

INFLUENCE OF SOIL AND WATER CHEMISTRY ON MARSH PLANT COMMUNITIES  
IN PALO VERDE NATIONAL PARK, COSTA RICA

By

ESTELLE S. ROBICHAUX

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For the little lion

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By

Estelle S. Robichaux

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Wetlands perform many important hydrologic and biogeochemical functions; for example, they generally improve water quality, provide flood protection and can retain nutrients such as phosphorous. Relatively little is known about wetlands in Central America, although the vital nature of tropical wetlands, on both the regional and global scale, is increasingly acknowledged. Palo Verde National Park (PVNP), located in Guanacaste Province, Costa Rica, is recognized under the Ramsar Convention on Wetlands of International Importance, due to its role as an important feeding and breeding ground for resident and migratory birds during the dry season. Once part of a large ranching operation, Palo Verde became a national park in the early 1980's and soon, the open marsh known as Palo Verde Lagoon, became overgrown with cattail (*Typha domingensis*). Many blamed this transformation on the removal of cattle from the area, and efforts to restore the marsh are ongoing.

The purposes of this study were: 1) to conduct a baseline analysis of soil and water chemistry in the marshes of PVNP; 2) to analyze plant species composition in relation to water and soil characteristics; and 3) to determine if *Typha domingensis* seeds establish preferentially in soils with specific conductivities. Fieldwork for this study was conducted during June and

July 2008. Soil and water samples were collected and plant species surveys conducted in eight different areas of the park.

Statistically significant differences were found among the areas for many soil and water characteristics (for soil: Ca, Mg, N, Cl, EC, sand and clay content; for water, Mg, K, Na, phosphate and Na). Species richness among the different areas was also statistically significant. Strong relationships between soil EC, Cl, S and K and species richness were found; water Fe, Na and depth were also highly related to species richness. Multivariate logistic regressions performed on the presence and absence of specific species found that soil N, P and K, water nitrate, P and depth all had statistically significant and magnitudinous effects. There were no statistically significant or notable results from the germination experiment.

Alternative hypotheses for the establishment of the extensive *Typha* marshes are supported by the findings of this study. It is hoped that the results of and synthesis provided by this research will raise additional research questions to further evaluate the cattle-grazing hypothesis, which is strongly established in the local community.

## CHAPTER 1 INTRODUCTION

The Palo Verde area wetlands are recognized to be of international importance to resident and migratory waterfowl. After becoming a national park, some of the marshes within Palo Verde National Park (PVNP) experienced dramatic changes in vegetative community structure and no longer provide desirable habitat for avifauna. The restoration of the Palo Verde marsh has been a priority of the Costa Rican conservation agenda for over a decade. The basis of the restoration efforts, however, is a scientifically unfounded hypothesis that the previous presence of cattle in the marshes helped control the growth and spread of *Typha domingensis*, and that their removal has allowed this invasive species to become dominant.

Given the ecological significance of these wetlands, an effort to determine verifiable causes of the changes observed in the wetland plant communities should be made. Any efforts made now are hindered by a lack of historical information and baseline data for almost every aspect of the system. Therefore, in addition to any conclusions drawn, any data collected will serve as a baseline dataset and will increase knowledge of the biophysical aspects of this system.

The studies conducted in PVNP were based on hypotheses that the factors more likely to have influenced the establishment of *Typha domingensis* are soil and water chemical characteristics, rather than the presence or absence of cattle. The knowledge gained about this system, through both field and experimental research, will increase understanding of the ecological framework within which the management and scientific communities must operate. Armed with greater knowledge of the biotic and abiotic interactions taking place within the park, more effective and scientifically based restoration techniques can be researched and implemented.

## Research Objectives and Proposed Hypotheses

- **Objective 1:** To conduct a baseline analysis of water and soil chemistry throughout the marshes of PVNP.
  - **Hypothesis:** There will be statistically significant differences in concentrations of the major nutrients and cations between the marshes located in the *Typha*-dominated areas and those not in that area.
- **Objective 2:** To analyze area plant species composition in relation to water or soil characteristics.
  - **Hypothesis:** There will be statistically significant relationships between certain chemical components in soil and water, specifically the major cations and electrical conductivity, and plant species composition.
- **Objective 3:** To determine if *Typha domingensis* seeds will establish preferentially in soils with specific conductivities.
  - **Hypothesis:** *Typha domingensis* seeds will have higher rates of germination in soils of mid-range conductivity (1-3 mS/cm).

## Background Information

### Importance of Wetlands

Throughout history, wetlands have been viewed as menacing and gloomy places, offering little or no value to society or to industry. These perceptions have infiltrated everything from literature to historical representation, from language connotations to recent popular culture, where wetlands have been portrayed as miserable, dirty and ominous (Mitsch and Gosselink 2007). Today, we know that wetlands perform important functions in hydrologic and biogeochemical cycles, such as cleansing polluted water, preventing floods, recharging ground water aquifers and retaining sediment and nutrients (Zedler and Kercher 2005). They are also downstream receivers of human and natural waste and are essential in shoreline protection. Wetlands support an extensive and widely varied food web that services many industries and have also been recognized as vital in sustaining biodiversity (Gibbs 2000). Moreover, they are a

source of cultural and historical identity that is often important to local economies in the form of recreation or tourism (Barbier 1994).

### **Central American Wetlands**

For millennia, the resources provided by inland freshwater wetlands have been used for agriculture, timber and hunting throughout Central America (Ellison 2004). In Guanacaste Province, Costa Rica, the land that once supported the agricultural economies of indigenous tribes (Helwig 1969) became the heartland of the logging, farming and cattle ranching industries in Costa Rica at the outset of the 20<sup>th</sup> century (Becker 1943). As the ecological functions and economic reliance on these systems have become more widely recognized, the vital nature of tropical wetlands to their respective regions has become even more pronounced (Aylward and Barbier 1992, Barbier 1994).

In contrast to the many well-studied wetland areas in North America and Europe, the wetlands of Central America are, in many ways, *terra incognita*. Despite all Central American countries having adopted the 1971 Convention of Wetlands of International Importance, especially as Waterfowl Habitat (the “Ramsar Convention”), total wetland area within this region is still unknown and there is no universal wetland classification system defined among these countries (Finlayson and van der Valk 1995, Ellison 2004). The paucity of research in Central American wetlands has been greatly influenced by two factors: the lack of adequate access to these areas and the harsh, unwelcoming and sometimes even threatening environments.

This lack of knowledge is particularly acute when it comes to seasonal wetlands, which experience extreme conditions, exacerbating even further the limiting factors mentioned above (Sarmiento et al. 2006). The seasonal wetland areas within Palo Verde National Park (PVNP) are no exception, since no literature regarding the wetlands themselves has been published in scholarly journals and very little research conducted within them. Moreover, the Organization

for Tropical Studies (OTS), which manages the biological station within the park, classifies all the surrounding marsh areas as ‘lagoons’ and has no data on the soils in these areas. This is in stark contrast to the numerous studies and plethora of information available on the tropical dry forest system, also located within the park (e.g., Wetterer et al. 1998, Gillespie 1999, Gillespie and Walter 2001, Frankie et al. 2004).

### **Palo Verde National Park**

The land now contained within the Palo Verde National Park was once part of a large hacienda network owned by David Russell Stewart (a.k.a. George Wilson) and later, his sons, Donald and David Stewart Bonilla. This hacienda of nearly 30,000 ha was part of a 133,000 ha estate, which comprised approximately 13% of all of Guanacaste Province (Edelman 1992). From 1926 onwards, this land was primarily used for cattle ranching (Quesada and Stoner 2004). During the dry season, 10-15,000 cattle would roam and graze the low-lying areas of the hacienda, resulting in the overgrazing and trampling of marsh vegetation (McCoy and Rodríguez 1994). Consequently, during the wet season, floating vegetation and low-growing sedges would dominate the Palo Verde wetland. This open marsh with almost no tall emergent vegetation, in combination with its slow exsiccation, became an important breeding and feeding ground for approximately 60 species of both resident and nearctic migratory avifauna during the harsh dry season (McCoy and Rodríguez 1994, Ellison 2004).

In 1975, the Costa Rican government expropriated much of the Stewart land and later donated some of it to the Costa Rican Wildlife Service (McCoy and Rodríguez 1994, Quesada and Stoner 2004). On April 18, 1977, President Daniel Oduber Quirós declared 4,800 ha of this land the Dr. Rafael Lucan Rodríguez Caballero National Wildlife Refuge, the first national wildlife refuge in Latin America, and the Stewart family removed the last of the cattle from the former Palo Verde hacienda in 1979 (McCoy and Rodríguez 1994, Quesada and Stoner 2004).

In June of 1980, President Rodrigo Carazo Odio declared that nearly 10,000 ha adjacent to the Refuge would become Palo Verde National Park, put into executive order on July 2, 1981 (Evans 1999, Quesada and Stoner 2004). By November 1990, the park was expanded to include the Refuge and the neighboring Lomas Barbudal Biological Reserve, resulting in approximately 20,000 ha of land contained and protected within the park boundaries (Quesada and Stoner 2004). Palo Verde National Park, and other surrounding wetland areas, became recognized as wetlands of international importance under the Ramsar Convention in 1991 (Quirós et al. 2001).

After the Refuge and National Park were designated, a dramatic change in the vegetative community structure within the 6,000-ha Palo Verde wetland was observed. What had once been an open marsh, dominated by floating vegetation and almost no tall emergent vegetation, became the largest cattail (*Typha domingensis*) marsh in the region within a few years (McCoy and Rodríguez 1994). The thousands of birds that once graced the waters and skies of Palo Verde became displaced as *Typha* filled the marsh. The rapid changes in this well-known wetland were cause for alarm within the scientific and conservation communities. The hypothesis that occurred to many people, including renowned ornithologist F.G. Stiles, was that the cattle had been instrumental in sustaining the desired open water characteristics of the Palo Verde marsh (Hartshorn 1983).

The idea of this connection between the presence of the cattle and the state of the marsh quickly became accepted into the local scientific, conservation and ranching communities; after all, the correlation seemed obvious. As a result, in 1986, the Costa Rican Wildlife Service signed a five-year contract with a private cattle rancher that allowed them to graze up to 1,000 cattle in the Palo Verde Lagoon (McCoy and Rodríguez 1994, Quesada and Stoner 2004). Although the reintroduction of cattle into the area wetlands did not curtail the *Typha*-domination,

this idea attracted continued support because of the notion that such means would provide environmentally sustainable and steady income for local people (Quesada and Stoner 2004). In 1991, a group of private ranchers was given permission to graze cattle within the park and released approximately 4,000 more cattle into the area; the contract was renewed in 1998 and persists to this day (Quesada and Stoner 2004).

### ***Typha* as Invasive Species**

Species of the genus *Typha* are found all over the world in freshwater marshes, from Europe to the Everglades to Australia. Although in most cases specific species are native to a certain region, they are often considered invasive because their ability to rapidly colonize large areas and overtake other native plant habitat (Grace and Wetzel 1982). The genus is generally very resilient, some species being able to withstand extreme flooding (~2 m) and drought (~2 cm) for up to two months (Grace 1989, Fickbohm and Zhu 2006) and tolerating increased soil salinities (Miklovic and Galatowitsch 2005). *Typha* have also been documented to thrive under conditions of eutrophication and those otherwise intolerable to most plant species, such as acid seeps in coal mine drainage areas (Mitsch and Gosselink 2007).

Nutrient availability, specifically that of nitrogen, phosphorous and potassium, typically controls plant growth in wetland ecosystems. When one or any combination of these nutrients is increased, a positive response in plant growth, for many species, will be observed (Shardendu and Ambasht 1991, Verhoeven and Schmitz 1991, Sarmiento et al. 2006). *Typha*, however, exhibits exceptionally increased plant growth in response to nutrification (Newman et al. 1996). *Typha* are also allelopathic plants, meaning they produce phytotoxins that inhibit the germination of seedlings (McNaughton 1968, Gallardo et al. 1998), which serves as yet another enhancement of the species' aggressive properties.

An individual cattail head can produce up to 250,000 seeds (Sojda and Solberg 1993), which have the capability to successfully germinate and establish under flooded conditions of up to 75 cm (Yeo 1964), though they are unlikely to do so outside of controlled experiments (Shay and Shay 1986). *Typha* can germinate surprisingly well in the presence of NaCl and Na<sub>2</sub>SO<sub>4</sub> (Choudhuri 1968); *Typha latifolia* was observed to germinate very well (63% ± 10.2) in NaCl solutions with an osmotic pressure of 0.50 atm (0.735 ppt; 1.10 mS/cm). However, germination rates decreased rapidly with increased osmotic pressure, reaching only 35% ± 9.0 in a solution of 1.0 atm (1.470 ppt; 2.19 mS/cm) (Choudhuri 1968). Although *Typha* germination may be negatively affected by mildly brackish conditions (0.5-3 ppt), once a plant has successfully established it can flourish under the same, or even more extreme, conditions (Choudhuri 1968, Zedler et al. 1990, Miklovic and Galatowitsch 2005).

Zedler et al. (1990) found that *Typha orientalis* seedlings had an increased growth rate when treated with a 5 ppt (7.46 mS/cm) sea salt solution at 4 and 5 weeks, rather than a 0 ppt solution; plants under these brackish conditions also had higher survival rates (83%) than those treated with the 0 ppt solution (28%) at 28 weeks. In an experiment that observed biomass response to varying concentrations of NaCl solution (0-1000 mg L<sup>-1</sup>) combined with species competition, dramatically increased levels of *Typha angustifolia* biomass were recorded at the highest levels of NaCl concentration (Miklovic and Galatowitsch 2005). Consequently, once a *Typha* community is established it will be able to survive despite elevated levels of salinity, having a negative effect on species richness (Miklovic and Galatowitsch 2005, Jin 2008). The findings of Choudhuri (1968) and Zedler et al. (1990) formed the basis for the germination experiment hypothesis.

The robust nature of the *Typha* species allows it to withstand and flourish under conditions that result in the death of most species. Because of this, in the event of ecological disturbance, be it fire, flooding by fresh or saline water or eutrophication, the dominant vegetative community may perish and provide *Typha* with an opportunity to establish. Given the history of hydrologic and ecological manipulation of Palo Verde Lagoon, there is considerable certainty that it was these alterations that allowed for the easy establishment of *Typha* throughout the marsh.

### **An Unproductive Restoration Based on an Unsubstantiated Hypothesis**

An important fact, not often considered, is that until 1979 the Palo Verde Lagoon was connected to the Tempisque River by five ‘natural’ canals, which employed weirs that were used to maintain flooding within the lagoon during the dry season (Quesada and Stoner 2004).

Although the Tempisque carries freshwater down from the plains of Guanacaste into the Gulf of Nicoya, it is often mixed with the Gulf’s saline waters due to strong tidal influence (McCoy and Rodríguez 1994). After the cessation of the ranching operation, the weirs were removed and the canals filled in with sediment and the transformation of Palo Verde Lagoon into a *Typha*-dominated marsh began. Five years later, the cattle-grazing restoration method was put into place (McCoy and Rodríguez 1994, Quesada and Stoner 2004).

A number of other issues are associated with the development of this restoration program. One is that the cattle were never directly observed to graze on the cattail (Quesada and Stoner 2004), but consume the more herbaceous species both in the wetlands and the surrounding tropical dry forest (pers. obs.). It has also been shown that moderate grazing in tropical flooded savannas, a similar system with regard to seasonality and vegetative community structure, does not have a substantial effect on plant production (Sarmiento et al. 2004). Additionally, the restoration efforts for Palo Verde marsh were implemented without having predetermined

monitoring methods in place to ascertain impacts or changes within the system (Quesada and Stoner 2004).

Today, two methods of *Typha* control are employed within Palo Verde National Park. The first is the cattle grazing technique, which is utilized in all areas of the park, not just those dominated by *Typha*. The second technique is the use of *fangeo*, the mechanical crushing of cattails with paddle wheels. This method is effective in delaying *Typha* regrowth for a few seasons, but is expensive and produces short-term results. In fact, for the past several years, the scientific director of the OTS Biological Station has had to use the bulk of his research budget to fund the *fangeada* of the Palo Verde marsh (J. Zúñiga pers. comm.). Additionally, because there has been no rigorous or long-term research conducted regarding this restoration method, there may be unknown effects on the desired plant community, soil characteristics and decomposition dynamics.

In the case of Palo Verde National Park, there is no known documentation of the state of the wetland areas before its time as a cattle ranch; there is no record as to whether *Typha* was absent, present or dominant in this system. Also, other than the area known as Palo Verde marsh, there is no knowledge of purposeful hydrologic or other system manipulation before, during or after the hacienda era, yet there are extensive *Typha*-dominated marshes in the southern half of the park (Catalina sector). Given the history of the Palo Verde wetland and the nature of *Typha* species discussed above, the hypothesis of cattle grazing having controlled cattail growth is unfounded.

Moreover, in the northern part of the park, an area known as la Varillal, there is no *Typha* present at all. There is, however, a considerable amount of *Mimosa pigra* in that area, another plant that is often viewed as invasive and indicative of disturbance. It is interesting that two

areas, with no real barriers between them, could both experience such extensive disturbance that each would be overrun by a very distinctive invasive species.

With this in mind, the questions raised are: What was the historical vegetative species composition of the area wetlands? Why has cattail invaded other areas of the park (i.e., Catalina sector)? Is it even invasive? Why did it not establish throughout the *entire* park? Are the restoration efforts currently employed effective? Given that the system is no longer hydrologically altered or managed, is it even possible to eradicate the cattail?

### **Summary**

While this study will not deal with all of the questions mentioned above, the two relevant questions are: Why has cattail invaded other areas of the park? and; why did it not establish throughout the entire park? This research was focused on beginning to answer these questions. It is hoped that these answers will help the scientific and management communities begin to understand the dynamics of this system. As greater appreciation of biogeochemical influences, outside environmental impacts and system parameters develops, more effective and efficient restoration methods can evolve and be implemented.

Chapter 2 of this thesis provides a thorough description of the study area, Palo Verde National Park, and detailed information on the field, laboratory, experimental and statistical methods used throughout this study. Results addressing each of the objectives of this study – information on soil and water chemistry, analysis of plant community composition and outcome of the germination experiment – are described in Chapter 3. The final chapter of this thesis will attempt to provide explanations of the potential mechanisms underlying the patterns, and exceptions, seen in the results. These interpretations will be used to assess the hypotheses proposed for this study; these conclusions will be related back to the overarching concept of restoration.

## CHAPTER 2 METHODS

A number of different methods were used to collect and analyze data for this study. Field methods included plant species surveys and the collection of soil and water samples. These samples were sent to the University of Costa Rica, where the majority of the chemical analysis took place. Some aspects of the analysis, however, were conducted in the laboratory at Palo Verde. The statistical analysis of each dataset varied. For soil and water chemistry data, basic descriptive statistics, analysis of variance and t-tests were applied. Several regression models were used to analyze plant community and germination experiment data.

### **Study Area**

This study was conducted in the seasonally flooded freshwater marshes of Palo Verde National Park (10° 20'N, 85° 20'W). PVNP, in Guanacaste Province, Costa Rica, has its southern border at the convergence of the Tempisque and Bebedero Rivers, approximately 8 km north of where the Tempisque flows into the Gulf of Nicoya (Figure 2-1). The Tempisque River valley is characterized by savannah plains between the mountainous, forest-covered Nicoya Peninsula to the west and a volcanic mountain range, la Cordillera del Guanacaste, to the east (Helwig 1969). The river itself is subject to strong tidal fluctuations, having a range of nearly 3 m between high and low tides (McCoy and Rodríguez 1994); it is not known how far up the Tempisque River the saline waters of the Gulf of Nicoya travel.

This region of Costa Rica has two seasons – wet and dry. The wet season, usually beginning in mid-May and lasting until mid-November (Figure 2-2), is typified by clear blue skies in the morning and heavy afternoon thunderstorms. While average annual rainfall throughout the province is upwards of 1700 mm, the lower Tempisque is the driest area, receiving average rainfall of only 1200 mm (Helwig 1969, McCoy and Rodríguez 1994).

Temperatures average between 25°C and 30°C throughout the year, but can reach up to 38°C during the peak of the dry season (March-April) (Helwig 1969, McCoy and Rodríguez 1994).

These dramatically fluctuating environmental conditions are what drive the seasonal changes within the wetlands of Palo Verde National Park. Before the rains set in, apart from a few permanently flooded areas, the freshwater marshes around the park are dry, with their Vertisols exposed and cracked (McCoy and Rodríguez 1994, Gallaher and Stiles 2003), much like the hyperseasonal savannas of South America (Sarmiento et al. 2006). When the wet season arrives, the marshes quickly become inundated and remain so until the beginning of December when they gradually start to dry down. By March, most of the area wetlands no longer retain any water. Vertisols have very high clay content to depth, show evidence of movement, for example in the form of slickensides, and are present under such conditions that allow them to crack during the dry season and swell when saturated during the wet season (Comerma 1999). Each of these characteristics has either been previously documented or is presented here (McCoy and Rodríguez 1994, Gallaher and Stiles 2003).

The area known as the Palo Verde marsh exsiccates much more slowly than many of the other marshes in the area and is able to support many species of migratory and resident waterbirds during the dry season when other area marshes cannot (McCoy and Rodríguez 1994, Ellison 2004). It was this unique feature that was the primary driver behind the continued and expanding protection of this area as a national park and, eventually, its recognition under the Ramsar Convention.

### **Field Methods**

All field research was conducted between June 10 and July 16, 2008 at eight transects throughout the park, each being 2.5 – 5 km apart (Figure 2-3; Appendix A for a complete listing of study dates).

## **Plant Species Community Composition Surveys**

A nested design was used in conducting the plant surveys. At each transect location, 4-10 plots were chosen at random, stratified in linear segments of 100 m (Appendix A for plot coordinates). The start points for each transect and the locations for each plot were all chosen at random. Transects 1, 2 and 3 had 6 plots each; transect 4 had 10 plots; and transects 5, 6, 7 and 8 each had 4 plots.

At each plot location, two 1-m<sup>2</sup> quadrats, nested in a 20-m<sup>2</sup> quadrat, were established. After plant surveys for these quadrats were conducted, two satellite plots, at a distance between 10 and 15 meters on opposite sides of each main plot, were also established (Figure 2-4). Braun-Blanquet cover classes (1, < 1%; 2, 1-5%; 3, 6-25%; 4, 26-50%; 5, 51-75%; 6, 76-100%) were used to record percent cover for each species.

## **Soil and Water Sample Collection**

Within each of the eight transects, composite core soil samples of 100 cm<sup>3</sup> were taken, using a soil corer, at four plot locations. For transects 1, 2 and 3, samples were taken at plots 1, 3, 4 and 6; within transect 4, samples were taken at plots 1, 4, 7 and 10; and for transects 5, 6, 7 and 8, samples were taken at all four plots. Soil samples from an additional area were taken (Site 9; Figure 2-3) and used for in-house laboratory analysis and the germination experiment only.

A 2" soil corer was used to obtain 5-7 cm of soil; loose organic matter was removed from the tops of the cores. Each composite consisted of 4-5 cores taken from within a 2.5-m radius of the initial plot locations. Two 50-ml water samples were taken at the same locations as the soil samples.

## ***Typha domingensis* Seed Collection**

Seeds from 20 *Typha domingensis* seedheads were harvested from all transect areas where *Typha* was present (transects 1, 2, 3 and 4).

## **Laboratory Methods**

### **Soil Sample Analysis**

Prior to being dried, soil samples were stored in a laboratory refrigerator; each sample was oven dried at 105°C until a consistent weight was reached. After the soil samples were dried, 50-ml of each sample was hand-ground with mortar and pestle and passed through a 0.2-mm sieve. The remaining dried soil was bagged and stored. Using a volumetric flask, two 25-ml replicates of each sample were measured out and combined with 25-ml of distilled water in 50-ml centrifuge tubes; the samples were then mixed for one minute on a Vortex Maxi Mix II. All samples remained saturated for 24 hours before being spun in a Sorvall GLC-1 Bench Top Centrifuge. Due to the age and condition of the centrifuge the maximum frequency of rotation was approximately 1200 rpm, thus samples were spun for two hours at this speed. Once the samples had been centrifuged, the extracted pore water was measured for pH and conductivity using a Hanna HI9813 Grocheck Combo Meter. Before each laboratory session, the meter was calibrated for both pH and conductivity, using solutions with a measured pH of 7.0 and total dissolved solids of 1500 ppm, respectively.

### **Water Sample Analysis**

Of the two water sample replicates from each plot, one was refrigerated after collection and tested within 48 hours, while the other was frozen. Before testing, all samples were spun for 15 minutes in the Sorvall GLC-1 Bench Top Centrifuge in order to isolate any particulate organic matter. pH and conductivity were measured using the Hanna HI9813 Grocheck Combo Meter. Nitrate and phosphate were measured using a Hach DR/2010 Portable Spectrophotometer. Nitrate was analyzed following mid-range (0 to 4.5 mg/L  $\text{NO}_3^-$ ) protocols with NitraVer 5 Nitrate Reagent Powder Pillows (Hach Company 2000). Reactive phosphorus (0 to 2.50 mg/L  $\text{PO}_4^{3-}$ ) was analyzed following the ascorbic acid method using PhosVer 3

Powder Pillows; in several cases, phosphate levels were out of range for this method and the amino acid method (0 to 30.00 mg/L PO<sub>4</sub><sup>3-</sup>) protocols were thus followed (Hach Company 2000).

### University of Costa Rica Sample Analysis

The unanalyzed soil and water samples were sent to the Center for Agronomic Investigation at the University of Costa Rica in San José for analysis of nutrient content and other characteristics. Soil samples were analyzed for the following using Modified KCl-Olsen extraction solutions: pH, acidity, Ca, Mg, K, P, Zn, Cu, Fe, Mn and S. Cl, %N and soil texture were also analyzed.<sup>1</sup> Due to costs, soil samples were combined, resulting in *two* composite samples per transect rather than four. Each composite sample represents the soil chemical make-up of a *subtransect* (Figure 2-4). Water samples were analyzed for pH, NH<sub>4</sub><sup>+</sup>, NO<sub>3</sub><sup>-</sup>, Ca, Mg, K, P, Fe, Zn, Cu, Mn, Na and electrical conductivity (EC).

### Experimental Methods

The soils previously prepared and used to measure pH and conductivity were remixed and 15-ml of each rewetted soil sample were put in a Petri dish. While the soils were being prepared, the *Typha domingensis* seeds were soaked in distilled water to separate the viable seeds from the attached bristle hairs. Once the viable seeds were separated and gently dried using paper towels, they were counted out in groups of 100. Each of the 48 soil samples were planted with 100 of the *Typha* seeds and then placed in the station shade house. When necessary, equal amounts of

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<sup>1</sup> The following is a description of the procedures utilized at the Center for Agronomic Investigation (CIA) at the University of Costa Rica, translated from a description provided with the results report. The codes in parentheses refer to procedural sections within the CIA manual: pH procedures were conducted with water of pH 5.5 (CIA-SC09-01-02-P02). Acidity, Ca and Mg procedures were conducted with a KCl 1M solution; P, K, Zn, Fe, Mn and Cu procedures were conducted with an Olsen Modified pH 8.5 solution (CIA-SC09-01-02-P04). Acidity was determined by valuation (CIA-SC09-01-02-P05); P was determined by UV-Visual Spectrophotometer (CIA-SC09-01-02-P07); and all other elements were determined by Atomic Absorption Spectrophotometer (CIA-SC09-01-02-P06).

The values listed with each element indicate the general 'critical levels' of the extracting solutions used for the respective procedures: Acidity, 0.5; Ca, 4; Mg, 1; K, 0.2; P, 10; Zn, 3; Cu, 1; Fe, 10; Mn, 5; S, 12.

Please see (Silver et al. 1994) for more detail on Modified KCl-Olsen solutions.

distilled water were put into each dish in order to maintain a reasonable level of soil moisture. Germination was observed and recorded every 48 hours over a two-week period.

## **Statistical Methods**

### **Categorization and Exclusion of Transect 5 from Some Analysis**

Although the soil and water samples from transect 5 were used during analysis to establish the general trends of soil and water chemistry throughout the park, the data collected from plant community surveys were not used. Because of the “active” restoration of the Palo Verde Lagoon (the area where transect 5 was located), the plant communities cannot be said to accurately reflect the edaphic and hydrologic conditions of the area. These restoration activities may also have unknown effects on the seed bank, but since the data collected from transect 5 soil samples could not be determined as outliers, they were used in analysis of the germination experiment results.

Transects were grouped into southern and northern sites for some analysis. The southern site included transects 1, 2, 3 and 4; the northern site included transects 6, 7 and 8. The divisions were based on location and general plant community composition, the marshes in the southern site being dominated by *Typha domingensis* and those in the northern site by *Mimosa pigra*, another species associated with disturbance and often considered to be invasive. Transect 5 would have been grouped within the southern site, but was excluded from all categorized analysis.

### **Analysis of Soil and Water Chemistry**

For baseline soil and water data analysis, a number of descriptive statistics were applied to all components using Microsoft Excel. In order to become familiarized with the data, frequency histograms were constructed and measures of central tendency (mean, median, mode) and dispersion (range, variance, standard deviation, coefficient of variation) were calculated. These

calculations were applied to each transect (1-9) as well as to the site groupings (northern and southern). This suite of statistics will elucidate biogeochemical trends on a spatial scale and may indicate environmental influences, such as impacts from agriculture, ranching or proximity to the Tempisque River and Gulf of Nicoya. Pearson correlation coefficients were calculated, using the R statistical package, to determine whether any linear relationships existed between variables; these results could reinforce any inferences made regarding environmental influences.

To determine statistically significant differences between groups, ANOVAs were conducted on all variables among transects and T-tests between the northern and southern sites. Any statistically significant differences for specific variables among transects may highlight and reiterate the trends and influences revealed through basic statistical analysis. As variations in soil and water chemistry throughout the park are established and corroborated, an understanding of the system dynamics will begin to develop.

## **Analysis Plant Species Community Composition**

### **Linear regression analysis of species richness**

Species richness was calculated by counting the number of species found in each quadrat; averages were taken when species richness was needed for a different scale (i.e., by plot, subtransect or transect). These species richness values were used, in conjunction with soil and water chemistry data, to create scatter plots in Excel, which became the basis for regression equations and related coefficients of determination. Evaluating these data in such a manner allows for any tendencies of species richness to be revealed; that is, whether samples of high or low relative species richness are associated with high, low or mid-range concentrations of specific nutrients or other characteristics. How much of the variation in the response data (species richness) is explained by the independent variable (soil or water chemical variable) is

demonstrated through the coefficient of determination ( $R^2$ ); the higher the  $R^2$  value, the more variation is explained by the independent variable.

Using R, fixed-effects ANOVAs were conducted, based on multivariate linear models (lm), for several variable combinations. In order to minimize any issues of multicollinearity, all variables within a model equation had correlation coefficients of less than  $\pm 0.20$ . Once initial regressions were run, those variables whose coefficients were not statistically significant ( $p > 0.15$ ) were removed and ANOVAs calculated for the new iteration of regressions. These regressions were performed because, whereas single-variable regression can reveal interesting trends, plant species are not affected by only one chemical component. Multiple variables must be included in one instance to reflect more accurately potential reactions in nature.

There are assumptions made, substantiated by data, associating *Typha*-dominated areas with low species richness. Since the results of these regressions will provide information about which chemical components are associated with high, low or mid-range species richness, inferences can then be made regarding these chemical components and the predominance of *Typha* in certain areas.

### **Logistic regression analysis of the most abundant species**

The most abundant species, common to both the northern and southern sites, were ascertained by tallying each cover category for each species. The tally total was then multiplied by its cover category number (i.e., 1-6) and the results for each category added together. The species with the highest final numbers were determined to be the most abundant and were those used in further analysis. The presence or absence of each of these species within each subtransect was established; if a species was present in a quadrat, it was scored '1', and if it was absent from a quadrat, it was scored '0'. For each subtransect, the total number of present or absent occurrences for each species was totaled.

The determined presence or absence of each species and the initial variable combinations used in the multivariate linear models, binomial logistic regressions were performed in R (glm, binomial logit family). Two additional variable combinations were used for logistic regression; the first, containing all the variables noted to have high  $R^2$  values in the species richness analysis, and the second, based on the results of Sarmiento et al. (2006) and Caraco et al. (1989). As above, after the initial regressions were run, non-statistically significant variables were removed and the models were run again.

The results of these model iterations are presented in the form of variable coefficients, their levels of significance, likelihoods and graphic output that plots actual data and model fit. That is, on the x-axis of the graph, the actual number of occurrences for a species is plotted and on the y-axis, the model-predicted number of occurrences for a species given the independent variable data is plotted.  $G^2$ , the likelihood-ratio-chi-squared statistic, is used to compare the observed (x-axis) and expected (y-axis) of the response variable to assess the goodness of fit of the model.

Analyzing the presence or absence of specific species with respect to chemical components will build upon and help evolve the interpretations of biogeochemical interactions occurring within the system. The results from these models considering multiple variables for individual species will provide indications as to which elements in soil or water have the most influence on whether that species can successfully survive in an area. Having these specific results will allow for the definition of niche differentiation among plant species in this system. This kind of information can be essential in developing restoration goals and methods, as it often shapes or limits what can be done and in what manner.

### **Analysis of Germination Experiment**

As with the rest of the data gathered, the germination experiment data were subject to a set of descriptive statistical analysis in Excel and several regressions in R. A simple linear model,

based on 'site', 'transect' and conductivity, was the initial effort, using up to third order polynomials in the regression and then comparing model fits. A model using 'site' and 'transect' as nested random variables was subsequently used, also employing first and second order polynomials. These models were used to ascertain any relationships between the area within the park the soil was collected from, the specific location it was collected from, conductivity and *Typha* germination.



Figure 2-1. Location of Palo Verde National Park in Guanacaste Province, Costa Rica. Image source: University of Texas Libraries, Perry-Castañeda Library Map Collection, [http://www.lib.utexas.edu/maps/americas/costa\\_rica.gif](http://www.lib.utexas.edu/maps/americas/costa_rica.gif) [Accessed October 9, 2009].

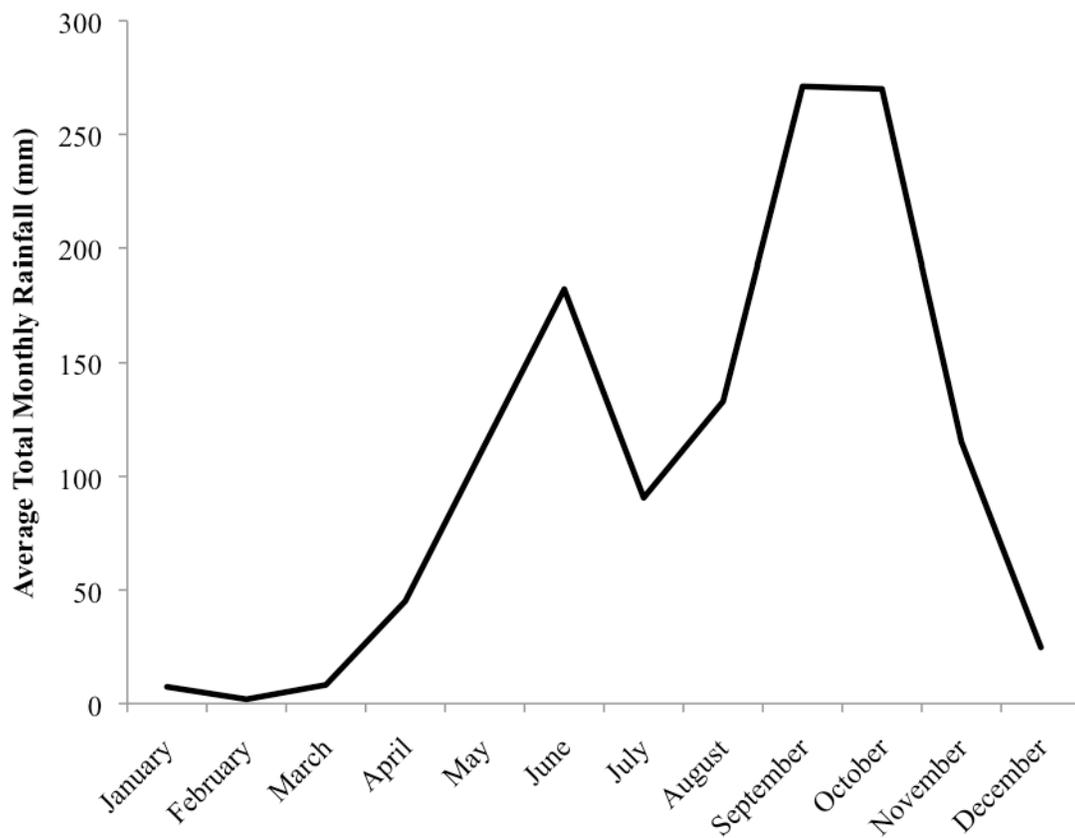


Figure 2-2. Average total monthly rainfall recorded at the Palo Verde marsh, OTS Biological Station. Data source: Organization for Tropical Studies, September 1996 – October 2007.

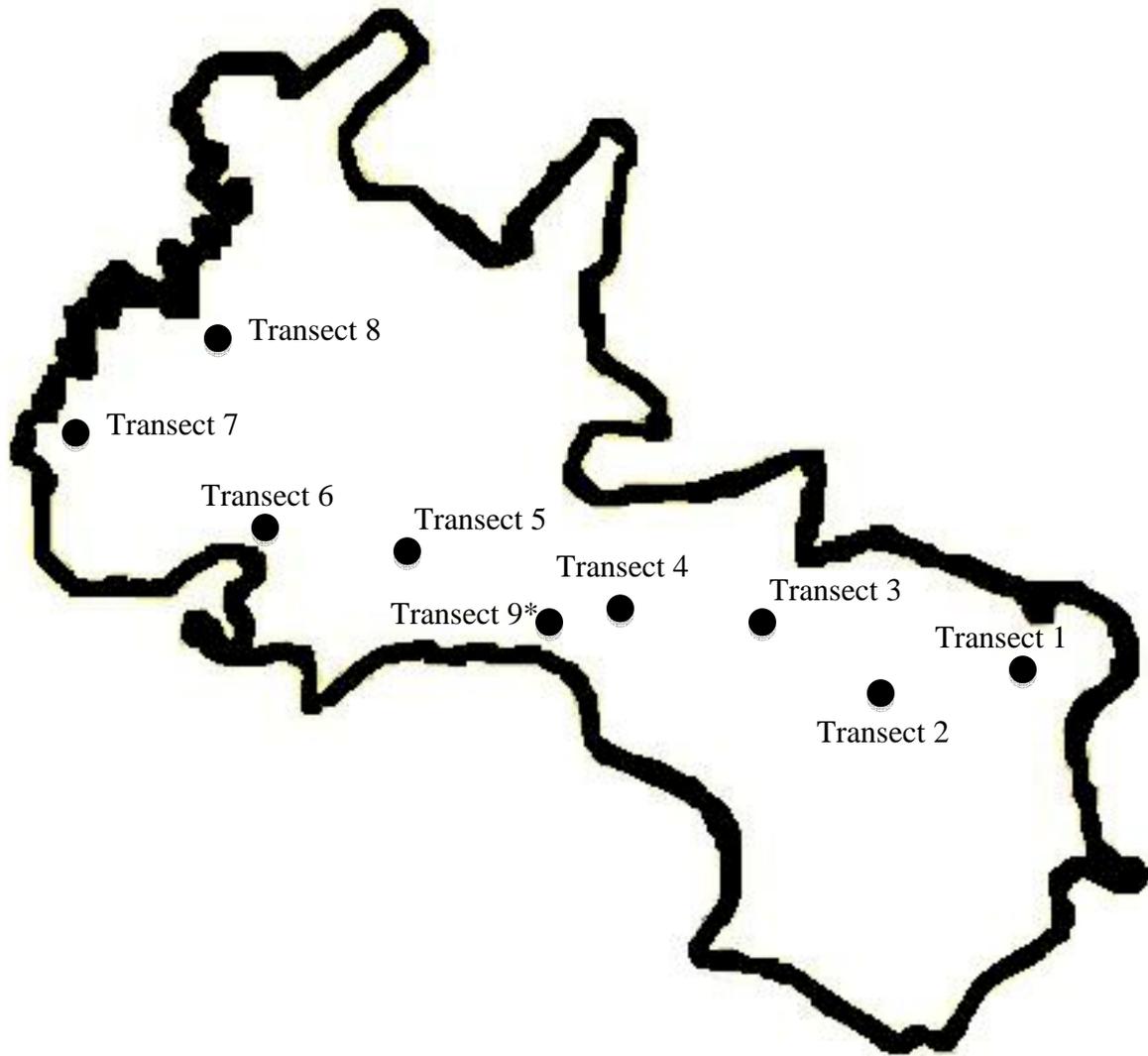


Figure 2-3. Palo Verde National Park boundary and transect locations

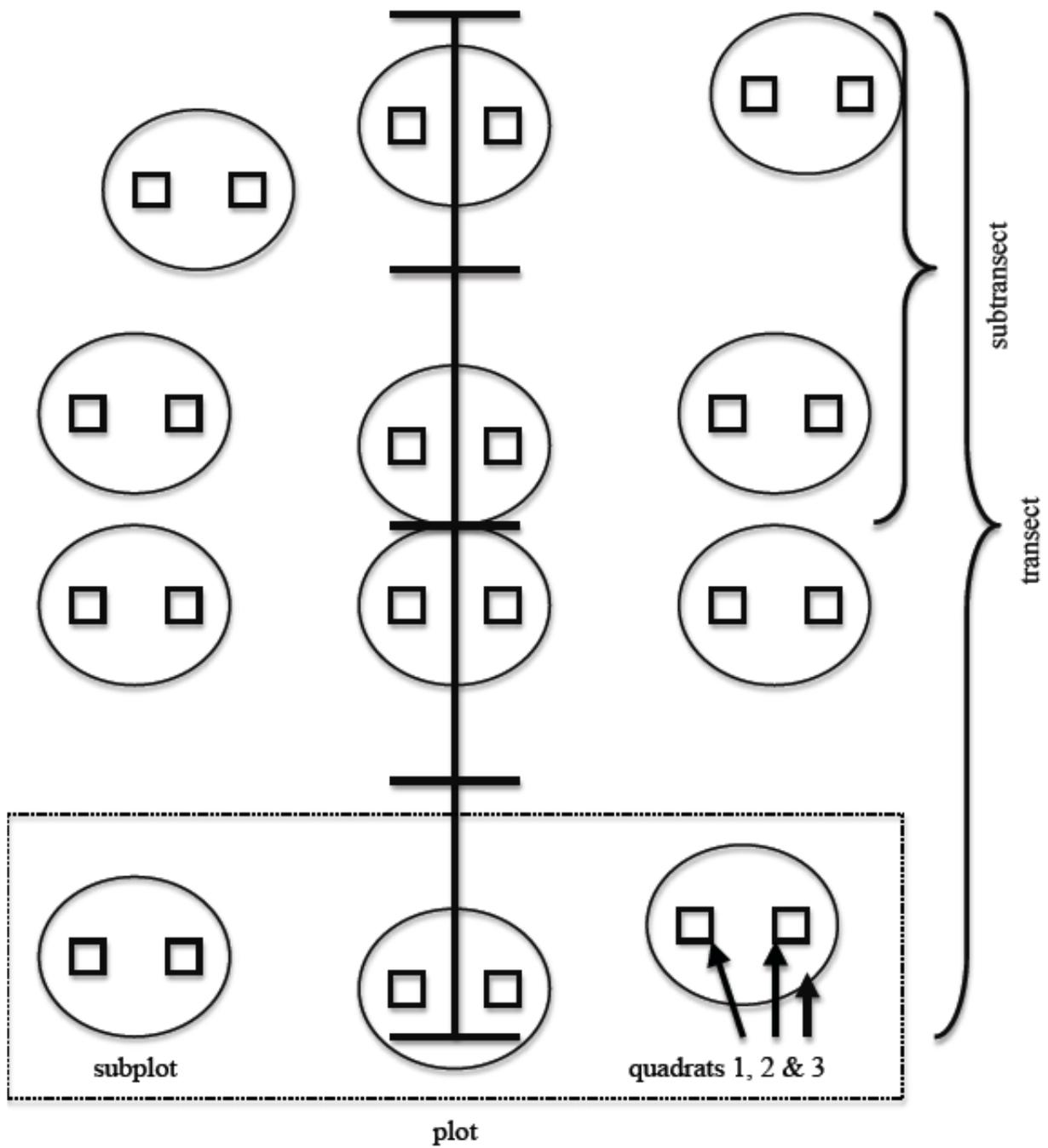


Figure 2-4. Transect design and layout. Figure is not to scale.

## CHAPTER 3 RESULTS

The results presented in this chapter are organized to address the specific objectives of this research. Generally, results are for analysis on the transect-level (1-8) are described, followed by those on the site-level (southern and northern). The first section describes patterns of different component groupings seen in the soil and water chemistry throughout the park. The second section gives the results of the regression models generated to analyze species richness and abundance. The final section details the outcome of the germination experiment.

### **Soil and Water Chemistry**

#### **Salinity Markers**

The analysis of soil and water samples conducted by the University of Costa Rica showed some marked trends across both transects and sites. Samples from transects 1, 2, 3, 4 and 5 showed substantially higher concentrations of soil Cl, soil S and water Na, all of which are salinity markers (Figure 3-1). ANOVA tests demonstrated statistically significant differences amongst transects for soil Cl ( $p = 0.0065$ ) and water Na ( $p = 0.0082$ ); although soil S did not prove to have statistically significant differences among transects ( $p = 0.3940$ ), the general trend in elemental concentration was present. These findings are supported by the higher electrical conductivity (EC) found in both the soil and water samples from transects 1, 2, 3, 4 and 5 (Figure 3-2). Transect 1 had the highest soil conductivity of these areas ( $5.03 \text{ mS/cm} \pm 0.73$  (1 SD)), followed by transect 5 ( $3.81 \text{ mS/cm} \pm 0.95$ ); transects 6, 7 and 8 all had average soil conductivities of  $0.87 \text{ mS/cm}$  (transect 6,  $\pm 0.15$ ; 7,  $\pm 0.16$ ; 8,  $\pm 0.11$ ). Water conductivity, however, was highest at transect 4 ( $0.380 \text{ mS/cm} \pm 0.272$ ).

Some of these trends seen across transects were shown to be statistically significant between sites using Student's t-test, while others were not. Soil Cl ( $p = 0.008$ ) was statistically

significant and soil S ( $p = 0.101$ ) slightly so, with higher levels being in the southern site (Cl,  $130.16 \text{ mg kg}^{-1} \pm 79.50$ ; S,  $87 \text{ mg L}^{-1} \pm 61.55$ ) rather than in the northern site (Cl,  $20.85 \text{ mg kg}^{-1} \pm 4.83$ ; S,  $44 \text{ mg L}^{-1} \pm 12.73$ ). The tendency was the same for both soil and water EC (soil,  $p = 0.001$ ; water,  $p = 0.018$ ; Appendix B for complete ANOVA and T-statistic tables). Conversely, water Na ( $p = 0.980$ ) showed no statistically significant differences between sites, presumably because of the large variance among the southern site transects ( $29.32 \text{ mg L}^{-1} \pm 34.84$ ).

### **Cations**

Concentrations of cations (Ca, Mg, K) in water had some statistically significant differences among transects (Ca,  $p = 0.1712$ ; Mg,  $p = 0.0044$ ; K,  $p = 0.0006$ ) and tended towards the same general trend seen in the salinity markers, with lower concentrations observed from transects 6, 7 and 8 (Figure 3-3). The measured effective cation exchange capacity (ECEC) of soil samples did not have the same tendency, however. Although concentrations of the specific cations varied significantly across transects (acidity,  $p = 0.1304$ ; Ca,  $p = 0.0019$ ; Mg,  $p = 0.0400$ ; K,  $p = 0.0884$ ), and the proportional concentrations were different amongst transects, the lowest cation concentrations were at transect 1 ( $26.02 \text{ cmol}^+ \text{ L}^{-1} \pm 6.43$ ) and the highest at transect 8 ( $51.47 \text{ cmol}^+ \text{ L}^{-1} \pm 1.41$ ). The concentrations found at all other transects ranged between 31 and  $38 \text{ cmol}^+ \text{ L}^{-1}$  (Figure 3-3).

Although water Ca was not statistically significant among transects, it was statistically significant between the northern and southern sites ( $p = 0.028$ ), as was water Mg ( $p = 0.072$ ). Water K, on the other hand, was highly statistically significant among transects, but not between sites ( $p = 0.506$ ). Overall soil ECEC ( $p = 0.026$ ) was statistically significant between sites, even though the significance of individual cations diverged greatly (acidity,  $p = 0.440$ ; Ca,  $p = 0.036$ ; Mg,  $p = 0.534$ ; K,  $p = 0.005$ ). As with the transect averages, cation concentrations in water were higher at the southern site transects (S-Ca,  $14.34 \text{ mg L}^{-1} \pm 4.30$ ; N-Ca,  $11.22 \text{ mg L}^{-1} \pm 1.97$ ) and

higher in soil at the northern site transects (S-ECEC,  $32.04 \text{ cmol}^+ \text{ L}^{-1} \pm 5.77$ ; N-ECEC,  $40.65 \text{ cmol}^+ \text{ L}^{-1} \pm 7.50$ ).

### **Nitrogen and Phosphorous**

Total N (TN) and P (TP) concentrations in the soil samples showed some interesting results as well. TN was highest at transect 5 ( $0.539 \% \pm 0.069$ ), followed by transects 7 and 8 would have the next highest levels of TN ( $0.422 \% \pm 0.083$  and  $0.322 \% \pm 0.025$ , respectively; Figure 3-4). Similarly, TP concentration was highest at transect 6 ( $19 \text{ mg L}^{-1} \pm 1.41$ ), followed by transects 1, 4 and 5, all of which had average concentrations of  $11.5 \text{ mg L}^{-1}$  ( $1, \pm 2.12$ ;  $4, \pm 13.43$ ;  $5, \pm 6.36$ ; Figure 3-5). For soil samples, TP did not have statistically significant differences among transects ( $p = 0.2683$ ), while TN did ( $p = 0.0018$ ). These results are intriguing because it would be expected that the highest levels of these important nutrients would be found in the most productive areas: those dominated by *Typha*.

For related concentrations found in water samples, the reverse was true. Nitrate did not have statistically significant differences amongst transects ( $p = 0.1691$ ) and ammonium was slightly statistically significant ( $p = 0.0779$ ; Figure 3-4); phosphorus ( $p = 0.0594$ ) and phosphate ( $p = 0.0010$ ), on the other hand, both show statistically significant differences among transects (Figure 3-5). Yet, between sites, nitrate was the only component in either water or soil that was even close to statistically significant ( $p = 0.119$ ).

### **pH**

Individually, neither soil nor water pH showed any obvious trend among transects (Figure 3-6), although water pH did prove to be statistically significant ( $p = 0.0507$ ). Soil pH for all transects was circumneutral, ranging from 5.5 to 6.6, and water pH slightly more basic, ranging from 6.7 to 7.5. It is noteworthy, however, that the differences between soil and water pH are greatest at transects 6 and 7 and least at transects 8 and 5.

The differences, or lack thereof, in pH among transects was reiterated by the absence of significance between the northern and southern sites for both soil and water pH. The differences seen in transect water and soil pH was masked in the site averages, showing slightly higher pH for both in the southern site (S: water,  $7.14 \pm 0.58$ ; soil,  $6.05 \pm 0.53$ . N: water,  $6.92 \pm 0.35$ ; soil,  $5.73 \pm 0.30$ ).

## **Texture**

A final soil characteristic of interest is texture. There were statistically significant differences in all components of soil content (sand,  $p = 0.0174$ ; silt,  $p = 0.0623$ ; clay,  $p = 0.0209$ ). Sand content decreased and clay content increased on the northern route from transect 1 to transect 4; for transects 6, 7 and 8, texture differences came from increases in sand content and decreases in silt content (Figure 3-7). Surprisingly, transect 5 had the highest level of sand content ( $41.9 \% \pm 3.5$ ) and, consequently, the lowest level of clay content ( $34.7 \% \pm 1.8$ ).

When comparing texture between the northern and southern sites, the overall differences in soil composition become quite clear. While there is no statistically significant difference in silt content ( $p = 0.245$ ) between sites, there are in both sand ( $p = 0.036$ ) and clay content ( $p = 0.016$ ). Following the trends seen among transects, the sand content in the southern site was higher than that in the northern site (S,  $24.02 \% \pm 8.32$ ; N,  $15.75 \% \pm 4.60$ ), and conversely for clay content (S,  $52.68 \pm 9.53$ ; N,  $63.09 \pm 3.04$ ). Despite any differences in specific soil content, all soil samples were classified by the UCR-CIA, using the American texture triangle, as either clay ( $n = 14$ ) or clay loam ( $n = 3$ ).

## **Correlations**

### **Salinity markers**

A number of interesting and statistically significant correlations were found between soil and water components (Appendix C for complete correlation matrix). The salinity markers

discussed above (soil Cl, S and EC; water Na and EC) generally have some kind of correlation between them. Soil Cl, S and EC are all statistically significantly and positively correlated with one another. Water Na and EC have a strong, positive correlation; soil EC is positively correlated with the two as well. However, neither soil Cl nor S is well correlated with water Na; soil Cl is positively correlated with water EC, though not highly.

### **Cations**

Water Ca has a positive correlation with water Mg and K, although it is not a very strong correlation, and with sand content; water Mg and K are positively and very statistically significantly correlated. Water Mg also has a strong, positive correlation with water Na and EC; water K is statistically significantly and positively correlated with water and soil P. There were, however, very few correlations between the cation concentrations in soil. Soil Ca has a strong negative relationship with soil K and silt content; soil Mg and ECEC both have strong positive correlations with clay content.

### **Nitrogen, phosphorus and pH**

Soil P and water  $\text{PO}_4^{3-}$  both have relatively strong, positive correlations with silt content. Soil N and Mg are statistically significantly and negatively correlated. Water  $\text{NH}_4^+$  has very strong and positive relationships with water Mn and Fe; water  $\text{NO}_3^-$  has a statistically significant, positive relationship with soil Mn. The salinity markers and some of the major cation in the water (Na, EC, Mg, K) have statistically significant, positive relationships with water pH; soil pH has a negative correlation with both soil Mn and Fe.

## **Plant Species Community Composition**

### **Linear Regressions of Species Richness**

Analysis of species richness on the subtransect, transect and site scales all showed highly statistically significant differences between their respective areas (Table 3-1). Before beginning

regression analysis, comparing species richness summary statistics with those of specific variables, visual patterns begin to emerge (Figures 3-1, 2, 3 & 8). In relation to species richness, the variables whose models had the highest coefficients of determination were primarily salinity markers: soil Cl, EC and S and water Na. Soil K, water Fe and water depth also had higher  $R^2$  values.

The variable with the highest  $R^2$ -value was soil EC (0.67357), followed by water depth (0.49409), soil Cl (0.48364), water Fe (0.4729), soil K (0.46802), water Na (0.36625) and soil S (0.32061). Most of these statistical models were based on polynomial equations; only soil K and S were exponentially-based (Figure 3-9). For soil EC, soil Cl, water Fe and water Na, there was a trend of high species richness in areas of low elemental concentration, with a gradual decrease in species richness with increase in concentration, and eventually an increase in species richness with further increase in concentration. For water depth, soil K and soil S, there was a decrease in species richness with an increase in the respective variables.

When multiple variables were placed in a linear model, the components that seemed to have the largest effects on species richness were not centered on salinity markers. The final regression equations were

$$\text{Sp.Rich} \sim -3.077 + 0.209 * \text{clay} + -0.207 * \text{soil Cu} + 0.012 * \text{soil Fe} + 28.384 * \text{soil N} + 0.152 * \text{water Fe} + -0.021 * \text{water Na} + -2.935 * \text{water NO}_3^- + 0.692 * \text{water P} + -0.050 * \text{water depth} \quad (3-1)$$

$$\text{Sp.Rich} \sim -1.040 + -6.313 * \text{soil K} + 11.734 * \text{soil N} + -0.302 * \text{soil Cu} + -0.206 * \text{sand} + -0.009 * \text{soil S} + 0.110 * \text{water Fe} + 2.310 * \text{water pH} + -0.005 * \text{water depth} \quad (3-2)$$

Soil N had a strong positive effect on species richness, while soil K had a strong negative effect (Table 3-2). Water pH had a positive effect and soil acidity a negative effect on species richness. Although water depth, water Fe, sand content and clay content were consistently statistically significant in the regression models, their coefficients were quite small.

## Logistic Regressions of the Most Abundant Species

Of the 51 plant species surveyed in the marshes (Appendix D), the most abundant species found in both the small (1 m<sup>2</sup>) and large (20 m<sup>2</sup>) quadrats were

- *Typha domingensis*
- *Mimosa pigra*
- *Eleocharis* spp.
- *Hymenachne amplexicaulis*
- *Nymphaea* spp.
- *Aniseia martinicensis*
- *Echinodorus paniculatus*
- *Sarcostemma clausum*
- *Croton argenteus*
- *Thalia geniculata*
- *Cyperus articulatus*
- *Oryza latifolia*
- *Paspalidium germinatum*

Despite these species being those generally most abundant, some of them were present only in a few subtransects. Because of this, some species did not return any successful regressions, including some of the more focal species such as *M. pigra*. A number of the regressions had several statistically significant variables, but only a few had this in addition to low residual deviance. *T. domingensis*, *Eleocharis* spp., *Nymphaea* spp., *A. martinicensis*, *E. paniculatus*, *S. clausum* and *T. geniculata* all returned statistically significant and good-fitting results for at least one model (Figure 3-10). The regressions for *M. pigra*, *H. amplexicaulis*, *O. latifolia* and *P. germinatum* all had at least one model run successfully, but the results were far from statistically significant. *C. argenteus* and *C. articulatus* did not have any successful regression output. The final regression equations for the successful models (Figure 3-10) on the presence or absence of these species were

$$\text{Ani.mar} \sim -5.276 + -0.138 * \text{sand} + 0.021 * \text{soil Fe} + 36.249 * \text{soil N} + -0.010 * \text{soil S} + -5.596 * \text{water NO}_3^- + 1.561 * \text{water pH} + 0.390 * \text{water PO}_4^{3-} \quad (3-3)$$

$$\text{Ech.pan} \sim 32.404 + -30.761 * \text{soil N} + -0.847 * \text{soil P} + -17.596 * \text{soil K} + -0.119 * \text{soil S} + 0.010 * (\text{soil P} * \text{soil S}) \quad (3-4)$$

$$\text{Ele.spp} \sim -8.233 + -0.062 * \text{soil Fe} + -0.019 * \text{soil Mn} + 0.014 * \text{water Na} + 4.483 * \text{water NO}_3^- + -0.069 * \text{water depth} \quad (3-5)$$

$$\text{Nym.spp} \sim 21.318 + 34.825 * \text{soil N} + -3.436 * \text{soil P} + 7.718 * \text{soil K} + -0.914 * \text{soil S} + 0.076 * (\text{soil P} * \text{soil S}) \quad (3-6)$$

$$\text{Sar.cla} \sim 34.340 + -0.379 * \text{clay} + -8.226 * \text{soil K} + 0.219 * \text{soil P} + -5.049 * \text{water EC} + -0.505 * \text{water Fe} + -2.041 * \text{water PO}_4^{3-} + -0.134 * \text{water depth} \quad (3-7)$$

$$\text{Tha.gen} \sim 35.790 + -0.510 * \text{soil Mg} + -3.18533 * \text{soil pH} + -3.008 * \text{water NO}_3^- + 0.595 * \text{water PO}_4^{3-} + -0.104 * \text{water depth} \quad (3-8)$$

$$\text{Typ.dom} \sim -10.586 + 0.060 * \text{soil Cl} + 5.610 * \text{soil EC} + -0.048 * \text{soil C} + 0.843 * \text{water Fe} + -0.327 * \text{water Na} + 0.124 * \text{water depth} \quad (3-9)$$

Because of the variation in inputs and response variables, it is difficult to note any general trends. However, there were a few consistencies observed. As seen in the species richness regressions, soil K had a strong negative effect on the presence or absence of *E. paniculatus* and *S. clausum*, and soil N had a strong positive effect on the presence or absence of *A. martinicensis* and *Nymphaea* spp. (Figure 3-10). While higher soil pH had a negative effect on *T. geniculata* presence, water pH had a positive effect on the occurrence *A. martinicensis* and *E. paniculatus*, as well as species richness. Water depth had a small negative, though generally statistically significant, effect on the presence of the modeled species, except for *T. domingensis*, which had a positive coefficient for water depth. Water nitrate, water P and clay content all varied in their effects on the presence or absence of specific species, but the coefficients were consistent in magnitude and statistical significance.

### **Germination Experiment**

While mean soil EC showed great variation among transects, average *Typha* seed germination did not have the same tendency (Figure 3-11). T-tests between southern and northern site conductivity and germination provided the same results: statistically significant

differences in EC ( $p < 0.001$ ) but none in germination ( $p = 0.664$ ). Plotting the conductivity and germination data did not reveal any obvious patterns either.

The simple linear model did not show any differences between the distinct polynomial regressions (2<sup>nd</sup> order,  $p = 0.6462$ ; 3<sup>rd</sup> order,  $p = 0.9363$ ), although all three models presented statistically significant coefficients for site and multiple transects (Table 3-3). Additionally, there was a substantial difference in the magnitude and significance of coefficients for transects from the southern versus the northern site. The linear mixed-effects model showed no statistically significant results, for the first or the second order polynomial regressions. Inputting ‘site’ and ‘transect’ as random nested variables did not provide for any results of note either.

### **Summary of Results**

Analysis of the soil and water chemistry data provided some very intriguing results, which may be explained by a number of different hypotheses. It can be concluded, however, that there are distinct differences in the soil and water chemistry between the southern and northern marshes. Whether these distinct characteristics are directly or indirectly responsible for variations in species richness and composition is unknown, but it can be said that there are definite connections between soil and water chemistry and plant species community composition. It is unfortunate that there were no viable results from the germination experiment. It could have given some insight into why *Typha domingensis* was able to initially establish in these marshes.

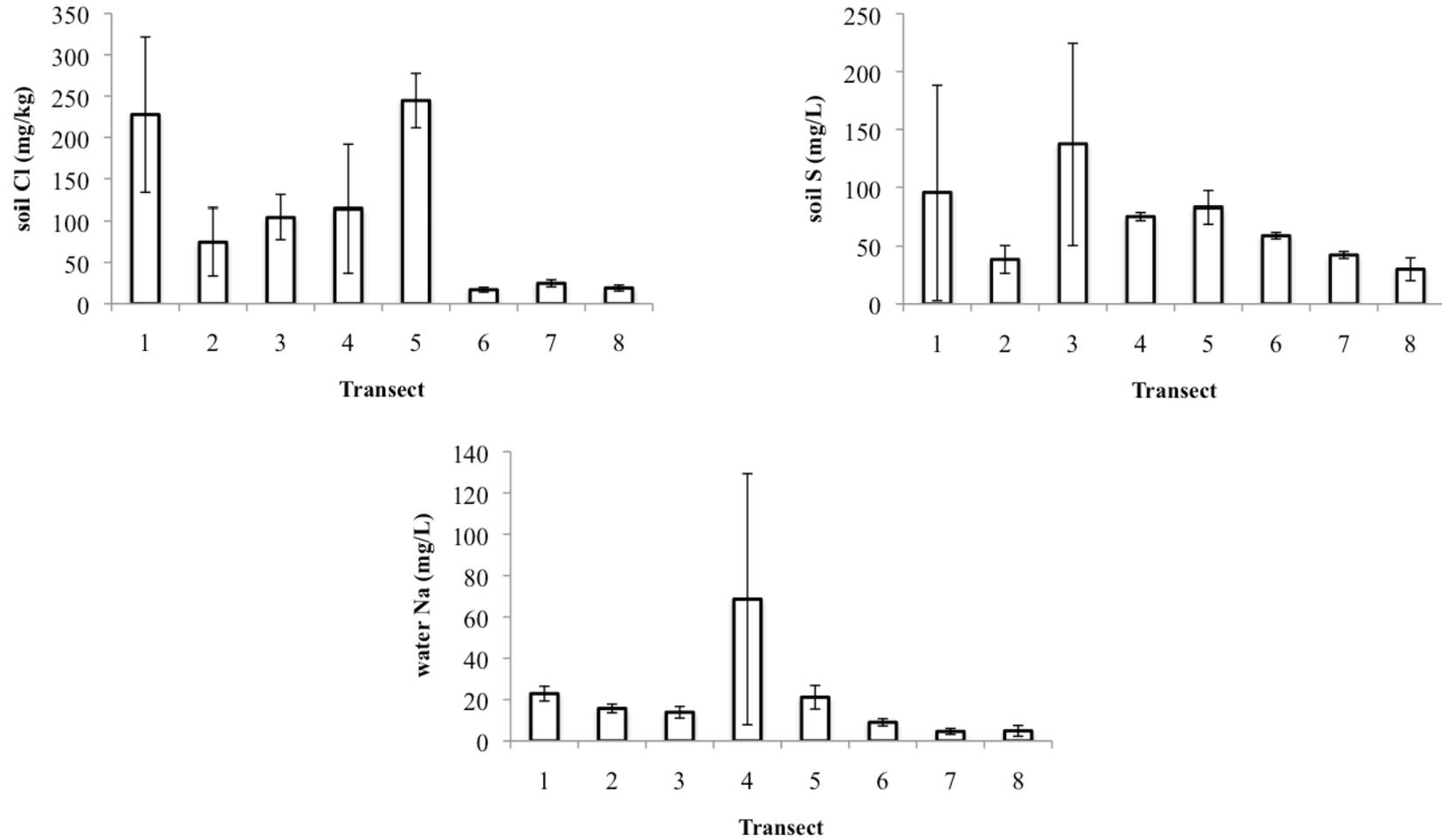


Figure 3-1. Transect averages. For salinity markers,  $\pm 1$  SD. For soil Cl, the calculated F-statistic = 7.1 ( $p = 0.0065$ ); for soil S,  $F = 1.2$  ( $p = 0.3940$ ); for water Na,  $F = 3.6$  ( $p = 0.0082$ ). Unless otherwise noted, sample sizes for variables in all figures are as follows: soil components,  $n = 2$  for all transects except transect 7, where  $n = 3$ ; water components,  $n = 4$  for transects 1, 2, 4, 5, 6 and 8,  $n = 5$  for transect 3, and  $n = 6$  for transect 7.

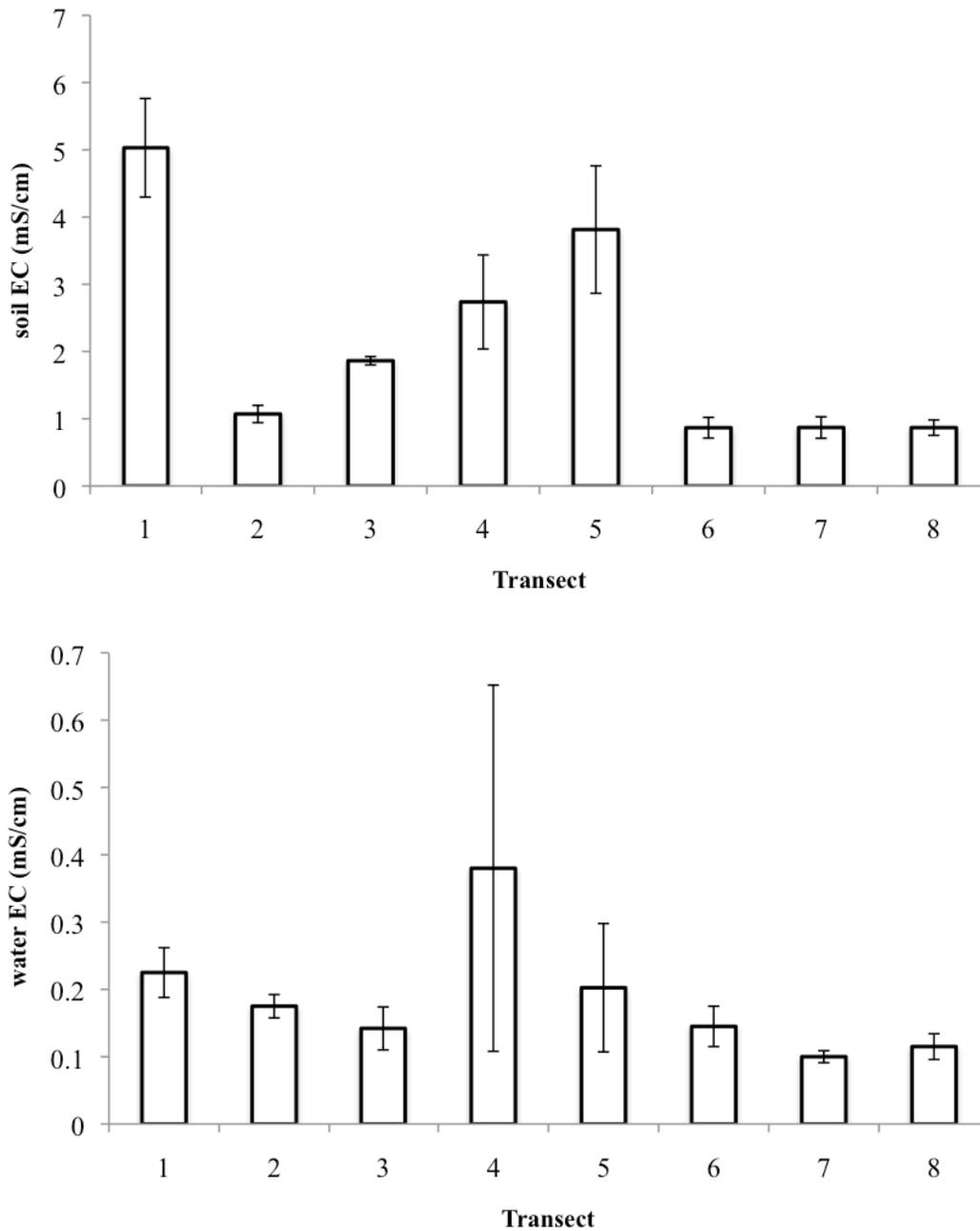


Figure 3-2. Transect averages. For electrical conductivity for soil and water,  $\pm 1$  SD. For soil EC, the calculated F-statistic = 100.4 ( $p < 0.0001$ ); for water EC,  $F = 2.9$  ( $p = 0.0247$ ). For soil measurements,  $n = 4$  for transects 1, 2 and 3,  $n = 3$  for transect 4,  $n = 8$  for transects 5, 6 and 8, and  $n = 16$  for transect 7.

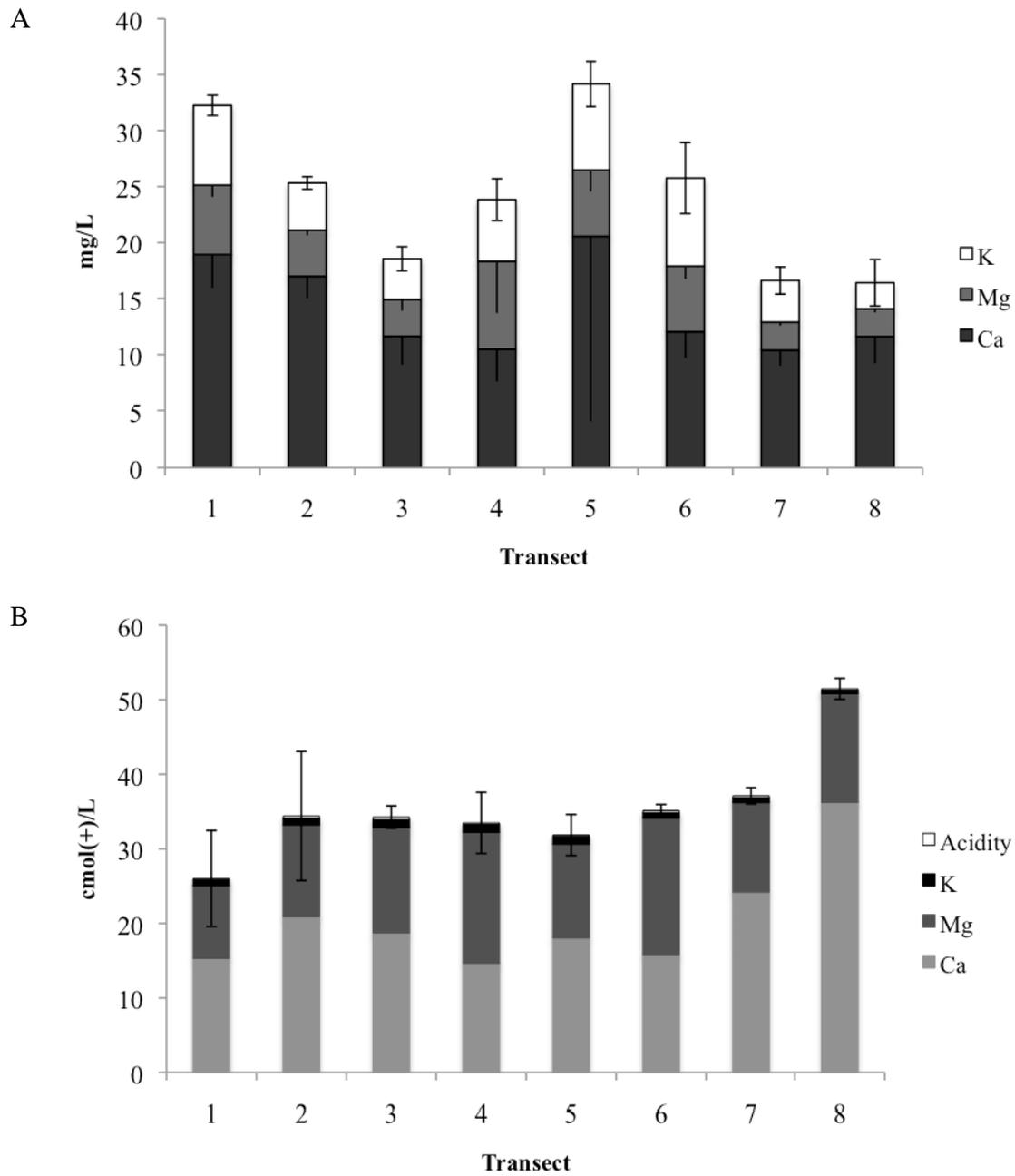


Figure 3-3. Transect averages. A) For dissolved cations in water and B) effective cation exchange capacity in soil,  $\pm 1$  SD. For soil ECEC, the calculated F-statistic = 5.8 ( $p = 0.0123$ ); for water Ca,  $F = 1.6$  ( $p = 0.1712$ ); for water Mg,  $F = 4.1$  ( $p = 0.0044$ ); for water K,  $F = 5.6$  ( $p = 0.0006$ ).

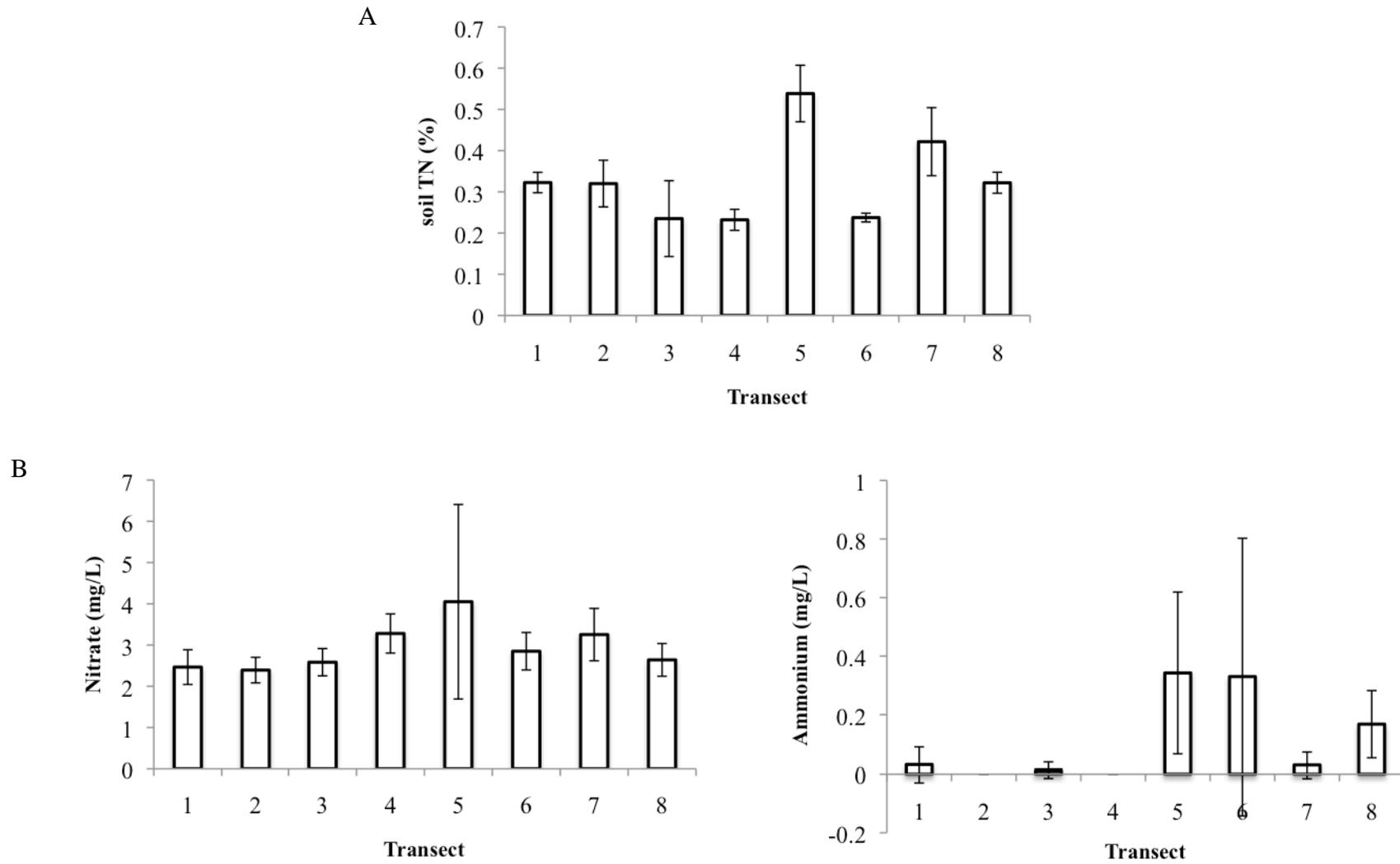


Figure 3-4. Transect averages. A) For nitrogen compounds in soil and B) in water,  $\pm 1$  SD. For soil TN, the calculated F-statistic = 10.5 ( $p = 0.0018$ ); for water  $\text{NO}_3^-$ ,  $F = 1.7$  ( $p = 0.1691$ ); for water  $\text{NH}_4^+$ ,  $F = 2.1$  ( $p = 0.0779$ ).

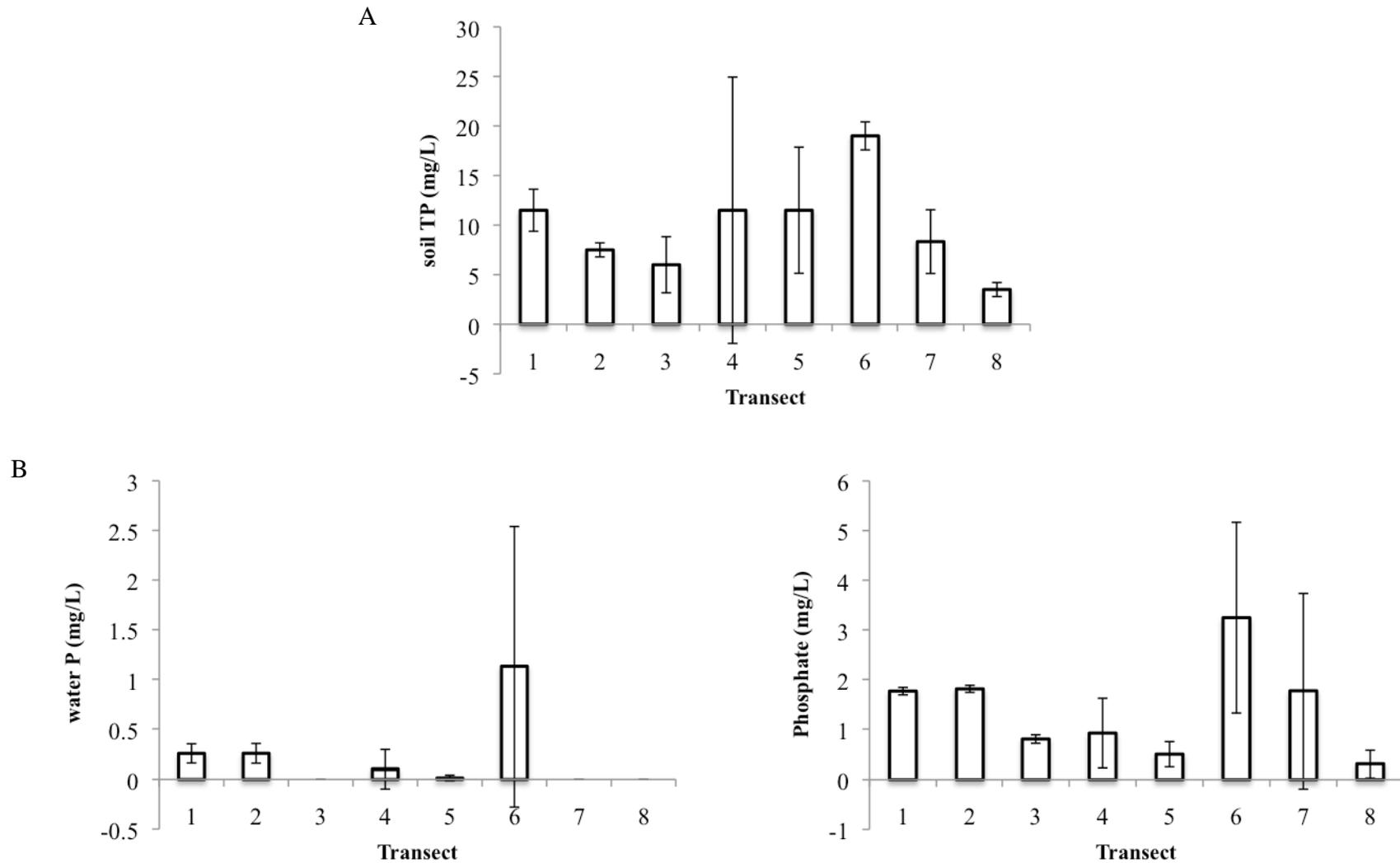


Figure 3-5. Transect averages. A) For phosphorous compounds in soil and B) in water,  $\pm 1$  SD. For soil TP, the calculated F-statistic = 1.6 ( $p = 0.2683$ ); for water P,  $F = 2.3$  ( $p = 0.0594$ ); for water  $\text{PO}_4^{3-}$ ,  $F = 5.2$  ( $p = 0.0010$ ). For water phosphate,  $n = 8$  for transect 7 and  $n = 7$  for transect 8; all other sample sizes are the same.

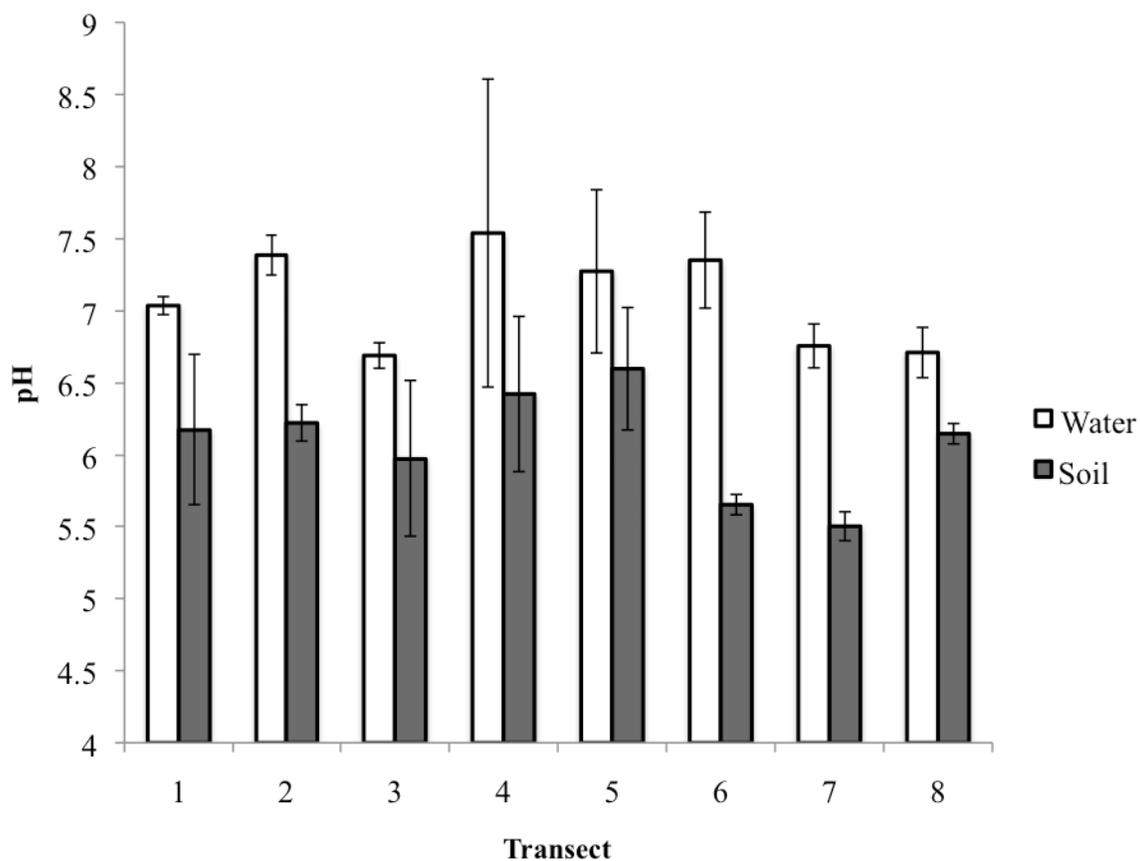


Figure 3-6. Transect averages. For water and soil pH,  $\pm 1$  SD. For soil pH, the calculated F-statistic = 1.4 ( $p = 0.3286$ ); for water pH,  $F = 2.4$  ( $p = 0.0507$ ).

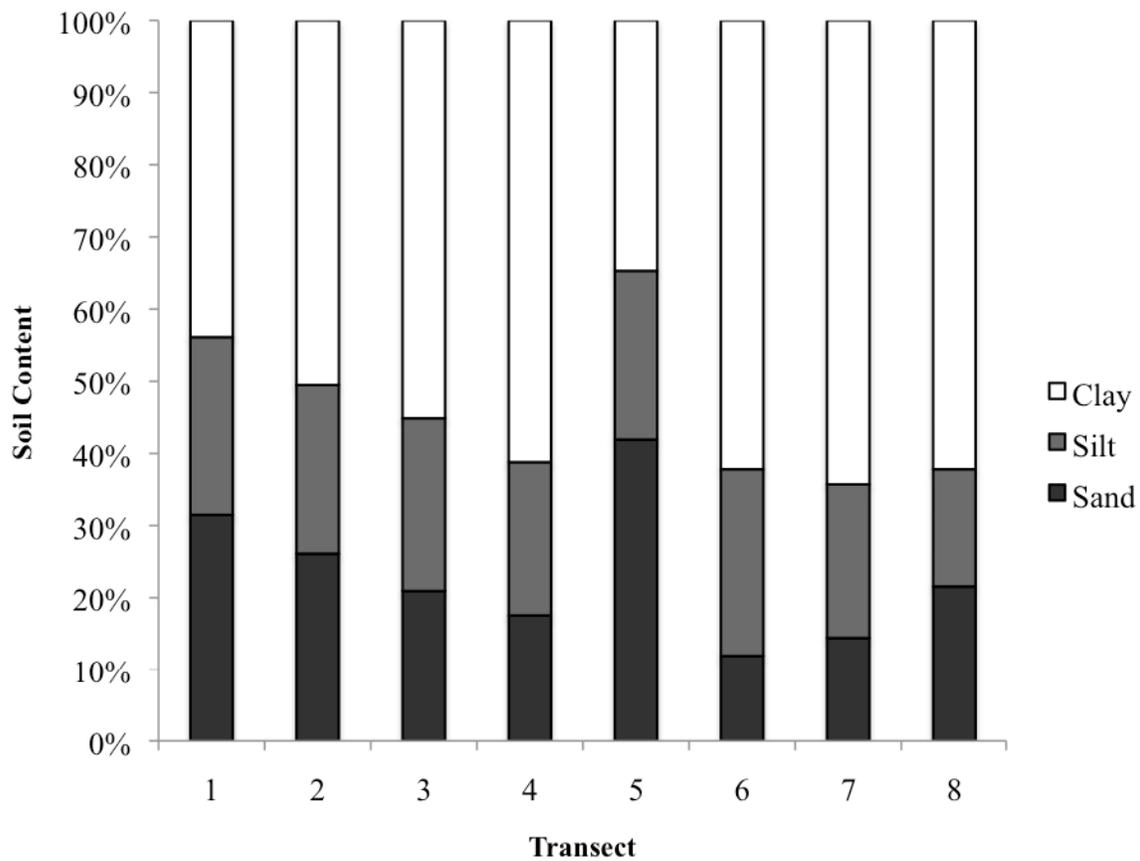


Figure 3-7. Transect averages. For soil content and texture. For sand content, the calculated F-statistic = 5.1 ( $p = 0.0174$ ); for silt,  $F = 3.2$  ( $p = 0.0623$ ); for clay,  $F = 4.8$  ( $p = 0.0209$ ).

Table 3-1. ANOVA and T-test table for species richness (# of species/1 m<sup>2</sup>) at multiple scales.

	df(b)	df(w)	F/T-statistic	<i>p</i> -value
Subtransect	13	226	29.40	<0.0001
Transect	6	233	29.46	<0.0001
Site	238		-7.99	<0.0001

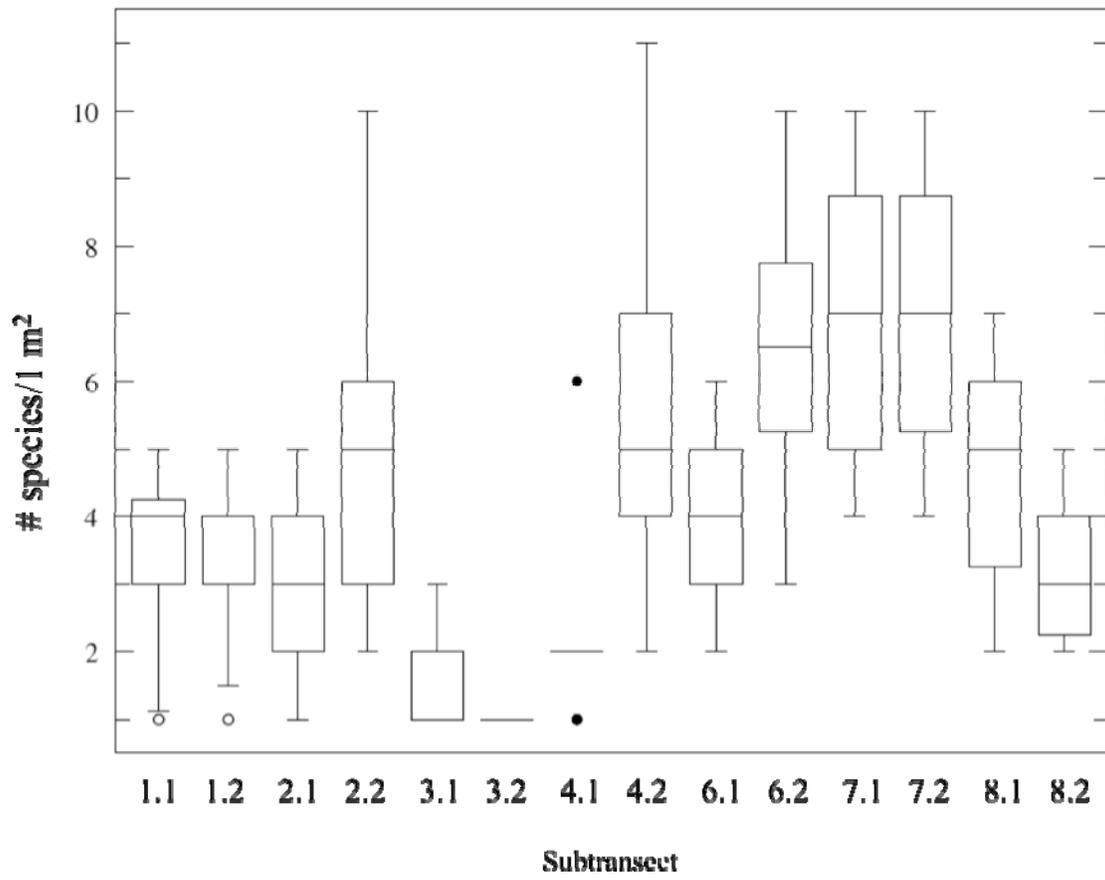


Figure 3-8. Box plot of species richness (per 1 m<sup>2</sup>) by subtransect.

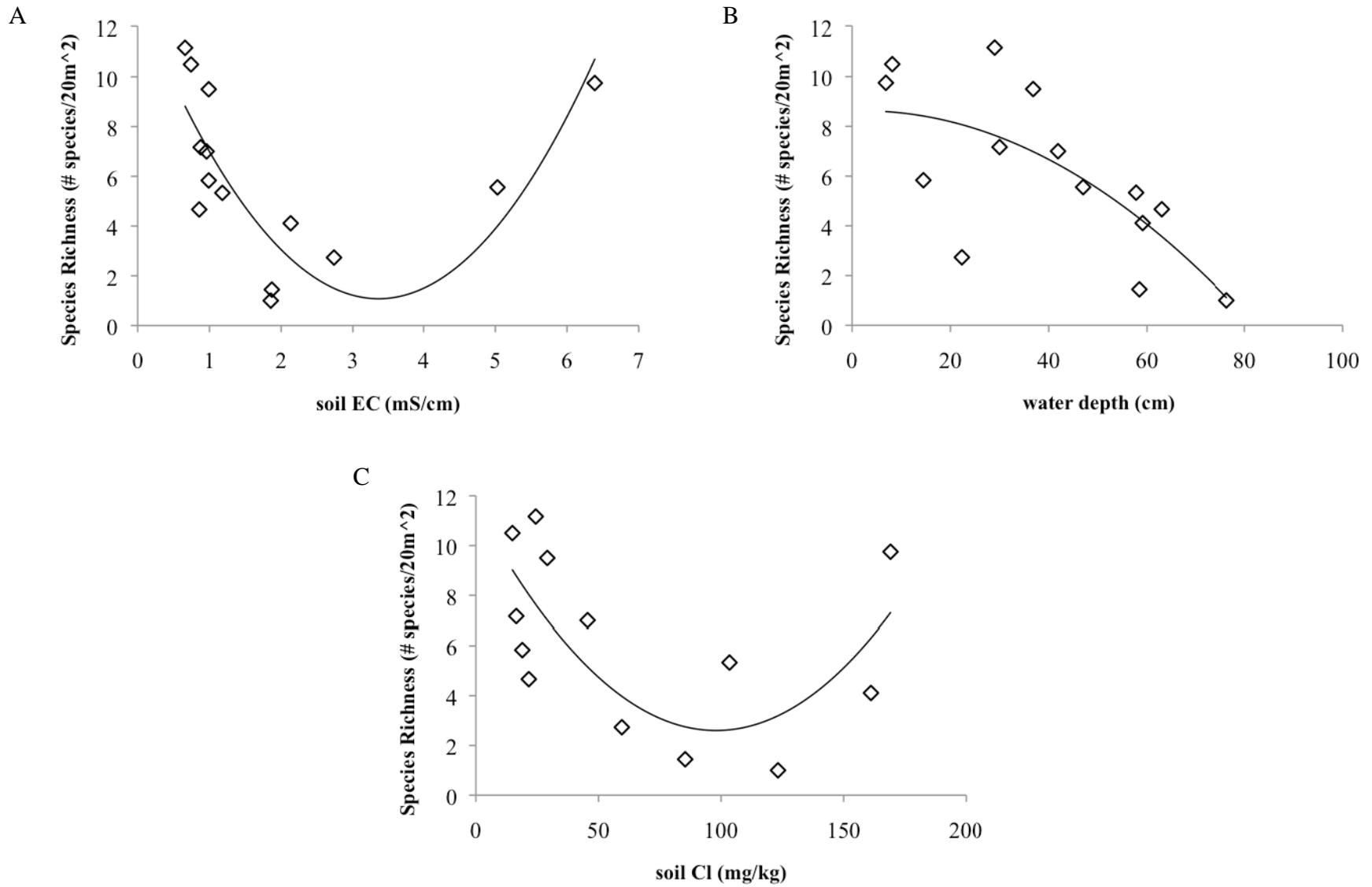


Figure 3-9. Trends in species richness. A) With respect to soil EC, B) water depth, C) soil Cl, D) water Fe, E) soil K, F) water Na and G) soil S.

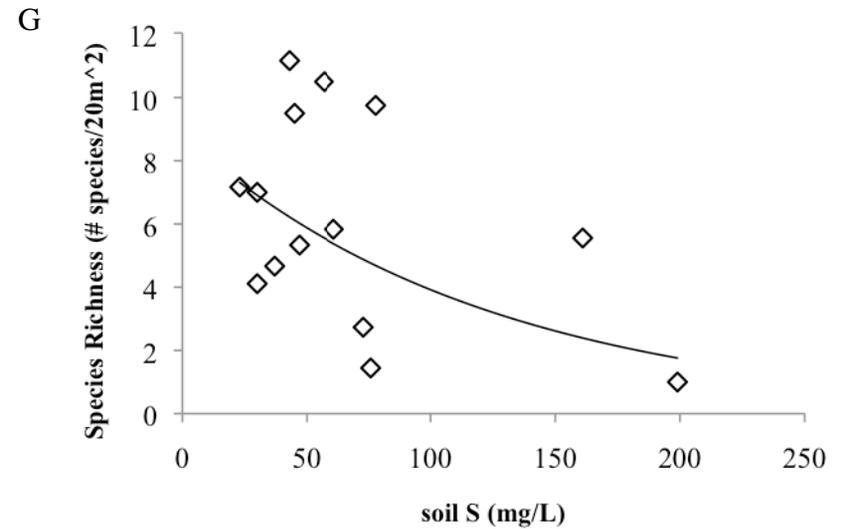
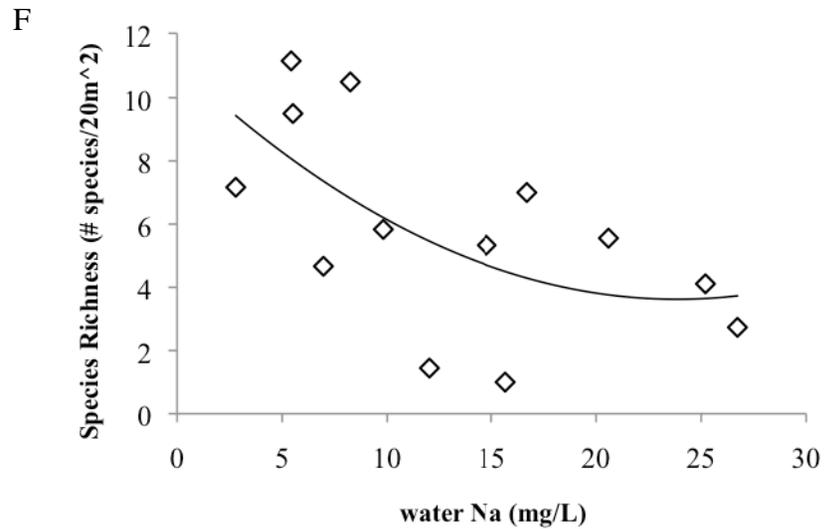
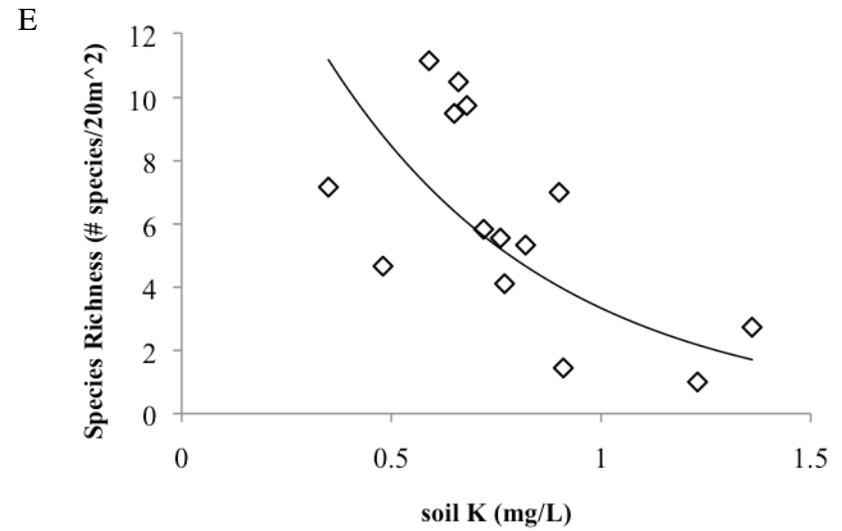
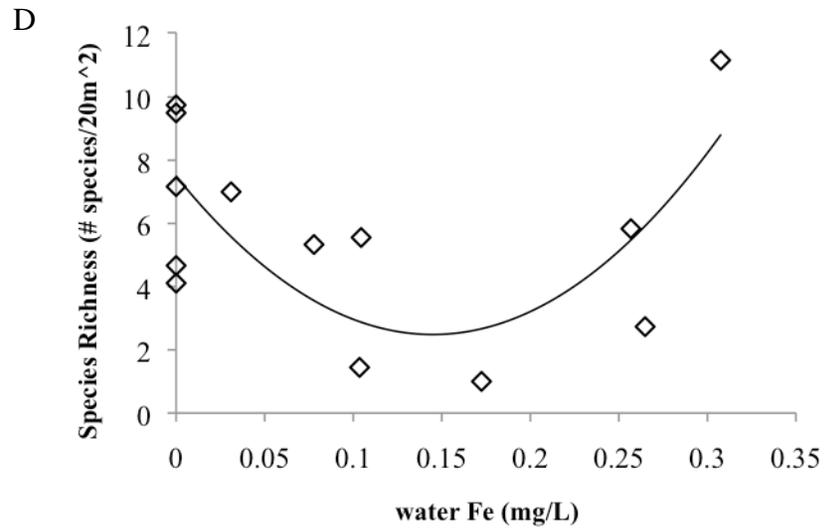


Figure 3-9. Continued.

Table 3-2. Linear model and ANOVA output for final regression equations for the response variable ‘Species Richness.’ Statistically significant coefficients: \*\*\*,  $p < 0.005$ ; \*\*,  $p < 0.01$ ; \*,  $p < 0.05$ .

	Coefficient	F-Statistic	$p$ -value	
Clay	0.20946	10.1830	0.0051	***
Soil Cu	-0.20685	3.9745	0.0616	*
Soil Fe	0.01149	0.2872	0.5986	
Soil N	28.38421	17.8656	0.0005	***
Water Fe	0.15184	3.7008	0.0703	*
Water Na	-0.02063	0.6673	0.4247	
Water NO <sub>3</sub> <sup>-</sup>	-2.93477	6.4816	0.0202	**
Water P	0.69215	2.1029	0.1642	
Water depth	-0.04981	5.4732	0.0310	**
	Sum Sq	Mean Sq	df	
Residuals	71.337	3.963	18	

	Coefficient	F-Statistic	$p$ -value	
Soil K		27.8673	4.28e-05	***
Soil N		5.8280	0.0260	*
Soil Cu		3.4978	0.0769	*
Sand		19.4115	0.0003	***
Soil S		0.4265	0.5216	
Water Fe		0.1549	0.6983	
Water pH		6.3321	0.0210	*
Water depth		0.0583	0.8119	
	Sum Sq	Mean Sq	df	
Residuals	62.680	3.299	19	

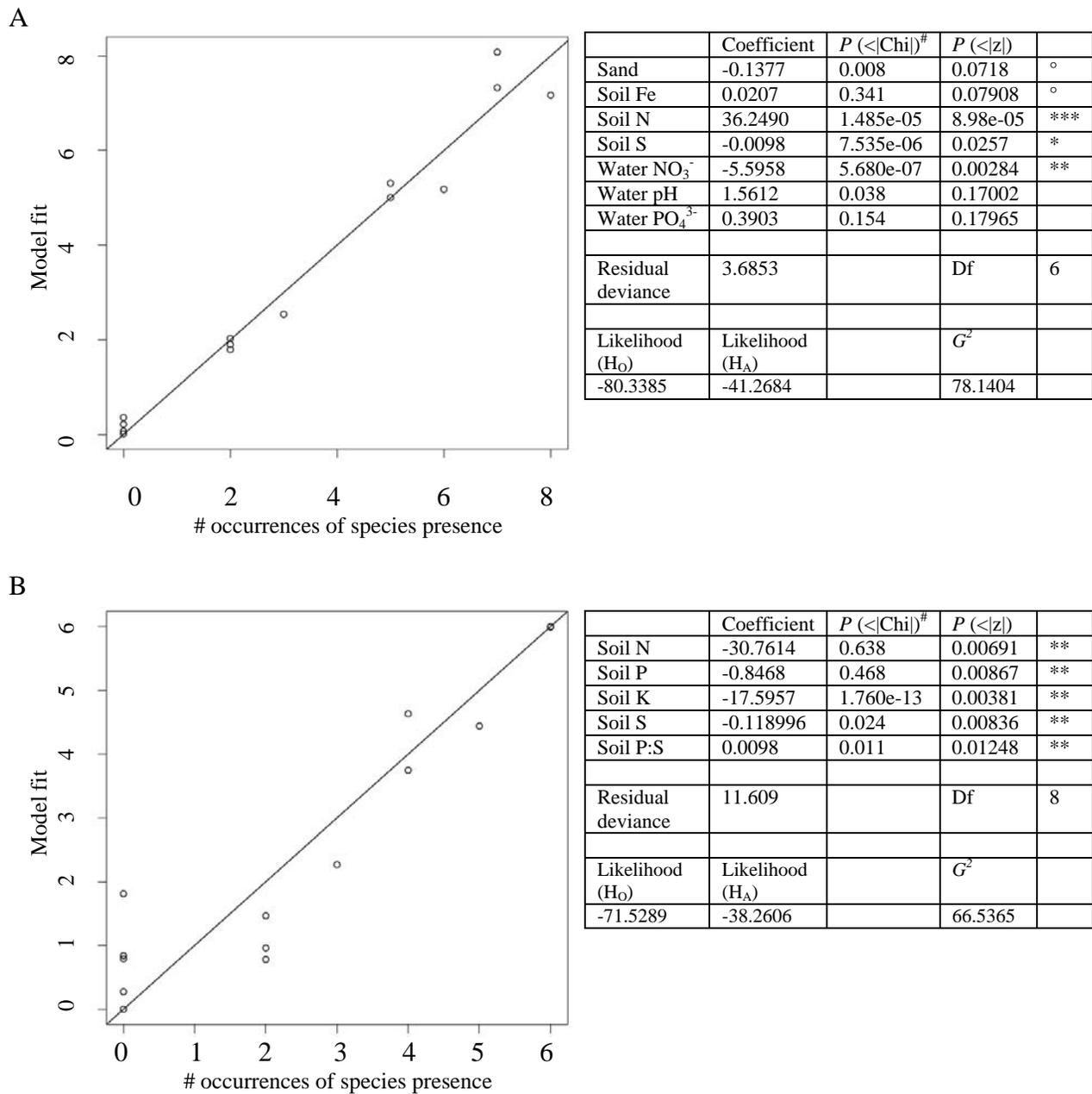
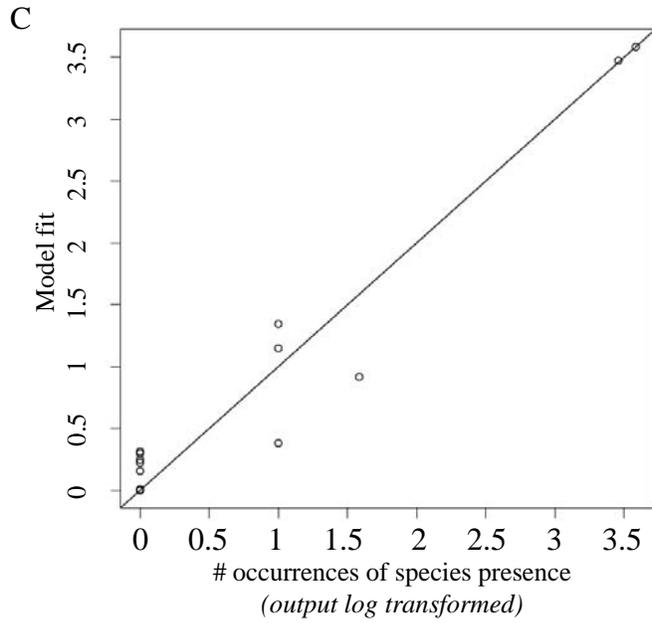
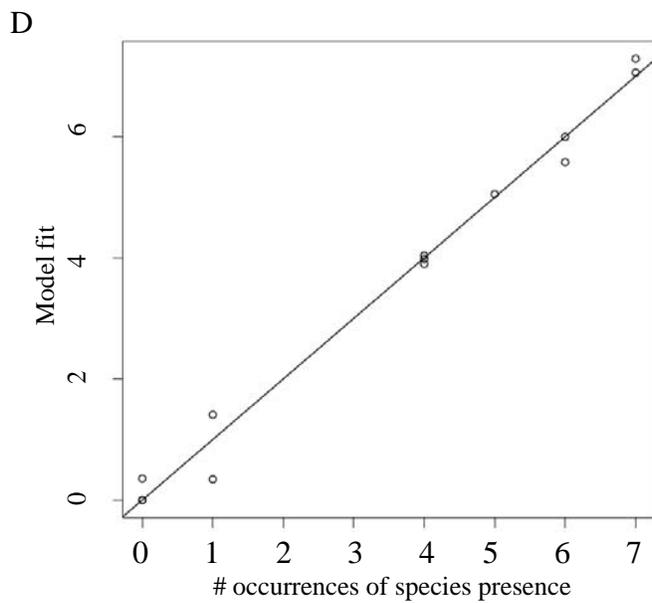


Figure 3-10. Output for logistic regressions. A) For the presence of *A. martinicensis*, B) *E. paniculatus*, C) *Eleocharis* spp., D) *Nymphaea* spp., E) *S. clausum*, F) *T. geniculata* and G) *T. domingensis*, with accompanying model equation output. Likelihoods are log values. <sup>#</sup> - Terms added sequentially, first to last. Statistically significant coefficients: \*\*\*,  $p < 0.001$ ; \*\*,  $p < 0.01$ ; \*,  $p < 0.05$ ; °,  $p < 0.1$ .



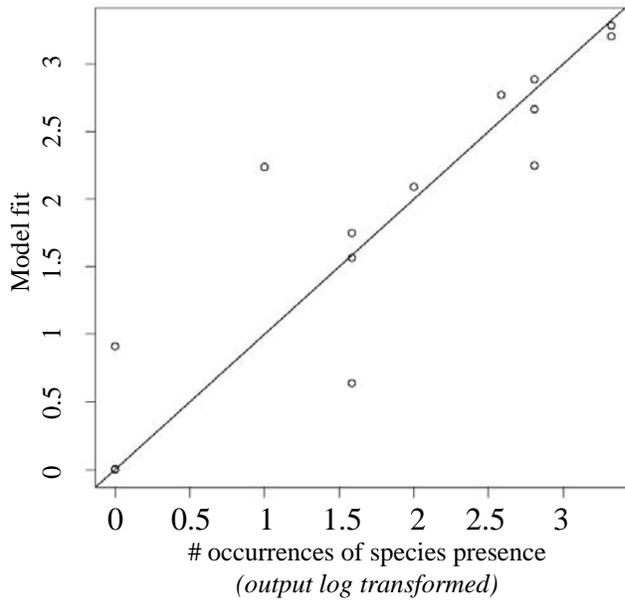
	Coefficient	$P (< \text{Chi} )^{\#}$	$P (< z )$	
Soil Fe	-0.0619	0.770	0.1784	
Soil Mn	-0.0194	0.570	0.0855	°
Water Na	0.01398	9.971e-08	0.37885	
Water NO <sub>3</sub> <sup>-</sup>	4.4833	1.4323-07	0.00657	**
Water depth	-0.0690	0.076	0.08007	°
Residual deviance	4.6084		Df	8
Likelihood (H <sub>0</sub> )	Likelihood (H <sub>A</sub> )		$G^2$	
-62.7188	-32.9159		59.6057	



	Coefficient	$P (< \text{Chi} )^{\#}$	$P (< z )$	
Soil N	34.82451	0.002	0.00104	***
Soil P	-3.4356	0.331	3.79e-05	***
Soil K	7.71836	5.149e-07	0.03948	*
Soil S	-0.9136	0.246	3.01e-05	***
Soil P:S	0.07635	6.89e-12	2.99e-05	***
Residual deviance	2.6851		Df	8
Likelihood (H <sub>0</sub> )	Likelihood (H <sub>A</sub> )		$G^2$	
-79.3876	-37.4478		83.8795	

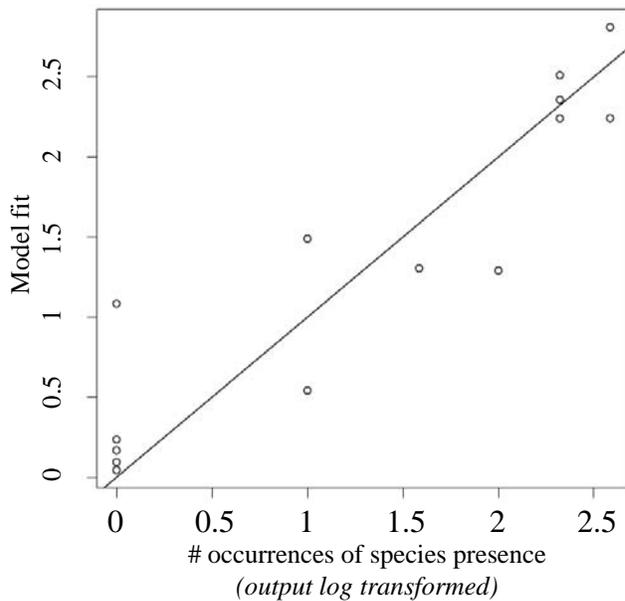
Figure 3-10. Continued.

E



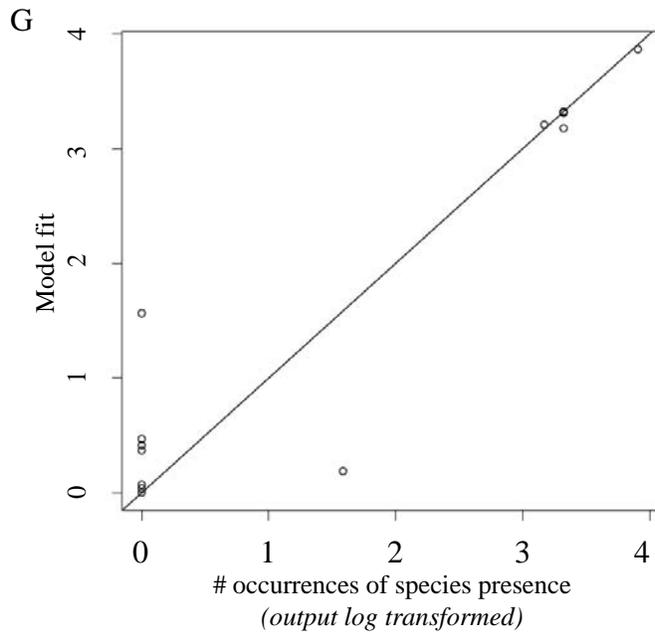
	Coefficient	$P (< Chi )^{\#}$	$P (< z )$	
Clay	-0.3790	0.018	0.0017	**
Soil K	-8.2265	0.011	0.0014	**
Soil P	0.2190	0.347	0.1419	
Water EC	-5.0493	0.143	0.0606	°
Water Fe	-0.5048	0.515	0.0496	*
Water PO <sub>4</sub> <sup>3-</sup>	-2.0411	1.189e-06	0.0004	***
Water depth	-0.1314	0.005	0.0163	*
Residual deviance	13.271		Df	6
Likelihood (H <sub>0</sub> )	Likelihood (H <sub>A</sub> )		G <sup>2</sup>	
-81.8226	-58.4409		46.7634	

F



	Coefficient	$P (< Chi )^{\#}$	$P (< z )$	
Soil Mg	-0.51009	0.024	0.00556	**
Soil pH	-3.1853	0.002	0.0097	**
Water NO <sub>3</sub> <sup>-</sup>	-3.0081	0.687	0.0031	**
Water PO <sub>4</sub> <sup>3-</sup>	0.5948	3.183e-06	0.0192	*
Water depth	-0.1038	4.995e-04	0.0099	**
Residual deviance	8.300		Df	8
Likelihood (H <sub>0</sub> )	Likelihood (H <sub>A</sub> )		G <sup>2</sup>	
-66.3592	-42.2474		48.2237	

Figure 3-10. Continued.



	Coefficient	$P (< \text{Chi} )^{\#}$	$P (< z )$	
Soil Cl	0.0600	0.810	0.02623	*
Soil EC	5.6099	0.002	6.08e-05	***
Soil S	-0.0480	4.932e-08	0.0006	***
Water Fe	0.8425	0.146	0.3042	
Water Na	-0.3274	7.580e-18	0.0056	**
Water depth	0.1240	0.001	0.0071	**
Residual deviance	16.708		Df	7
Likelihood ( $H_0$ )	Likelihood ( $H_A$ )		$G^2$	
-83.1777	-20.1465		126.062	

Figure 3-10. Continued.

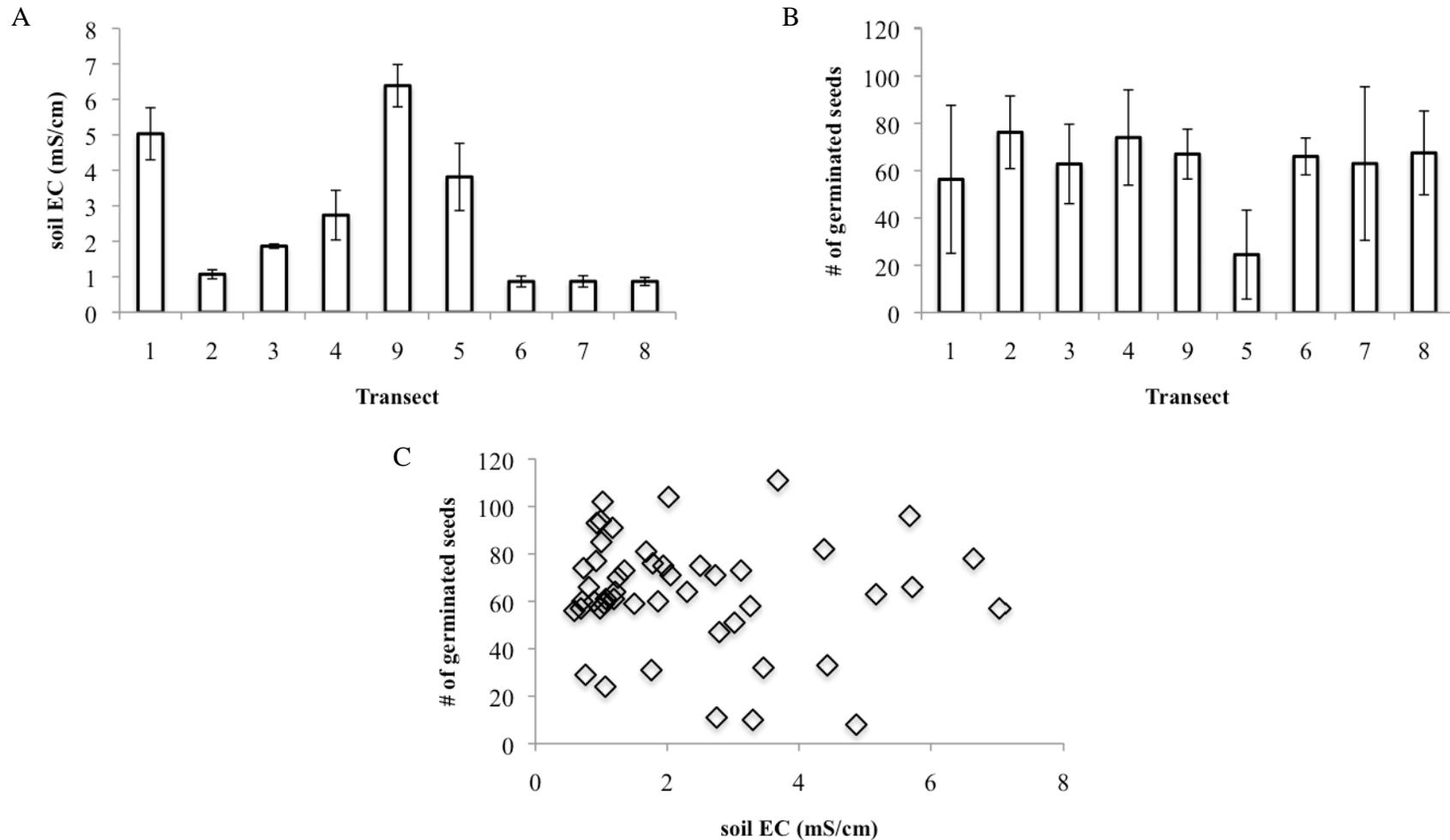


Figure 3-11. Transect averages. A) For soil electrical conductivity and B) *Typha* seed germination,  $\pm 1$  SD, and C) scatter plot of soil EC and total germination. For soil EC, the calculated F-statistic = 67.48 ( $p < 0.0001$ ; excluding transect 5); for seed germination,  $F = 0.59$  ( $p = 0.7562$ ; excluding transect 5). For soil measurements,  $n = 18$  for transect 2,  $n = 16$  for transect 7,  $n = 12$  for transects 1 and 3,  $n = 11$  for transect 4,  $n = 8$  for transects 5, 6 and 8, and  $n = 6$  for transect 9. For germination,  $n = 9$  for transect 2,  $n = 6$  for transects 1, 2, 3 and 7,  $n = 4$  for transects 5, 6 and 8, and  $n = 3$  for transect 9.

Table 3-3. Model output for first order polynomial regression of *Typha* seed germination. Multiple  $R^2 = 0.2143$ ; adjusted  $R^2 = 0.02944$ . F-statistic = 1.159 ( $p = 0.3514$ ).

	Coefficient	$p$ -value	
Site(S)	-35.739	0.0588	*
Transect(2)	40.551	0.0113	**
Transect(3)	20.317	0.1516	
Transect(4)	23.938	0.0650	*
Transect(6)	-1.264	0.9316	
Transect(7)	-3.989	0.7670	
Transect(8)	NA	NA	
Transect(9)	-17.329	0.4016	
mS (1 <sup>st</sup> )	104.156	0.0573	*

## CHAPTER 4 DISCUSSION

### **Review of Results**

Higher levels of salinity markers in soil and water were found in the southern area (Figure 3-1). These transects also had higher cation concentrations in the water, but the greatest concentrations of cations in soil were observed within the northern transects (Figure 3-3). In fact, the greatest concentration level in soil was found at transect 8, which had the lowest cation concentration in water; the lowest cation concentration in soil was found at transect 1, which had the second highest concentration level in water. Within the southern site transects, sand content decreased and clay content increased with increased distance from the river mouth. For the northern site transects, sand content increased and silt content decreased with distances further upstream.

N and P levels were high at some of the southern site transects, but were also surprisingly elevated for some of the northern site transects. Transects 7 and 8 had the second and third highest levels of total soil nitrogen, respectively (Figure 3-4), and transect 6 had the highest level of total soil phosphorus (Figure 3-5). Although there were no trends or statistically significant differences between pH levels of water or soil for the transects, there were great differences between the water pH and soil pH; that is, water pH was substantially higher than soil pH at each transect (Figure 3-6).

Soil Cl, S, K, EC and water Na, Fe and water depth explained much of the variation in species richness among subtransects using single-variable regressions (Figure 3-9). Multivariate linear models of species richness showed that the variables of soil N, K and water P, pH, EC and depth were both large in magnitude and statistically significant (Table 3-2).

Results from the logistic regressions run on the most abundant species produced strong models for several of the species, most of them containing some form of N, P or K in the variable selection (Figure 3-10). The presence or absence of *Typha*, however, was best modeled using salinity markers; none of the regressions run on *Typha* resulted in statistically significant and magnitudinous effects for nitrogen or phosphorus compounds.

The *Typha domingensis* germination experiment did not provide any statistically significant or noteworthy results. Although there were statistically significant differences among the specific soil porewater conductivities for the transects, there were no differences in germination totals. A scatter plot of these data revealed no patterns or trends of any kind (Figure 3-11).

## **Soil and Water Chemistry**

### **Environmental Influences**

#### **Seasonal variation**

When looking at the soil and water chemistry of wetlands, one must always keep in mind that the numbers of interest are *concentrations*. Concentrations change, often varying with the volume of water present in the wetland. This is especially true when considering seasonal wetlands (Sarmiento et al. 2004), whose dynamic hydrology results in continual changes in soil conditions and available nutrients.

Although this study did not address the seasonal variation that occurs in the area marshes, it is important to recognize these cyclic trends with regard to timing of sample collection. A study conducted in a tropical freshwater wetland in India, with similar climatic patterns to those seen in the Palo Verde region, found that, during the months of June and July,  $\text{NO}_3^-$ ,  $\text{PO}_4^{3-}$  and Ca concentrations in water were very high, K very low and Mg concentrations were on the rise (Shardendu and Ambasht 1991). Sodium showed no distinct seasonal pattern. These exact

trends would probably not be observed in the marshes of Palo Verde National Park, because of their hyperseasonality, but we would expect something quite similar.

Since this study made no effort to track seasonal changes within the Palo Verde wetlands, it is impossible to know whether these trends in concentrations would be present or not.

However, K concentrations found in the water around Palo Verde seem to be particularly high, relative to Ca and Mg concentrations (Figure 3-3). This is the opposite of what was found by Shardendu and Ambasht (1991). While it may be the case that K concentrations would have continued to increase over the following months, K is typically not more dominant than Mg in tropical wetlands (Shardendu and Ambasht 1991, McDowell and Asbury 1994).

Beyond the flux of water due to seasonality, such dynamics may bring about other responses. For example, the continual wetting and drying of soil can result in mineral accumulation (Johnson and Steingraeber 2003), which will lead to higher electrical conductivity. These seasonal changes could partially explain why soil ECs are much higher at some transects than their corresponding water ECs (Figure 3-2) and do not tend to follow the same spatial pattern.

Soils throughout the park were found to be slightly acidic relative to water (Figure 3-6), which is a trend also seen in calcareous mires (Johnson and Steingraeber 2003); these differences might be intensified by seasonal variation. During the wet season, soil sulfur will reduce to  $S^{2-}$ ; once the marshes dry out the sulfur will oxidize into  $SO_4^{2-}$ . Increased sulfate concentrations have been shown to dramatically decrease pH in wetlands (Mossmark et al. 2008). Since many of the marshes had been flooded for less than a month and pH can be slow to change, this may still be a reasonable explanation for the low pH levels, even though soil samples for this study were taken during the wet season.

## Geology

It is not unusual to find differences in concentration levels when comparing elemental compositions of soil and water. Some of those noted within PVNP might be due, in part, to seasonal variation. Although it is not immediately obvious, there is a vast difference in the overall concentrations of Ca and Mg in soil and water (Figure 3-3). Throughout the park, calcium constitutes approximately 58% of the total cation concentration (Ca, Mg, K) in both soil and water; Mg, on the other hand, comprises nearly 39% of soil cation concentrations but only 20% in water. While these findings are in accordance with the results of the study carried out in the tropical freshwater wetland in India, they might be altered by rainwater runoff from the large limestone ridges that dominate the central area of the park. Presumably, such a considerable influx of calcium carbonate could skew the results of this study, making it appear to reflect those of the Shardendu and Ambasht (1991) study, even if they do not.

Unexpected patterns in spatial variation of cation concentrations in soil might also be explained by runoff from the limestone ridges within the park. The lagoons of the south are large and, in some places, very far from the limestone outcroppings that dominate the skyline. The marshes of the north, on the other hand, are much smaller and are much closer to the ridges. Higher cation concentrations in water within the southern marshes could be accounted for by their proximity to the river; higher cation concentrations in soil, particularly Ca, within the northern marshes could be accounted for by their proximity to the limestone ridges.

Differences in soil texture might also contribute to varying levels of cation concentration throughout the park. Higher clay content in soil results in higher total surface area of the soil particles, allowing for the adsorption of more cations onto soil particles (Mengel et al. 2001). Soil from transect 1 was found to have one of the lowest clay contents within the park (Figure 3-7); this could easily explain the low concentrations of cations in this area, despite the proximity

of both the Tempisque and the Gulf of Nicoya. The extremely high concentrations of cations in soil found at transect 8 could be the result of both high clay content and its location between two limestone ridges.

### **Tempisque River and Gulf of Nicoya**

Proximity to the Tempisque River and the Gulf of Nicoya could explain some of the spatial patterns seen in soil concentrations of specific elements, particularly in the southern area marshes. The natural levees along the Tempisque River generally keep its waters, the recipient of nitrogen-loaded runoff from agricultural fields to the north and the saline waters from the Gulf of Nicoya to the south (McCoy and Rodríguez 1994, Kress et al. 2002, Tabash Blanco 2007), from flowing into the Palo Verde marshes. During extreme rain events or tropical storms, the river will flood and overtop the levees. There is also speculation that the Palo Verde and Nicaragua Lagoons, where the southern marshes are located, were previously the main channel of the Tempisque River (E. González, pers. comm.).

Elevated levels of salinity markers, such as sulfur and chloride, and phosphorus (Figures 3-1 and 3-5) in the southern marshes could be explained by the presence of relict marine deposits. Inland saline lakes and wetlands often exist due to the remnants of their former marine landscapes (Strehlow et al. 2005). High levels of P are also found in areas known to have been previously inundated by marine waters (Hein 2004, Benito et al. 2005, Kametaka et al. 2005). Although very specific conditions are required for major phosphate deposits to occur (Orris and Chernoff 2004), the concept of marine sedimentary deposits of phosphate is plausible in the setting of Palo Verde due to a presumably slow sedimentation rate, warm climate and stable basin conditions (Hein 2004, Orris and Chernoff 2004). Given that S is often deposited with P in such situations (Nathan and Nielsen 1980, Hein 2004), this hypothesis could explain the high levels of both P and S in the southern area of the park.

Higher levels of N in the northern marshes (Figure 3-4) might be explained by occasional inundation by the nitrified waters of the Tempisque River. Relatively recent flooding of the southern marshes by the Tempisque could be the source of elevated concentrations of soil Cl, S and water Na as well. What is curious, however, is that Cl concentrations were highest for transects 1 and 5, while transect 3 had the highest S concentration and the highest Na levels were found at transect 4. These discontinuities may be explained by more localized hydrologic and biogeochemical interactions.

### **Potential Impacts of the Former and Current Ranching Operations**

Because of the dominant presence of *Typha domingensis* in Palo Verde Lagoon and Catalina sector (the southern site), it would be expected that the highest levels of nitrogen and phosphorus compounds would be found there (McCormick et al. 1996, Newman et al. 1996, Noe et al. 2001). This, however, was not the case (Figures 3-4 and 3-5). As discussed previously, there is active cattle-grazing throughout the marshes of Palo Verde. Some of the shallower marsh areas are also used as pastures for the caballeros' horses; the marsh where transect 6 was located is one of these areas. Continuous deposition of nutrient-rich organic matter (in the form of feces) could potentially be the cause for such elevated levels of phosphorus compounds in this area. Soil P concentrations throughout the park were generally high and could be justified under the same hypothesis: that more than 50 years of grazing cattle in the marshes of Palo Verde has dramatically altered soil chemistry through the continual deposition of such nutrient-rich organic matter.

### **Plant Species Community Composition**

There are several interesting points with regards to the analysis of species composition throughout the park marshes, the first of which is the marked trend seen in salinity markers and species richness (Figure 3-9). Most of the trendlines show the *opposite* of what is typically

observed in species richness response to nutrients (Pausas and Austin 2001). Generally, species richness is low at low nutrient levels and begins to increase when nutrient levels are increased; once a 'critical point' is reached, species richness will start to decline as nutrient levels continue to rise. The contrary trend seen here may be due, in part, to the elements of focus, the concentration range and this *Typha*-dominated system. Moreover, even though single variable regressions can give us insight into simple patterns and trends observed throughout a landscape, ecosystems and biogeochemical dynamics are much more complex than one dimension is capable of capturing (Bedford et al. 1999, Pausas and Austin 2001).

The *Typha* species' numerous and vigorously productive properties, including resilience in the presence of salinity (Zedler et al. 1990) and the ability to colonize rapidly (Grace and Wetzel 1982), have been discussed previously. These factors, combined with data that show the subtransects with only one or two species (*T. domingensis* dominated; Figure 3-8) have high concentrations of chloride, sulfur or sodium (Figure 3-1), support the hypothesis that the soil and water characteristics in the different marshes do indeed influence plant species composition. These areas give *Typha* a competitive advantage over other species because of its robust nature. The fact that the transect area with the most *Typha* (transect 3) has the lowest concentration of soil P (Figure 3-5) may be a very important factor in determining the biogeochemical dynamics of this specific system. Additionally, the successful iteration of a salinity-centric model for *Typha* abundance, rather than one related for P, reinforces the idea that these characteristics have, in one way or another, allowed *Typha* to establish and become the dominant species.

The pattern seen between species richness and soil K concentration is easily interpreted in support of this hypothesis as well. The areas dominated by *T. domingensis*, an emergent macrophyte, will generally be much more productive and have much higher biomass per unit

area than the areas dominated by herbaceous or even small shrub species, such as *H. amplexicaulis* or *M. pigra* (Brinson et al. 1981). In European wetlands, higher species richness has been associated with lower levels of biomass in K- or K/N-limited systems (Venterink et al. 2003). If higher aboveground biomass is associated with the *Typha* dominated areas, then the validity of the continuously decreasing trend of species richness with greater soil K concentrations seen in these data (Figure 3-9) is upheld.

Multivariate logistic regressions performed on the presence and absence of specific species demonstrated the strong influence of nitrogen and phosphorous components (Figure 3-10). The combination of variables that yielded the most exciting results was that inspired by the work of Sarmiento et al. (2006) and Caraco et al. (1989). In a flooded savanna in Venezuela, areas fertilized with N, P or N and P showed little to no increase in primary and biomass production; however, when a fertilizer combining N, P, K and S was used, the observed increases in production were remarkable (Sarmiento et al. 2006). A review of aquatic systems suggests that relative phosphorus release from sediment may in part be regulated by the concentration of sulfate present (Caraco et al. 1989). The high and frequent levels of significance for all of the terms, including the interaction between S and P, demonstrates that this is a first-generation model for understanding the biotic and abiotic reactions occurring in this system.

### **Germination Experiment**

Unfortunately, the results of the germination experiment provided no results to support the hypothesis presented here. It is interesting to note, however, that there was equally high levels of germination throughout the park, other than at transect 5 (Figure 3-11). The measured soil conductivity for the samples from transect 5 was lower than that from transects 1 and 9, but higher than all the other transects. This low level of germination implies that there are other factors at work in that particular marsh. It could be that the continued *fangeada* does have long-

term effects either on the viability of *T. domingensis* seeds or through the rapid release of toxic compounds (McNaughton 1968) into the soil through the crushing process.

These effects might have been easily captured by having control samples of unplanted soil from several of the different soils. Limitation in necessary supplies in field situations is an unfortunate reality and one that is central to the lack of controls in this experiment. All available resources were used to obtain the maximum amount of data possible. Retrospectively, a few samples could have been foregone in order to allow for control samples.

### **Overall Synthesis**

Although this study did not address the cattle-grazing restoration method utilized within Palo Verde National Park, evidence that contradicts its foundations has been provided. To begin with, the removal of the weirs that connected Palo Verde Lagoon to the Tempisque River certainly had more to do with the establishment of *Typha* than the removal of the cattle. Secondly, cattle do not eat *Typha*; they prefer to consume the more herbaceous species. Finally, since there is no historical information on the plant community structure of these marshes before they were used as cattle grazing pastures, it is impossible to know whether these wetlands even need restoring.

Data that point to other possible hypotheses for the invasion of *Typha domingensis* have also been provided. That many areas of the marshes in both the southern and northern areas of PVNP have a dominant invasive species present (*T. domingensis* or *Mimosa pigra*) suggests that the entire park has seen some kind of disturbance, which gave these plants an opportunity to establish, and that there are underlying reasons why *Typha* flourished in the south and *Mimosa* in the north. The most obvious reasons for this, supported by the data presented in this thesis, are differences in soil and water chemistry between the two areas.

The southern area of PVNP has been shown to have much higher concentrations of elements indicative of marine influences – chloride, sulfur and sodium – in the soil. Even though the soils of the northern area marshes have higher cation concentrations – another salinity indicator – these can be explained with higher clay content in soil and proximity to limestone outcroppings. The water of the southern area, however, has much higher cation concentrations than those found in the north. This is congruous with the hypothesis that the southern area marshes are subject to much greater marine influences, whether current or relict, than the northern area marshes.

It is difficult to draw direct conclusions from some of the analysis conducted on the plant species communities. It is unlikely that variations in soil and water chemistry have directly caused species richness to decline. What is more likely is that such conditions inhibited regrowth rates of other species after a disturbance event and that *Typha* was able to quickly establish and colonize the area rapidly. Thus, the question remains *how* specific soil and water chemical characteristics influence the establishment of *Typha domingensis* in Palo Verde National Park.

Despite this, and the lack of results from the germination experiment, it is hoped that this research will begin the process of debunking the cattle-grazing hypothesis and restoration technique. Unfortunately, because the McCoy Rodríguez (1994) paper is one of the few published works specifically addressing the Palo Verde wetlands, its unsubstantiated hypothesis continues to receive recognition and support, even by some of the most well-known wetlands ecologists of today. In the most recent edition of their renowned book *Wetlands* (4<sup>th</sup> edition), Bill Mitsch and James Gosselink (2007) state, in their section discussing Palo Verde National Park, that “[c]uriously, the diversity of birds was partially maintained because of cattle grazing”

(76). This demonstrates how powerful one publication can be. The results from this research will begin to counteract the pervasiveness of illogical hypotheses and ineffective restoration methods. However, continued research will be necessary to reinforce and develop these findings.

### **Recommendations for Future Research**

While the research presented in this thesis lays out the initial fundamentals necessary to understanding the biogeochemical dynamics within the marshes of Palo Verde National Park, it is not yet complete. Many other aspects with respect to the system and associated research need to be addressed. It is now known that there are considerable differences in soil and water chemistry in the different areas of the park. What needs to be undertaken next is research that begins to address ‘why.’ The distinct characteristics of the salinity markers are readily explained by the proximity of the southern area marshes to the mouth of the Tempisque River. However, it may be relevant to know to what extent the river, rather than the degree to which relic deposits, is currently influencing these characteristics. There were also statistically significant differences found in concentrations of the major cations, nitrogen, copper and manganese in soil and water samples. Further research into system specific biogeochemical or hydrologic functions should be pursued in order to understand not only the origin of these differences, but also their effects.

It should be recognized that there was a lack of specificity in the chemical analysis conducted for this research. While it is important to have the baseline knowledge of elemental composition in soil and water, it is also essential that the concentrations of different compound forms be measured. For instance, there were no statistically significant differences found in soil phosphorous, an element that is known to have a large influence on plant growth and plant community structure. But it was total phosphorous that was measured in soil samples, rather

than bioavailable phosphorous, which is what actually influences plant productivity (Grunwald et al. 2006).

Other components integral to system dynamics and function that are not addressed in this thesis are the use of historical data, such as flooding and fire history, and overall hydrology (Sarmiento and Pinillos 2001). This is primarily because this information is inexistent. There are data, however, that could be used to create pseudo-historical data. Water level data for the Palo Verde marsh are available for the past several years; these could be used to generate a benchmark for comparative water levels throughout the park. Unfortunately, for some years, data for the critical period of the onset of the rainy season are missing. Information regarding fire history of the park is also available; these data, however, are on a very coarse scale and give no details other than the dates of the fires. The scale of these data are very important, as was noted this summer when fire spread throughout Catalina sector, but the roads functioned as large firebreaks and protected large areas of this sector from the fire (pers. obs.).

Besides this research, there are two other, ongoing projects involving Palo Verde National Park. The first is doctoral research being conducted by Michael J. Osland, at Duke University, studying the response of plant communities to seasonal flooding, grazing and the mechanical crushing of cattails. This study will be the first scientifically rigorous research conducted on the effects of the current restoration techniques employed in the park. The second is a fire ecology study that was carried out this summer, in conjunction with the research presented here, by Steven J. Hall, of the University of Wisconsin and UCLA-Berkeley, and myself. This project was focused on studying the seedbank and re-emergent plant communities after intense fire and subsequent flooding in the *Typha* marshes of Catalina sector. It is hoped that the results from

this and future research will be used to inform conservation policy and restoration efforts within Palo Verde National Park.

### **Conclusions**

The marshes within Palo Verde National Park have been the subject of ongoing restoration efforts for over two decades. The results have been far from desirable. The broader aim of this research was to provide objective information on the ecological conditions of these marshes, intending to demonstrate to the management and conservation agencies involved with PVNP that the restoration methods currently employed need reevaluating. This study has successfully shown that:

- Differences in soil and water chemistry between the northern and southern areas of the park are statistically significant.
- Specific soil and water characteristics are related to species richness and the presence or absence of specific plant species.

These initial findings, combined with continued research into the ecological history, and hydrologic and biogeochemical characteristics of this system will provide a scientifically based foundation for management of the park and the development of a long-term restoration plan.

APPENDIX A  
METADATA

Table A-1. Plot locations and sample collection and processing dates. P = plant; S = soil;  
W = water.

Transect	Plot	Latitude (10°)	Longitude (85°)	Data Collection	Sample Processing (W)	Sampling Drying (S)
1	1	19.195'	13.481'	P, S, W – 6/12/08; S – 6/20/08	6/14/08	6/19/08; 7/15/08
1	2	19.075'	13.490'	P – 6/20/08		
1	3	18.993'	85.488'	P, S, W – 6/12/08; S – 6/20/08	6/14/08	6/17/08; 7/13/08
1	4	18.929'	13.503'	P, S, W – 6/12/08; W – 6/20/08	6/21/08	6/19/08
1	5	18.957'	13.595'	P – 6/20/08		
1	6	18.935'	13.658'	P, S, W – 6/12/08	6/14/08	6/19/08
2	1	18.999'	14.878'	S, W – 6/11/08; P, S – 6/25/08	6/13/08	6/19/08; 7/9/08
2		18.952'	14.964'	S – 6/11/08		6/19/08
2		18.943'	14.987'	S – 6/11/08		6/17/08
2	2	18.928'	15.046'	P – 6/25/08		
2		18.902'	15.103'	S – 6/11/08		6/17/08
2	3	18.887'	15.149'	S, W – 6/11/08; P, S – 6/25/08	6/13/08	6/17/08; 7/9/08
2	4	18.935'	15.167'	S, W – 6/11/08; P, S – 6/25/08	6/13/08	7/9/08
2	5	18.983'	15.287'	P – 6/25/08		
2	6	18.990'	15.329'	S, W – 6/11/08; P, S – 6/25/08	6/13/08	7/13/08
3	1	19.759'	16.368'	S, W – 6/11/08; P, S – 6/23/08	6/13/08	6/17/08; 7/9/08
3	2	19.749'	16.449'	P – 6/23/08		
3	3	19.754'	16.478'	S, W – 6/11/08; P, S – 6/23/08	6/13/08	6/19/08; 7/9/08
3	4	19.738'	16.570'	S, W – 6/11/08; P, S – 6/23/08	6/13/08	6/17/08; 7/9/08
3	5	19.732'	16.609'	P – 6/23/08		
3	6	19.728'	16.706'	S, W – 6/11/08; P, S – 6/23/08	6/13/08	7/13/08
4	1	19.733'	18.068'	P, S, W – 6/14/08	6/16/08	7/13/08
4	2	19.690'	18.129'	P – 6/14/08		
4	3	19.664'	18.160'	P – 6/14/08		
4	4	19.653'	18.190'	P, S, W – 6/14/08	6/16/08	7/13/08
4	5	19.630'	18.263'	P – 6/14/08		
4	6	19.585'	18.300'	P – 6/13/08		
4	7	19.559'	18.327'	P, S, W – 6/13/08	6/16/08	7/9/08
4	8	19.533'	18.355'	P – 6/13/08		
4	9	19.509'	18.379'	P – 6/13/08		
4	10	19.496'	18.418'	P, S, W – 6/13/08	6/16/08	7/13/08

Table A-1. Continued.

Transect	Plot	Latitude (10°)	Longitude (85°)	Data Collection	Sample Processing (W)	Sample Drying (S)
5	1	20.607'	20.370'	P, S, W – 7/8/08	7/10/08	7/17/08
5	2	20.533'	20.365'	P, S, W – 7/8/08	7/10/08	7/17/08
5	3	20.485'	20.360'	P, S, W – 7/9/08	7/10/08	7/17/08
5	4	20.433'	20.349'	P, S, W – 7/9/08	7/10/08	7/17/08
6	1	20.543'	21.934'	P, W – 6/17/08; S – 6/18/08; W – 7/16/08	6/19/08; 7/20/08	7/17/08
6	2	20.571'	21.884'	P, W – 6/17/08; S – 6/18/08	6/19/08	7/17/08
6	3	20.602'	21.855'	P, S, W – 6/18/08	6/19/08	7/17/08
6	4	20.577'	21.959'	P, S, W – 6/18/08	6/19/08	7/17/08
7		21.836'	24.141'	S, W – 6/10/08	6/13/08	6/19/08
7	1	21.811'	24.161'	P, S, W – 7/16/08	7/20/08	7/18/08
7	2	21.891'	24.192'	P, S, W – 6/26/08; W – 7/16/08	6/27/08; 7/20/08	7/9/08
7	3	21.931'	24.234'	P, S, W – 6/26/08	6/27/08	7/9/08
7	4	22.001'	24.251'	P, S, W – 6/27/08	6/27/08	7/9/08
7		22.034'	24.186'	S, W – 6/10/08	6/13/08	6/19/08
7		22.146'	24.251'	S – 7/16/08		7/18/08
7		22.210'	24.231'	S, W – 6/10/08	6/13/08	6/17/08
8	1	22.630'	22.581'	P, S, W – 6/15/08; W – 6/26/08	6/16/08; 6/27/08	7/17/08
8	2	22.650'	22.629'	P, S, W – 6/15/08; W – 6/26/08	6/16/08; 6/27/08	7/17/08
8	3	22.671'	22.697'	P, S, W – 6/15/08	6/16/08	7/17/08
8	4	22.707'	22.746'	P, S, W – 6/15/08; W – 7/16/08	6/16/08; 7/20/08	7/17/08

### Notes on Soil and Water Sample Processing

Beyond the risk of the typical potential sources of error – sampling, equipment or statistical error – in this study there was the added risk of error due to sample processing. When storing soil and water samples, there is the potential that properties of chemical components will change. Any microbes within the samples themselves will continue to do what they do best – reduce nitrogen, sulfur, phosphorous, etc., perhaps transforming them into gaseous forms that are easily released from the samples when exposed to air or when dried (Carter and Gregorich 2008). While certain procedures can be used to help minimize these changes, some alterations in sample chemistry are inevitable.

Length of, temperature of and moisture levels during storage can affect the amounts of extractable nutrients and cations from soil (Allen and Grimshaw 1962, Shuman 1980, Meyer and Arp 1994, Silver et al. 1994). The degree and type of drying, whether air-dried or oven-dried at 105°C or at an intermediate temperature, will also have an effect on microbial activity or other soil properties (Carter and Gregorich 2008). Once dried, even the method and intensity of grinding can impact the extractable levels of some nutrients (Neary and Barnes 1993, Silver et al. 1994). For this study, many of these issues are not of particular concern because the type of analysis conducted was for total elemental composition. Despite the damaging effects of drying soil at 105°C, it was necessary under the humid conditions to obtain the reference standard for moisture content (Carter and Gregorich 2008).

The accuracy of field equipment is always in question, though they provide for very timely testing of samples. The portable spectrophotometer used to measure nitrate and phosphate levels was calibrated regularly and used with as much precision as possible. It would have been more accurate to use the low-range procedures for nitrate measurements, but the only available reagent was that for the mid-range procedures. These measurements, however, were not used in analysis, since the University of Costa Rica analysis included nitrate concentrations. Phosphate measurements were used in analysis and are in accordance with the phosphorus levels found in soil, though water phosphorous concentrations reported by UCR were much lower than those observed for phosphate. This may be, in part, due to bacteria or plankton present in the water that could change phosphorus concentrations during sample storage (Worsfold et al. 2005).

APPENDIX B  
ANOVA AND T-TABLES

Table B-1. ANOVA table for soil variables.

	df(b)	df(w)	F-ratio	<i>p</i> -value
pH	7	8	1.4	0.3286
Acidity	7	8	2.3	0.1304
Ca	7	8	10.4	0.0019**
Mg	7	8	3.8	0.0400*
K	7	8	2.8	0.0884
ECEC	7	8	5.8	0.0123*
% AS	7	8	2.6	0.1066
EC	8	44	100.4	<0.0001***
P	7	8	1.6	0.2683
Zn	7	8	2.8	0.0847
Cu	7	8	6.9	0.0069**
Fe	7	8	1.0	0.4749
Mn	7	8	8.6	0.0035**
S	7	8	1.2	0.3940
Cl	7	8	7.1	0.0065**
% N	7	8	10.5	0.0018**
% Sand	7	8	5.1	0.0174*
% Silt	7	8	3.2	0.0623
% Clay	7	8	4.8	0.0209*

Table B-2. T-table for soil variables.

	df	T <sub>OBS</sub>	<i>p</i> -value
pH	13	1.4	0.183
Acidity	13	0.8	0.440
Ca	13	-2.3	0.036*
Mg	13	-0.6	0.534
K	13	3.3	0.005**
ECEC	13	-2.5	0.026*
EC <sup>#</sup>	14	4.3	0.001***
P	13	-0.3	0.793
Zn	13	0.3	0.784
Cu	13	-1.1	0.290
Fe	13	0.03	0.972
Mn	13	-2.9	0.013*
S <sup>#</sup>	6	1.9	0.101
Cl <sup>#</sup>	6	3.9	0.008**
% N	13	-1.5	0.153
% Sand	13	2.3	0.036*
% Silt	13	1.2	0.245
% Clay	13	-2.8	0.016*

Table B-3. ANOVA table for water variables. All groups have  $df(b) = 7$ ,  $df(w) = 24$ .

	F-ratio	<i>p</i> -value
pH	2.4	0.0507
Ca	1.6	0.1712
Mg	4.1	0.0044**
K	5.6	0.0006**
EC	2.9	0.0247*
P	2.3	0.0594
PO <sub>4</sub> <sup>3-</sup>	5.2	0.0010**
NH <sub>4</sub> <sup>+</sup>	2.1	0.0779
NO <sub>3</sub> <sup>-</sup>	1.7	0.1691
Fe	1.1	0.4116
Na	3.6	0.0082**

Table B-4. T-table for water variables.

	df	T <sub>OBS</sub>	<i>p</i> -value
pH	26	1.3	0.205
NH <sub>4</sub> <sup>+,#</sup>	11	0	1
NO <sub>3</sub> <sup>-</sup>	26	-1.6	0.119
PO <sub>4</sub> <sup>3-,#</sup>	11	-1.2	0.255
Ca	26	2.3	0.028**
Mg	26	1.9	0.072*
K	26	0.7	0.506
EC <sup>#</sup>	11	2.8	0.018**
P <sup>#</sup>	11	0.4	0.667
Fe <sup>#</sup>	11	-1.0	0.332
Na <sup>#</sup>	11	0.03	0.980

# - Unequal population variances. \*\*\*,  $p < 0.001$ ; \*\*,  $p < 0.01$ ; \*,  $p < 0.05$

APPENDIX C  
PEARSON CORRELATION COEFFICIENTS

Table C-1. Correlation coefficient table for soil and water elemental variables.

	Water.pH	Water.NH4	Water.NO3	Water.PO4	Water.Cu	Water.Mg	Water.K	Water.P	Water.Fe
Water.NH4	-0.120								
Water.NO3	-0.050	-0.028							
Water.PO4	0.274	-0.016	0.208						
Water.Cu	0.296	-0.187	-0.330 *	0.083					
Water.Mg	0.823 ***	-0.082	0.134	0.191	0.354 **				
Water.K	0.525 ***	-0.065	0.178	0.478 **	0.404 **	0.696 ***			
Water.P	0.365 *	0.302	0.126	0.609 ***	0.086	0.308	0.650 ***		
Water.Fe	-0.027	0.915 ***	0.066	0.122	-0.132	0.019	0.074	0.426 **	
Water.Mn	-0.024	0.921 ***	0.053	0.112	-0.118	0.021	0.054	0.397 **	0.998 ***
Water.Na	0.755 ***	-0.173	0.131	-0.035	0.128	0.849 ***	0.326 *	0.014	-0.062
Water.EC	0.787 ***	-0.181	0.087	0.083	0.262	0.902 ***	0.416 **	0.066	-0.103
Soil.pH	0.185	-0.148	-0.232	-0.354	-0.006	0.075	-0.193	-0.138	-0.125
Soil.Acidity	-0.072	-0.180	-0.197	0.144	0.086	0.266	-0.016	0.171	-0.105
Soil.Ca	-0.460 *	0.087	-0.070	-0.227	-0.208	-0.644 **	-0.637 **	-0.252	-0.132
Soil.Mg	0.266	0.295	0.047	-0.037	-0.417	0.231	0.132	0.273	0.284
Soil.K	0.145	-0.306	-0.108	-0.052	0.096	0.271	0.204	-0.046	-0.082
Soil.ECEC	-0.326	0.196	-0.052	-0.233	-0.369	-0.515 *	-0.549 **	-0.128	-0.011
Soil.P	0.438	0.352	0.057	0.390	0.113	0.568 **	0.726 ***	0.517 *	0.426
Soil.Zn	0.139	-0.146	0.180	0.209	0.410	0.332	0.327	-0.042	-0.121
Soil.Cu	-0.216	0.238	-0.054	-0.193	-0.322	-0.155	-0.080	0.092	0.033
Soil.Fe	0.232	0.023	0.178	0.342	0.313	0.476 **	0.631 **	0.283	0.038
Soil.Mn	-0.017	0.159	0.469 *	0.341	-0.577 **	-0.025	0.144	0.308	0.143
Soil.S	-0.032	-0.158	-0.241	-0.081	0.142	0.152	0.194	-0.024	-0.043
Soil.Cl	0.271	-0.304	-0.256	-0.102	0.489 *	0.470 **	0.308	-0.092	-0.176
Soil.N	-0.099	-0.164	0.419	0.133	-0.026	-0.182	-0.257	-0.224	-0.201
Soil.EC	0.413	-0.286	-0.112	-0.123	0.257	0.626 **	0.309	-0.062	-0.152
Sand	-0.001	-0.258	-0.338	-0.162	0.489 *	0.054	-0.007	-0.194	-0.246
Silt	0.049	0.000	-0.098	0.463 *	0.263	0.124	0.553 **	0.370	0.160
Clay	-0.018	0.238	0.351	-0.031	-0.554 **	-0.098	-0.210	0.034	0.165

Table C-1. Continued.

	Water.Mn	Water.Na	Water.EC	Soil.pH	Soil.Acidity	Soil.Ca	Soil.Mg	Soil.K	Soil.ECEC
Water.Na	-0.073								
Water.EC	-0.094	0.985 ***							
Soil.pH	-0.106	0.252	0.226						
Soil.Acidity	-0.120	-0.327	-0.326	-0.127					
Soil.Ca	-0.120	-0.440	-0.465 *	0.078	-0.072				
Soil.Mg	0.274	0.195	0.159	0.075	0.044	-0.068			
Soil.K	-0.093	0.289	0.279	-0.038	0.379	-0.676 ***	0.134		
Soil.ECEC	-0.004	-0.335	-0.374	0.103	-0.031	0.909 ***	0.354	-0.560 **	
Soil.P	0.415	0.197	0.252	-0.235	-0.066	-0.697 ***	0.441	0.184	-0.478 *
Soil.Zn	-0.115	0.213	0.275	-0.160	-0.531	-0.298	-0.632 **	-0.148	-0.556 **
Soil.Cu	0.037	-0.168	-0.168	0.239	-0.239	0.491	0.527 *	-0.430	0.674 ***
Soil.Fe	0.032	0.168	0.240	-0.523 *	-0.028	-0.595 **	-0.206	0.163	-0.650 **
Soil.Mn	0.118	-0.095	-0.155	-0.530 *	0.266	-0.067	0.432	-0.063	0.115
Soil.S	-0.054	0.099	0.113	-0.160	-0.129	-0.317	0.059	0.488 *	-0.266
Soil.Cl	-0.170	0.417	0.463 *	0.147	-0.312	-0.490 *	-0.341	0.385	-0.602 **
Soil.N	-0.198	-0.026	-0.053	-0.103	-0.262	0.311	-0.617 **	-0.516 *	0.024
Soil.EC	-0.147	0.679 ***	0.681 ***	0.328	-0.355	-0.483 **	0.011	0.407	-0.449
Sand	-0.223	0.073	0.123	0.483 *	-0.050	-0.090	-0.716 ***	0.008	-0.383
Silt	0.139	-0.200	-0.144	-0.456	0.418	-0.675 ***	-0.139	0.486 *	-0.686 ***
Clay	0.152	0.011	-0.057	-0.267	-0.117	0.347	0.715 ***	-0.197	0.622 **

Table C-1. Continued.

	Soil.P	Soil.Zn	Soil.Cu	Soil.Fe	Soil.Mn	Soil.S	Soil.Cl	Soil.N	Soil.EC	Sand	Silt
Soil.Zn	0.175										
Soil.Cu	0.031	-0.304									
Soil.Fe	0.088 **	0.381 **	-0.215								
Soil.Mn	0.281	-0.347	0.040	0.177							
Soil.S	0.069	0.045	-0.173	-0.025	-0.108						
Soil.Cl	0.058	0.512 *	-0.384	0.193	-0.496 *	0.727 ***					
Soil.N	-0.487	0.531 *	-0.325	-0.017	0.022	-0.384	-0.085				
Soil.EC	0.107	0.303	-0.102	0.096	-0.331	0.693 **	0.849 ***	-0.164			
Sand	-0.290	0.416	-0.295	0.103	-0.699 ***	-0.090	0.473 *	0.173	0.238		
Silt	0.560 **	0.179	-0.500 *	0.517 *	0.308	0.359	0.243	-0.239	0.017	-0.007	
Clay	0.049	-0.454	0.430	-0.297	0.564 **	-0.057	-0.532 **	-0.067	-0.245	-0.920 ***	-0.384

\*\*\*, p < 0.01; \*\*, p < 0.05; \*, p < 0.1.

APPENDIX D  
PLANT SPECIES LIST

Plants species found while conducted surveys in PVNP, listed by life-form and function.

\*, multiple listing.

See (Crow 2002) for more information on individual species.

Trees, shrubs or suffrutescent

- *Bactris guineensis*
- *Coccoloba venosa*
- *Crateva palmeri*
- *Croton argenteus*
- *Ipomoea carnea*
- *Ludwigia* spp. (*L. erecta*, *L. octovalvis*)
- *Mimosa pigra*
- *Pithecellobium lanceolatum*
- *Tabebuia rosea*

Plants free-floating on surface

- *Azolla microphylla*
- *Eichhornia crassipes*
- *Lemna aequinoctialis*
- *Limnobium laevigatum*
- *Pistia stratiotes*
- *Salvinia* spp. (*S. auriculata*, *S. minima*)
- *Spirodela polyrhiza*
- *Wolffiella welwitschii*

Rooted plants, with leaves and/or stems floating on surface

- *Neptunia natans*
- *Nymphaea* spp. (*N. amazonum*, *N. prolifera*, *N. pulchella*)
- *Paspalum repens*

Emergent plants

- *Ammannia coccinia*
- *Canna glauca*
- *Cyperonina palustris*
- *Echinodorus paniculatus*
- *Heliotropium indicum*
- *Kosteletzkya depressa*
- *Ludwigia* spp. (*L. erecta*, *L. octovalvis*)\*
- *Malachra* spp. (*M. alceifolia*, *M. radiata*)
- *Neptunia natans*\*
- *Polygonum segetum*
- *Thalia geniculata*

- *Typha domingensis*
- *Vigna longifolia*
- Family Cyperaceae
  - *Cyperus articulatus*
  - *Cyperus* spp. (*C. digitatus*, *C. gigantean*)
  - *Eleocharis* spp. (*E. elegans*, *E. mutata*, *Eleocharis* sp. (round))
  - *Fimbristylis spadicea*
- Family Poaceae
  - *Echinochloa colona*
  - *Hymenachne amplexicaulis*
  - *Leersia hexandra*
  - *Oryza latifolia*
  - *Paspalidium germinatum*
  - *Paspalum repens*\*

Facultative wetland plants and terrestrial plants with high flooding tolerance

- *Aniseia martinicensis*
- *Cayaponia attenuata*
- *Chamaesyce thymifolia*
- *Croton argenteus*\*
- *Echinochloa colona*\*
- *Ipomoea piurensis*
- *Sarcostemma clausum*

## LIST OF REFERENCES

- Allen, S. E. and H. M. Grimshaw. 1962. Effect of low-temperature storage on the extractable nutrient ions in soils. *Journal of the Science of Food and Agriculture* **13**:525-529.
- Aylward, B. A. and E. B. Barbier. 1992. Valuing environmental functions in developing countries. *Biodiversity and Conservation* **1**:34-50.
- Barbier, E. B. 1994. Valuing environmental functions: Tropical wetlands. *Land Economics* **70**:155-173.
- Becker, H. F. 1943. Land utilization in Guanacaste Province of Costa Rica. *Geographical Review* **33**:74-85.
- 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.
- Benito, M. I., R. de la Horra, J. F. Barrenechea, J. López-Gómez, M. Rodas, J. Alonso-Azcárate, A. Arche, and J. Luque. 2005. Late Permian continental sediments in the SE Iberian Ranges, eastern Spain: Petrological and mineralogical characteristics and palaeoenvironmental significance. *Palaeogeography Palaeoclimatology Palaeoecology* **229**:24-39.
- Brinson, M. M., A. E. Lugo, and S. Brown. 1981. Primary production, decomposition and consumer activity in freshwater wetlands. *Annual Review of Ecology and Systematics* **12**:123-161.
- Caraco, N. F., J. J. Cole, and G. E. Likens. 1989. Evidence for sulphate-controlled phosphorus release from sediments of aquatic systems. *Nature* **341**:316-318.
- Carter, M. R. and E. G. Gregorich. 2008. *Soil sampling and methods of analysis*. Second edition. CRC Press, Boca Raton, FL.
- Choudhuri, G. N. 1968. Effect of soil salinity on germination and survival of some steppe plants in Washington. *Ecology* **49**:465-471.
- Comerma, J. 1999. Vertisols. Pages 783-817 *Soil taxonomy: A basic system of soil classification for making and interpreting soil surveys*. U.S. Department of Agriculture, Natural Resources Conservation Service, Washington, D.C.
- Company, H. 2000. DR/2010 Spectrophotometer Procedures Manual. Hach Company, Loveland, CO.
- Crow, G. E. 2002. *Aquatic plants of Palo Verde National Park and the Tempisque River Valley*. Instituto Nacional de Biodiversidad, Santo Domingo de Heredia, Costa Rica.
- Edelman, M. 1992. *The logic of the latifundio: The large estates of northwestern Costa Rica since the late nineteenth century*. Stanford University Press, Stanford, CA.

- Ellison, A. M. 2004. Wetlands of Central America. *Wetlands Ecology and Management* **12**:3-55.
- Evans, S. 1999. *The green republic: A conservation history of Costa Rica*. First edition. University of Texas Press, Austin, TX.
- Fickbohm, S. S. and W. Zhu. 2006. Exotic purple loosestrife invasion of native cattail freshwater wetlands: Effects on organic matter distribution and soil nutrient cycling. *Applied Soil Ecology* **32**:123-131.
- Finlayson, C. M. and A. G. van der Valk. 1995. Wetland classification and inventory: A summary. *Vegetatio* **118**:185-192.
- Frankie, G. W., A. Mata, and S. B. Vinson. 2004. *Biodiversity conservation in Costa Rica: Learning the lessons in a seasonal dry forest*. University of California Press, Berkeley.
- Gallaher, C. M. and C. A. Stiles. 2003. Using soils to understand ecosystem change in wetlands in Palo Verde National Park, Costa Rica. *in* Geologic Society of America Annual Meeting, Seattle, WA.
- Gallardo, M. T., B. B. Martin, and D. F. Martin. 1998. An annotated bibliography of allelopathic properties of cattails, *Typha* spp. *Florida Scientist* **61**:52-58.
- Gibbs, J. P. 2000. Wetland loss and biodiversity conservation. *Conservation Biology* **14**:314-317.
- Gillespie, T. W. 1999. Life history characteristics and rarity of woody plants in tropical dry forest fragments of Central America. *Journal of Tropical Ecology* **15**:637-649.
- Gillespie, T. W. and H. Walter. 2001. Distribution of bird species richness at a regional scale in tropical dry forest of Central America. *Journal of Biogeography* **28**:651-662.
- Grace, J. B. 1989. Effects of water depth on *Typha latifolia* and *Typha domingensis*. *American Journal of Botany* **76**:762-768.
- Grace, J. B. and R. G. Wetzel. 1982. Niche differentiation between two rhizomatous plant species: *Typha latifolia* and *Typha angustifolia*. *Canadian Journal of Botany* **60**:46-57.
- Grunwald, S., R. Corstanje, B. E. Weinrich, and K. R. Reddy. 2006. Spatial patterns of labile forms of phosphorus in a subtropical wetland. *Journal of Environmental Quality* **35**:378-389.
- Hartshorn, G. S. 1983. Plants: Introduction. Pages 118-183 *in* D. H. Janzen, editor. *Costa Rican natural history*. University of Chicago Press, Chicago, IL.
- Hein, J. R. 2004. The Permian Earth. Pages 3-18 *in* J. R. Hein, editor. *Life cycle of the phosphoria formation: from deposition to the post-mining environment*. Elsevier Science, Amsterdam.

- Helwig, J. F. 1969. Problems of social and economic development in the Province of Guanacaste, Costa Rica. University of Kansas.
- Jin, C. H. 2008. Biodiversity dynamics of freshwater wetland ecosystems affected by secondary salinisation and seasonal hydrology variation: a model-based study. *Hydrobiologia* **598**:257-270.
- Johnson, J. B. and D. A. Steingraeber. 2003. The vegetation and ecological gradients of calcareous mires in the South Park valley, Colorado. *Canadian Journal of Botany* **81**:201-219.
- Kametaka, M., M. Takebe, H. Nagai, S. Zhu, and Y. Takayanagi. 2005. Sedimentary environments of the Middle Permian phosphorite-chert complex from the northeastern Yangtze platform, China; the Gufeng Formation: a continental shelf radiolarian chert. *Sedimentary Geology* **174**:197-222.
- Kress, N., S. L. Coto, C. L. Brenes, S. Brenner, and G. Arroyo. 2002. Horizontal transport and seasonal distribution of nutrients, dissolved oxygen and chlorophyll-a in the Gulf of Nicoya, Costa Rica: a tropical estuary. *Continental Shelf Research* **22**:51-66.
- McCormick, P. V., P. S. Rawlik, K. Lurding, E. P. Smith, and F. H. Sklar. 1996. Periphyton-Water Quality Relationships along a Nutrient Gradient in the Northern Florida Everglades. *Journal of the North American Benthological Society* **15**:433-449.
- McCoy, M. B. and J. M. Rodríguez. 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 Word and New*. Elsevier Science.
- McDowell, W. H. and C. E. Asbury. 1994. Export of carbon, nitrogen, and major ions from three tropical montane watersheds. *Limnology and Oceanography* **39**:111-125.
- McNaughton, S. J. 1968. Autotoxic feedback in relation to germination and seedling growth in *Typha latifolia*. *Ecology* **49**:367-369.
- Mengel, K., E. A. Kirkby, H. Kosegarten, and T. Appel. 2001. The soil as a plant nutrient medium. Pages 15-110 *Principles of Plant Nutrition*. Kluwer Academic Publishers, Dordrecht, The Netherlands.
- Meyer, W. L. and P. A. Arp. 1994. Exchangeable cations and cation exchange capacity of forest soil samples: Effects of drying, storage, and horizon. *Canadian Journal of Soil Science* **74**:421-429.
- Miklovic, S. and S. M. Galatowitsch. 2005. Effect of NaCl and *Typha angustifolia* L. on marsh community establishment: A greenhouse study. *Wetlands* **25**:420-429.
- Mitsch, W. J. and J. G. Gosselink. 2007. *Wetlands*. Fourth edition. John Wiley & Sons, Inc., Hoboken, NJ.

- Mossmark, F., H. Hultberg, and L. O. Ericsson. 2008. Recovery from groundwater extraction in a small catchment area with crystalline bedrock and thin soil cover in Sweden. *Science of the Total Environment* **404**:253-261.
- Nathan, Y. and H. Nielsen. 1980. Sulfur isotopes in phosphorites. Pages 73-78 in Y. K. Bendor, editor. *Marine phosphorites - Geochemistry, occurrence, genesis*. Society of Economic Paleontologists and Mineralogists, Jerusalem, Israel.
- Neary, A. J. and S. R. Barnes. 1993. The effect of sample grinding on extractable iron and aluminum in soils. *Canadian Journal of Soil Science* **73**:73-80.
- Newman, S., J. B. Grace, and J. W. Koebel. 1996. Effects of nutrients and hydroperiod on *Typha*, *Cladium*, and *Eleocharis*: Implications for Everglades restoration. *Ecological Applications* **6**:774-783.
- 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.
- Orris, G. J. and C. B. Chernoff. 2004. Review of world sedimentary phosphate despoits and occurrences. Pages 559-573 in J. R. Hein, editor. *Life cycle of the Phosphoria Formation: From deposition to the post-mining environment*. Elsevier Science, Amsterdam.
- Pausas, J. G. and M. P. Austin. 2001. Patterns of plant species richness in relation to different environments: An appraisal. *Journal of Vegetation Science* **12**:153-166.
- Quesada, M. and K. E. Stoner. 2004. Threats to the conservation of tropical dry forest in Costa Rica. Pages 266-280 in G. W. Frankie, A. Mata, and S. B. Vinson, editors. *Biodiversity conservation in Costa Rica: Learning the lessons in a seasonal dry forest*. University of California Press, Berkeley, CA.
- Quirós, G., M. Solano M., and J. Gamboa E. 2001. Palo Verde Ramsar Information Sheet.
- Sarmiento, G. and M. Pinillos. 2001. Patterns and Processes in a Seasonally Flooded Tropical Plain: The Apure Llanos, Venezuela. *Journal of Biogeography* **28**:985-996.
- Sarmiento, G., M. Pinillos, M. P. d. Silva, and D. Acevedo. 2004. Effects of Soil Water Regime and Grazing on Vegetation Diversity and Production in a Hyperseasonal Savanna in the Apure Llanos, Venezuela. *Journal of Tropical Ecology* **20**:209-220.
- Sarmiento, G., M. P. d. Silva, M. E. Naranjo, and M. Pinillos. 2006. Nitrogen and Phosphorus as Limiting Factors for Growth and Primary Production in a Flooded Savanna in the Venezuelan Llanos. *Journal of Tropical Ecology* **22**:203-212.
- Shardendu and R. S. Ambasht. 1991. Relationship of nutrients in water with biomass and nutrient accumulation of submerged macrophytes of a tropical wetland. *New Phytologist* **117**:493-500.

- Shay, J. M. and C. T. Shay. 1986. Prairie marshes in western Canada, with specific reference to the ecology of five emergent macrophytes. *Canadian Journal of Botany* **64**:443-454.
- Shuman, L. M. 1980. Effects of soil temperature, moisture, and air-drying on extractable manganese, iron, copper, and zinc. *Soil Science* **130**:336-343.
- Silver, W. L., F. N. Scatena, A. J. Johnson, T. G. Siccama, and M. J. Sanchez. 1994. Nutrient availability in a montane wet tropical forest: Spatial patterns and methodological considerations. *Plant and Soil* **164**:129-145.
- Sojda, R. S. and K. L. Solberg. 1993. Management and control of cattails. *Fish and Wildlife Leaflets* **13**:1-7.
- Strehlow, K., J. Davis, L. Sim, J. Chambers, S. Halse, D. Hamilton, P. Horwitz, A. McComb, and R. Froend. 2005. Temporal changes between ecological regimes in a range of primary and secondary salinised wetlands. *Hydrobiologia* **552**:17-31.
- Tabash Blanco, F. A. 2007. A biogeochemical model for the Gulf of Nicoya, Costa Rica. *Revista De Biologia Tropical* **55**:33-42.
- Venterink, H. O., M. J. Wassen, A. W. M. Verkroost, and P. C. d. Ruiter. 2003. Species Richness-Productivity Patterns Differ between N-, P-, and K-Limited Wetlands. *Ecology* **84**:2191-2199.
- Verhoeven, J. T. A. and M. B. Schmitz. 1991. Control of plant growth by nitrogen and phosphorus in mesotrophic fens. *Biogeochemistry* **12**:135-148.
- Wetterer, J. K., D. S. Gruner, and J. E. Lopez. 1998. Foraging and Nesting Ecology of *Acromyrmex octospinosus* (Hymenoptera: Formicidae) in a Costa Rican Tropical Dry Forest. *The Florida Entomologist* **81**:61-67.
- Worsfold, P. J., L. J. Gimbert, U. Mankasingh, O. N. Omaka, G. Hanrahan, P. Gardolinski, P. M. Haygarth, B. L. Turner, M. J. Keith-Roach, and I. D. McKelvie. 2005. Sampling, sample treatment and quality assurance issues for the determination of phosphorus species in natural waters and soils. *Talanta* **66**:273-293.
- Yeo, R. R. 1964. Life history of common cattail. *Weeds* **12**:284-288.
- Zedler, J. B. and S. Kercher. 2005. Wetland resources: Status, trends, ecosystem services, and restorability. *Annual Review of Environmental Resources* **30**:39-74.
- Zedler, J. B., E. Paling, and A. McComb. 1990. Differential responses to salinity help explain the replacement of native *Juncus kraussii* by *Typha orientalis* in Western Australian salt marshes. *Austral Ecology* **15**:57-72.

## BIOGRAPHICAL SKETCH

Estelle Scheuermann Robichaux was born at St. Anne General Hospital in Matthews, Louisiana. With Bayou Lafourche located just across Highway 1, it was a very fitting beginning for Estelle. A long line of fishermen, hunters and farmers helped pave her family's way to Baton Rouge, where she grew up. As a child, she became a fledgling environmentalist – keen to start an environmental rights campaign, trying to get people to recycle and attempting to go vegetarian (that one didn't really work out). Over the years, these proclivities took a back seat to the “normal life” of being a teenager; but she always enjoyed the feel of the wind and sea spray on her face, as her father raced his boat across Lake Barre, surrounded by mysterious marshes and inky waters.

Estelle attended Wellesley College, majoring in economics and French, intending to become involved in international economic policy. She abandoned these plans after attending a semester abroad with the School for Field Studies, on South Caicos, TCI, BWI. The months spent studying tropical marine ecology, resource management and environmental economics reawakened her enthusiasm for conservation, this time in the form of academic ambition.

Desiring to become a well-rounded environmental policymaker, Estelle decided she would have to attend graduate school and focus on the natural sciences. After working for the Florida Fish & Wildlife Conservation Commission's Research Institute in St. Petersburg, she was accepted into the Master's program of the School of Natural Resources and Environment at the University of Florida. Within a few months, for she had decided that she wanted to focus her research, and her career, on wetlands. Having completed her Masters degree, with a concentration in wetland sciences, she will continue her studies at UF as a doctoral student in the IGERT Adaptive Management: Wise Use of Water, Wetlands & Watersheds program.