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Water Table and Nutrient Dynamics in Neotropical Savannas and Wetland Ecosystems

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UNIVERSITY OF MIAMI

WATER TABLE AND NUTRIENT DYNAMICS IN NEOTROPICAL SAVANNAS AND WETLAND ECOSYSTEMS

By

Randol M. Villalobos-Vega

A DISSERTATION

Submitted to the Faculty
of the University of Miami
in partial fulfillment of the requirements for
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WATER TABLE AND NUTRIENT DYNAMICS IN NEOTROPICAL SAVANNAS AND WETLAND ECOSYSTEMS

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Water Table and Nutrient Dynamics in Neotropical Savannas and Wetland Ecosystems (May 2010)

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The Tropical savannas of central Brazil (cerrado) and the Everglades wetland (Florida) ecosystems are ideal systems to study landscape spatial mosaics and their interactions. Both ecosystems show a variety of plant physiognomies distributed within small spatial scales and elevation gradients. Such variety of plant physiognomies provide an opportunity to investigate the roles of climate, topography, nutrient availability and water table dynamics as determinants of plant physiognomic distributions, and their role in shaping regional systems. South Florida Wetlands and the tropical savannas of central Brazil are examples of hydrologically-controlled ecosystems. In hydrologically-controlled ecosystems water sources, the availability of nutrients, and the patterns of water movement play important roles in determining vegetation structure and function.

The main objective of this study was to understand ecosystem level processes that shape different physiognomies in two hydrologically-controlled ecosystems. I conducted field work at the IBGE ecological reserve, a field experimental station located in Brasilia, Brazil. I also worked at the Everglades National Park in an area located near the south entrance of the Park in Homestead, Florida. I carried out three interconnected studies investigating water and nutrient dynamics: (1) In a Brazilian savanna I manipulated

levels of litter input and measured changes to soil properties, organic matter decomposition and tree growth. I found that changes in litter input affect soil physicochemical properties and soil biochemical processes. I also found that litter dynamics influence tree growth through their effects on soil physicochemical properties. (2) I also studied the effect of water table depth and its temporal variation on spatial patterns of vegetation distribution in the cerrado landscape. I monitored diurnal and seasonal changes in water table depth along two tree-density and topographic gradients. In addition, I measured woody species composition, growth rates of four tree species, litter production, soil nutrients, and nutrient resorption efficiency along those two gradients. I found that water table depth has an important role in determining the spatial distribution of cerrado physiognomies; it also affects tree growth, species composition and nutrient resorption efficiency. (3) In the Everglades I studied patterns of underground water uptake by two vegetation types. I monitored seasonal and diurnal changes in water table depth in a Hammock forest, in a stand dominated by the invasive woody species *Schinus terebinthifolius*, as well as the water level in an adjacent lake. I estimated stand level transpiration using two different approaches: with sap flow measurements and diurnal oscillations in water table levels. Then, I calculated the total quantity of groundwater withdrawn by evapotranspiration for the wet and dry seasons in the Hammocks and in the exotic invaded site and then compared the results. I found that water uptake by Everglades trees is well coupled to diurnal changes in water table depth and that the amount of water withdrawn from the groundwater was larger during the wet season than during the dry season. Finally, I detected hydrological feedbacks between different vegetation types and nearby bodies of water. Results of this study contributes to the current knowledge of ecosystem level processes in tropical and subtropical ecosystems where water circulation and water availability play a dominant role in shaping vegetation structure and function.

Dedication

I would like to dedicate this dissertation to my family, my wife and my good friends.

My parents taught me that there is no need of money to pursue your dreams and that nothing substitute hard work and honesty. You have been always with me in every single step of this process and in every decision I make.

My wife has been unconditional. Thank you so much dear Catarina for making my life even better. Thank you so much for helping me in every single step of this process, this dissertation is also yours.

My dear friends, you know who you are. I am so fortunate for having friends that blindly believe on my capabilities and always supported me in every possible way. You are my extended family.

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The field work carried out to produce this dissertation was labor intensive and its completion was possible only with the help of many people. I would like to thank

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Chapter 1

General introduction

Often, for convenience or simplicity, it is assumed that variability in ecosystem processes is negligible over space and time. This assumption of invariability has helped to foster the study of ecosystem process by diminishing the complexity due to variability (Pickett and Cadenasso 1995). However, incorporating variability is essential for gaining insight into ecological processes at a landscape scale. This is the case for ecologists who are interested in understanding interactions and processes among landscape spatial mosaics, in particular, fluxes of nutrients and water among different plant physiognomies that compose the landscape.

The presence of such different plant physiognomies implies an intrinsic complexity at the landscape level. Understanding the origin, structure and function of the different physiognomies, and the interactions among them, has important implications for management and conservation purposes. It is important to understand the pieces in order to appreciate the whole; therefore, scaling up from local processes to ecosystem processes is important for understanding the overall dynamics.

The Tropical savannas of central Brazil (cerrado) and the Everglades wetland (Florida) ecosystems are ideal systems to study landscape spatial mosaics and their interactions, because in both ecosystems there are a variety of plant physiognomies distributed within small spatial scales and elevation gradients. Such variety of plant physiognomies provide an opportunity to investigate the roles of climate, topography, nutrient availability and water table dynamics as determinants of plant physiognomic distributions, and their role in shaping regional systems.

Plant species composition and productivity largely reflect the prevailing climate, seasonal and annual variability in rainfall and temperature play a central role in dictating the dynamics of plant populations over time (see Prentice 1992). Substantial variability in climate occurs across and even within ecosystems, but broad scale climate variables alone cannot account for the spatial and functional vegetation patterns at local scale (Archer and Smeins 1991). Soil and topography influence plant distribution, growth, and abundance over the landscape, through regulation of the availability of moisture, which in turn affects nutrient availability (Nachabe et al., 2005). Water table dynamics (seasonal and diurnal fluctuations) also exert a strong influence on plant distributions and function, mainly through its effects on soil waterlogging (see Lenssen 2003; Visser and Voesenek 2004; Jackson and Colmer 2005; Mendoza et al., 2005; Santiago 2000).

In hydrologically-controlled ecosystems (such tropical savannas and wetlands) water sources and the availability of nutrients (Saha et al., 2009), as well as the patterns of water movement (either lateral or vertical) play important roles in determining vegetation structure and function. Hydrologically-controlled ecosystems are of particular interest because of the relatively high relevance that water supply and water cycle play in shaping the landscape. The hydrology and nutrient dynamics in combination with local climate and elevation gradients may result in different plant physiognomies that occupy sites also associated to those interactions. For example, vegetation influences water and nutrient cycles, and is a key factor for many atmospheric feedbacks (Moreira et al., 1997;

Sternberg et al., 2002). Climate and soil also influence the structure and spatial patterns of vegetation (Ridolfi et al., 2000; Porporato et al., 2001). In general, soil water moisture is influenced by rainfall inputs, runoff, deep water movement, and the physical and chemical characteristics of the soils (Porporato 2002). However, in hydrologically-controlled systems, water circulation patterns, seasonality of precipitation, and the hydrology of the region are more important in influencing ecosystem structure and function than the soil properties themselves.

The south Florida Wetlands (e.g., Everglades National Park) and the tropical savannas of central Brazil (cerrado) are good examples of hydrologically-controlled ecosystems. Strong seasonal fluctuations in rainfall and extended (well-defined) dry seasons characterize both ecosystems. The Everglades and the Brazilian cerrado receive similar annual rainfall (about 1500 mm per year) and both ecosystems experience similar duration of the dry season (approximately 4 months) (Oliveira 2005; Saha et al., 2009; respectively). Despite their similarities, these ecosystems have important hydrological differences. In the Everglades, the direction of the water flow is primarily horizontal due to a shallow water table and proximity to the ocean. In contrast, the direction of the water flow in the cerrado is primarily vertical, due to relatively well-drained soils, shallow topography, and relatively deep water tables.

Water movement patterns in both systems influence not only water availability for plants, but also the vegetation structure. For example, in the Everglades, changes in plant physiognomies correspond to small differences in elevation with respect to the water level (Ewe et al., 1999). Differences in elevation among marshes, saw grass, cypress domes, mangroves, pinelands and Hammocks, are usually measured in centimeters.

Hammocks (also called hardwood Hammocks) is the physiognomy located at the highest elevations in south Florida wetlands. They are isolated stands of broadleaf trees that occur in narrow bands, typically of few hundred meters wide (Snyder et al., 1990) or forming distinct "tree islands" usually surrounded by contrasting vegetation (Tomlinson 2001).

In the cerrado, shallow topographic gradients are correlated with a gradient of plant physiognomies from open savannas, at higher elevations, to closed savannas at lower elevations (Bucci et al., 2008). The water table depth and nutrient availability appears to change consistently along this topographic gradient. The water table apparently is deep in the upper portions of the topographic gradient and shallow in the lowest parts, and soils are more fertile in the upper parts than in the lower parts of the gradient (Furley 1998, De Araujo Neto et al., 1986; Goodland and Pollard 1973). However, differences in soil nutrient content among cerrado physiognomies are not as large and predictable as those found in the Everglades.

Description of study sites

This dissertation has three components; two were conducted in a Neotropical savanna ecosystem in central Brazil. The third component was conducted in a Wetland ecosystem at the Everglades National Park, Florida, USA. Although, these ecosystems receive a similar amount of annual rainfall and experience long dry seasons, they differ highly in their pattern of water movement. Both, similarities and differences allowed me to study several plant physiognomies at different scales. In the Brazilian savannas, I studied patterns of physiognomic distribution in relation to abiotic factors such as nutrient distribution, concentration of toxic elements in the soil, fire frequency and water table depth. I evaluated the effects of litter accumulation on soil physicochemical properties and tree growth in a cerrado *sensu stricto*, a type of physiognomy with abundant evergreen and brevi-deciduous trees and an herbaceous understory (Giambelluca et al., 2009). In the Everglades National Park, where the pattern of physiognomic distribution is better understood, I studied water table dynamics in relation to patterns of water consumption by Hardwood Hammock Forests. Hardwood Hammocks are the physiognomy that occurs at the highest elevation in the Everglades National Park, composed of evergreen broadleaf trees. I also studied patterns of lateral water flow by comparing two vegetation types; one native (Hammock Forest) and one non-native (stand dominated by the invasive tree *Schinus terebinthifolius* Raddi) with an open water body (Hidden Lake).

Tropical savannas of central Brazil (cerrado)

Savannas of central Brazil (cerrado) exhibit consistent differences in tree cover along shallow elevation gradients (Goodland 1971; Eiten 1972; Lopes and Cox 1977). Vegetation varies from open savannas with relatively few trees, most of which are small, in the lower portions of the topographic gradient (*campo sujo*) to closed savannas or woodlands with a relatively high density of taller trees in the upper portions of the gradient (cerradão) (Giambelluca et al., 2009). Herbaceous plant abundance follows the opposite trend with continuous coverage in open savannas to very low coverage in closed savannas and woodlands (Hoffmann et al., 2005). According to Haridasan (1992) cerrado *sensu stricto* is the most extensive physiognomy in the cerrado region of central Brazil and in the past occupied more than 65% of the cerrado region which extends over 180 million hectares. This author argues that cerrado *sensu stricto* is the result of the dystrophic soils and its interaction with climate and intermittent fires.

I conducted field work in at the IBGE ecological reserve, a field experimental station located 35 km south of the center of Brasilia, Brazil (latitude 15◦56'S , longitude 47◦53' W, altitude 1 100 m). The IBGE includes extensive areas of all major physiognomies of cerrado vegetation. Annual precipitation in the reserve ranges from 880 to 2,150 mm with a mean of approximately 1,500 mm (Bucci et al., 2005). There is a distinct dry season that extends from May through September with the months of June, July, and August being nearly rainless (Bucci et al., 2005). Mean annual temperature is about 22°C, with small seasonal changes. Maximum diurnal air temperature differences, can be as large as 20◦C during a typical day in the dry season. The soils are deep oxisols with a high percentage of clay and are well-drained (Bucci et al., 2005).

Everglades wetland ecosystem

A variety of plant physiognomies occur in this ecosystem along shallow topographic gradients of about 3 m: mangroves, cypress domes, long and short hydroperiod marshes, sawgrass savannas, bayheads, pinelands and tropical hardwood hammocks in ascending order of elevation (Saha et al., 2009). Most the other physiognomies are named after the dominant species, for example sawgrass (*Cladium jamaicensis* Crantz), cypress domes (*Taxodium sp*), mangroves (several species of mangroves) and pinelands dominated by slash pine (*Pinus elliottii* Engelm). There are also large differences in soil nutrients among plant physiognomies within the Everglades ecosystems. For example, nutrients are more abundant in Hammock soils than in pineland soils (Saha et al., 2009).

I conducted field work at the Everglades National Park in a Hammock stand located near the main entrance of the Park in Homestead, the south entrance of the Park (lat 25°23’ 09”, long 80° 37’ 20”). The Everglades is characterized by hot, wet summers and warm, dry winters, with lowest average temperature of 12°C. About 80% of the rainfall occurs from May to October and the mean annual temperature is about 27 °C. Annual rainfall averages 1470 mm but can vary widely when hurricanes cross the region (Chen and Gerber 1990; Snyder et al., 1990).

Objectives

The main objective of my dissertation research was to understand ecosystem level processes that shape different physiognomies in two hydrologically-controlled ecosystems: The tropical savannas of central Brazil (cerrado) and the Everglades Wetland ecosystem of south Florida. I carried out three interconnected studies investigating water and nutrient cycles to address the following questions:

Chapter 2

2.1 Do changes of litter input (removal or addition) affect soil physicochemical properties (e.g. soil temperature, soil moisture content, soil nutrient content) and soil biochemical processes (e.g. litter decomposition) in the tropical savannas of Brazil?

2.2 Do litter dynamics (i.e., litter fall, changes in litter input and litter decomposition) influence tree growth through their effects on soil physicochemical properties?

Chapter 3

3.1 What is the role of water table depth dynamics in determining the spatial distribution of cerrado physiognomies?

3.2 What is the effect of water table depth dynamics on tree growth along physiognomic and topographic gradients in the tropical savannas of Brazil?

Chapter 4

4.1 Is water uptake by Everglades Hammock trees coupled to diurnal changes in water table depth? If so, what is the difference in water uptake between wet and dry seasons?

4.2 Is there a difference in water table utilization between Everglades Hammock forest and a nearby forest invaded by exotic species?

To answer the first two questions I manipulated litter levels in a Brazilian savanna (cerrado) and measured changes to soil properties, organic matter decomposition and tree growth. Over a three year period, I manipulated litter levels in a cerrado *sensu stricto* in the central Brazilian plateau, and then measured properties of the soil, including soil respiration, soil temperature, soil gravimetric water content and soil nutrient and carbon content. I also measured changes in leaf area index of woody plants, as well as litter production and stem growth of the six most common tree species.

Even though the role of water table in determining plant physiognomies and physiognomic distribution in the cerrado has been debated for many years, a systematic study of water table in relation to topographic-tree density gradients has not been conducted. To address this issue, in Chapter 3, I studied the effect of water table depth and its temporal variation on spatial patterns of vegetation distribution and related ecosystem processes. I monitored diurnal and seasonal changes in water table depth along two topographic gradients in a cerrado landscape of the Brazilian plateau for over a year. I also measured woody species composition, growth rates of four tree species, litter production, soil nutrients, and nutrient resorption efficiency along these topographic gradients.

To study patterns of underground water uptake by Hammock trees and the effect of changing management practices on underground water, in Chapter 4, I monitored seasonal and diurnal changes in water table depth for 2 years in a Hammock forest, in a stand dominated by invasive woody species, and in an adjacent lake. I measured sap flow during consecutive days in several individuals of the most common species in both vegetation types. I used daily average sap flow per tree, sapwood cross-sectional area and stem diameter of all trees in each site to scale up tree water utilization to stand level transpiration. I compared diurnal oscillations in water table levels during the wet season to the dry season to evaluate seasonal patterns evapotranspiration and tree transpiration.

With this information, I calculated the total quantity of groundwater withdrawn by evapotranspiration during a day for the wet and dry season in the Hammocks and in the exotic *Schinus* invaded sites.

Results of this study will increase knowledge of ecosystem level processes in tropical and subtropical ecosystems where water circulation and availability play a dominant role in shaping vegetation structure and function.

Chapter 2

Leaf litter manipulations alter soil physicochemical properties and tree growth in a Neotropical savanna

Summary

In tropical savannas it remains unclear if leaf litter influences tree growth and physiology by altering soil properties. To address this issue we performed a long-term experiment in a Brazilian savanna cerrado in which litter levels were manipulated, and the resulting changes to soil properties, organic matter decomposition and tree growth were quantified. Over a three year period we manipulated litter levels in a cerrado *sensu stricto* in the central Brazilian plateau, creating plots with no litter- 'litter removal', natural levels of litter- 'natural litter' and double the natural levels of litter- 'double litter', with five plots per litter treatment. We measured properties of the soil, including soil respiration, soil temperature, soil gravimetric water content as well as soil nutrient and carbon content. We also measured changes in leaf area index of woody plants, litter production and stem growth of the six most common tree species. Compared to litter removal plots, plots with double litter had lower soil temperature and increased soil water content in the uppermost layers of soil, which may have resulted from changes in microclimate due to thicker litter cover. Plots with double litter also showed an increase in root activity and litter decomposition, consistent with the higher soil respiration rates found. Removal plots showed the lowest rates of soil respiration, but differences between treatments decreased

during the dry season. Rates of litter decomposition were faster in the double litter plots (compared to removal plots), as was nutrient content in the upper 5 cm of soil. Nitrogen and Phosphorus levels in removal and natural litter plots were similar throughout the extent of our study; in double litter plots they exhibited 22 % and 44% increments, respectively. Carbon content in the soil also increased substantially in the litter addition plots during the experimental study and was lower for the removal plots at the end of the experiment. Of the most common six tree species, only one, *Sclerolobium paniculatum*, had a significant increase in stem growth due to litter addition; growth of the other five species were not affected. Nutrient cycling in plots with natural litter levels was in a closed loop; most nutrients released by litter decomposition and mineralization were absorbed and reutilized immediately by plants. Thereby nutrient leakage outside the system was minimized and soil fertility in the nutrient deficient cerrado soils remained fairly constant through time. Litter addition resulted in greater nutrient availability and soil fertility in the upper soil layers of the double litter plots but remained relatively similar between removal and natural litter plots. *Sclerolobium paniculatum*, a fast growing tree with shallow roots was the only species able to successfully exploit the nutrients released by the decomposing litter in the double litter plots.

Background

Even though it is widely recognized that litter fall and leaf decomposition play key roles in nutrient cycling and soil conservation in terrestrial ecosystems, only a few studies have focused on Neotropical Savannas (Valenti et al., 2008), consequently more research is required for understanding the role of litter in this specific habitat. There is information available on the seasonality of litter fall, litter decomposition and its relationship with climate, but it is not yet fully understood how litter influences plant growth by altering soil properties in Neotropical savannas.

Litter has two major roles in forest and savanna ecosystems: (i) it is an important component of nutrient and carbon cycling and (ii) it forms a protective layer on the mineral soil surface, helping to regulate soil microclimate (Sayer 2006). Long-term litter manipulation (e.g. litter addition or removal) can affect ecosystem carbon turnover, soil nutrients and several biophysical and biochemical soil properties such as diurnal temperature fluctuations, water availability and bulk density of upper soil layers (Sayer et al., 2006; Peng et al., 2003). Litter manipulation may also affect both root activity and microbial communities, including those of decomposing organisms which may affect soil respiration rates (Sayer 2006; Ryan and Law 2005). If soil chemical composition is modified as a consequence of litter removal or addition, tree growth and carbon allocation patterns may change as well. Because litter interacts with many variables simultaneously, predicting the consequences of changes to litter inputs at the ecosystem level is challenging. Experiments removing and adding litter are needed to provide an empirical basis for assessing its role on ecosystems, particularly in savannas. It may be easier to predict responses to changes in litter inputs on rich soils. Neotropical savannas, however, are among the most nutrient poor tropical ecosystems worldwide; therefore predicting the consequences of litter manipulation is uncertain.

Nitrogen and/or phosphorus limitations to tree growth are widespread in the tropics, and severe in the Neotropical savannas of central Brazil (cerrado) (Haridasan

2000, 2001). Cerrado soils are old oxisols and are nutrient deficient with low pH and cation exchange capacity (Furley and Ratter 1988; Furley 1999; Haridasan 2000). A long-term fertilization experiment in cerrado soils showed that (1) total leaf surface area and basal area per tree increased with added nitrogen , and (2) despite being adapted to chronic nutrient limitations, woody cerrado species can exploit increases in nutrient availability by allocating resources to maximize carbon gain and enhance growth (Bucci et al., 2006). Increases in above-ground productivity of trees receiving nitrogen fertilization support the notion that cerrado trees are N limited, however, a highly efficient and complete resorption of P in leaves during senescence, supports the notion that cerrado trees are also P limited (Kozovits et al., 2007). Fertilization experiments provide information on the nature of nutrient limitation for ecosystem function, but may produce artifacts on nutrient cycling due to the large amount of fertilizer added once or a few times. Furthermore, the chemical composition of the nutrients in fertilizers may differ from those released by litter decomposition, and there is a potential for interactions with other nutrients, as well as non-desirable effects on soil decomposing organisms. Litter manipulations, and particularly increases of litter inputs, may enhance nutrient availability (e.g. N and P) without the potential artificial effects of fertilizers.

Savannas of central Brazil are highly seasonal environments characterized by a five months dry season, followed by seven months wet season. Evaporative demand is higher during the dry season, when relative humidity is low. During the dry season cerrado plants may become water stressed due to the combination of high evaporative demand, low precipitation, and consequently low water potentials in the upper soil layers (Bucci et al., 2008). Despite the stressful conditions that persist through the dry season, most tree species maintain active leaves and produce new leaves during this period, even before the beginning of the wet season (Franco et al., 2005; Lenza and Klink 2006). Litter accumulates mainly during the dry season because most trees shed their leaves at this time and decomposition rates are low (Kozovits et al., 2007). The majority of litter decomposition occurs at the beginning of the wet season, when soil water content is high and litter is still abundant (Kozovits et al., 2007). In savannas, the water balance between rainfall and evaporation losses is so tight that runoff and infiltration are negligible and nutrients should be recycled efficiently to reduce losses (Sarmiento 1984).

Our objective was to assess the long-term effects of litter manipulations on tree growth, organic matter decomposition and soil physical and chemical properties in a savanna. We tested the hypothesis that adding leaf litter to the Brazilian cerrado will: (1) decrease the temperature and increase the water content of soils, (2) increase the rate of organic matter decomposition and soil respiration, (3) increase the concentration of nutrients, and (4) increase stem growth and leaf production of trees. Opposite effects are expected for the removal treatment.

Materials and Methods

Study system and experimental design

The study was carried out at the Instituto Brasileiro de Geografia e Estatistica (IBGE) Ecological Reserve, a field experimental station located 33 km south of Brasilia, Brazil (lat. 15^{o} 56’, long 47^{o} 53’ W, alt. 1100 m). The IBGE includes areas of all major physiognomies of cerrado vegetation from open to closed savannas, and evergreen gallery forest restricted to flood plains of small rivers and streams. Annual precipitation in the reserve ranges from 880 to 2150 mm with a mean of 1500 mm (www.recor.org.br). There is a pronounced dry season from May through September with the months of June, July, and August being nearly rainless. Mean annual temperature averages 22^{o}C. Maximum and diurnal air temperature differences can be as large as 20^{o}C during a typical dry season day. The study site was located in an area protected from fire for at least 30 years. Two 320 x 50 m areas (parallel to a narrow abandoned dirt road) were divided into 40 m segments. In each segment the corner of a 20 x 20 m plot was randomly located with two conditions: (1) plots had to be at least ten meters away from the dirt road and (2) plot edges had to be at least five meters from the border of each segment. Fifteen permanent plots were established.

An exhaustive inventory of all woody stems with diameter >5 cm (30 cm above the soil surface) was conducted in all plots. We selected the six most abundant species for intensive monitoring: *Qualea grandiflora* Mart. (Vochysiaceae)*, Caryocar brasiliense* Camb. (Caryocaraceae)*, Ouratea hexasperma* (A.St.-Hil.) Bailll. (Ochnaceae)*, Sclerolobium paniculatum*Vogel. (Fabaceae)*, Scheflera macrocarpa* (Cham. & Schltdl) Frodin. (Araliaceae) *and Miconia pohliana* Cogn. (Melastomataceae) (Fig. 2.1). The 15 permanent plots were grouped in three blocks of similar tree basal area and species composition. Three treatments were randomly assigned within each block: removal of litter (from here on ‘litter removal’), addition of litter (‘double litter’) and no litter manipulation (‘natural litter’). To prevent litter accumulation in litter removal plots, litter collection roughly followed the natural cycle of litter fall, hence litter removal was more frequent during the dry season when leaves are shed. The litter collected was placed in plastic bags, weighed and transported to the litter addition plots in the same block, where it was spread on the forest floor. Litter removal/addition treatments were carried out roughly once a month during the dry season from July 2004 to August 2007.

Soil water content and temperature

Soil water content was expressed on a gravimetric basis. Five soil samples were collected at random locations within each of the 15 experimental plots during the dry season (September, 17 of 2007). Samples were collected at 3, 30 and 60 cm depth and immediately placed in tin canisters. Samples were weighed and then oven dried at 105 °C until they approached constant weight to obtain gravimetric water content.

Upper soil surface temperature was measured in three 1 x 1m subplots in one randomly selected plot of each of the three treatments. Since all the experimental plots were located in a homogenous savanna stand with similar leaf area index and soil type, we expect our measurements to reflect the overall treatment effects. Soil temperature at 1, 5, 15 and 30 cm was continuously monitored with copper-constantan thermocouples. Temperatures were measured every minute, and 30 minute averages were recorded using a data logger (CR10 X, Campbell Scientific, Logan, UT). These measurements were obtained during a three days period from October 18 to October 21 of 2005.

Rate of litter decomposition

A decomposition experiment was performed to assess the rates of litter decomposition in the three litter treatments. The leaf mass per unit area (LMA) of the six most abundant species was measured to choose three species with similar leaf phenology but representing a large range of LMA: *S. macrocarpa*, *S. paniculatum* and *O. hexasperma*. Senescent leaves of these focal species were collected by gently shaking the trees at the end of the dry season of 2006 from August to September. The litter samples were sun-dried and stored at room temperature until the beginning of the experiment in November of 2006.

Each litter decomposition bag (20 x 20 cm, 1mm mesh size) was filled with 10 g of air-dry leaves from one of the three focal species; sealed with rustless staples and individually marked. The bags were placed in the field at the onset of the 2007 rainy season so that there was sufficient soil moisture and an active community of decomposers. Water content of air-dry samples ratio was determined by oven drying subsamples of the senesced leaves.

Litter bags were placed in 2 x 2 m subplots that were randomly located within each experimental plot. Each subplot had a total of 18 litter bags divided in 6 sets with 3 litter bags per set (one per species). Each set of bags was connected by a cord to make easier the collection of individual sets. The bags were placed in contact with the ground, underneath the most recently fallen leaves. Five collections were carried out throughout 14 months. The first collection was done 20 days after the beginning of the experiment and the remaining four were done after 2, 3, 5 and 4 months. Once the litter bags were collected, the litter was oven-dried at 55°C until it approached constant weight. Roots or other plant parts were removed prior to the collection of the litter bags.

Soil respiration

Soil respiration (CO_2 flux) was measured in each plot using a Li-6400-09 soil respiration chamber attached to the Li-6400 portable photosynthesis system (LI-COR Inc., Lincoln, Nebraska, USA). The method includes scrubbing CO_2 and then measuring the rate of CO_2 increase inside the chamber. The ambient air CO_2 concentration (the target) was determined by laying the soil chamber on its side on the ground and observing the displayed CO_2 concentration. Measurements were taken during cycles that begin below ambient CO_2 concentration (determined by the user, also called ΔCO_2) and finished when it reaches the same ΔCO_2 above the target. Knowing the relationship between the CO_2 ambient concentration and CO_2 fluxes for a particular soil location, the CO_2 flux is determined by extrapolation. Target values were set before every measurement cycle. The ΔCO_2 was usually set at 5μmol mol^{-1} or at 10μmol mol^{-1} depending on the CO_2 fluxes recorded prior to the measurements.

To measure soil respiration, thin-walled PVC collars were inserted in four randomly placed locations within each plot. The collars were installed at least one day before measurements to avoid recording artificial amounts of CO_2 fluxes caused by the disruption of the soil due to collar insertion. The collars were 10 cm in diameter and approximately 7 cm in height. The insertion depth of the collars was 3 cm, to minimize cutting of fine roots. This insertion depth was chosen because it has been shown that soil respiration rates decrease with increasing depth of collar insertion (Wang et al., 2005). Soil temperatures were measured simultaneously with soil respiration using a Li-Cor soil temperature probe Type E.

The structure data collection was hierarchical (nested design). In the first three collections (August 2006, November 2006 and August 2007) we had two consecutive days of measurements with three measurements per subplot and four subplots per treatment plot. For the last collection (October 2007), we had only one day of measurements.

Soil Nutrients

To evaluate soil nutrient availability and soil pH, four soil samples at varying depths (5, 10, 25 and 50 cm) were collected from each plot at a random location from 2004 to 2008. Samples were collected using an auger, and placed in plastic bags and transported to the laboratory for analysis. Soil pH was measured in 1:2.5 soil-water suspension and in 1M KCl, exchangeable Ca, Mg and Al were determined in soil extracts of 1 M KCl and exchangeable K and available P, Fe, Mn, Zn and Cu in Mehlich's extract of a diacid mixture of 0.05 M HCl and 0.0125 M H_2SO_4. The cations in soil extracts were determined by atomic absorption spectrophotometry and P by colorimetry (Allen 1989). Total N in soil was determined by Kjeldahl digestion and distillation. Soil organic carbon was determined by the method of Walkley and Black (Allen 1989).

Stem growth

Fifteen trees of each of the six focal species were selected to measure stem growth. When possible, three individuals per species per plot were included. Dendrometer bands were installed on all trees. Dendrometers were made manually and consisted of a stainless steel tape encircling a tree stem, with one end passing through a collar (which is attached to the other end) and connected back to itself with a stainless steel spring, as described by Cattelino et al. (1986). Three months after dendrometer installation (allowing for stem-dendrometer adjustment) a permanent mark was made on the metal band next to the collar. As stem diameter increases, the mark moves away from the collar and the spring is stretched, keeping the dendrometer tight. A flexible ruler was used to measure stem diameter changes with an accuracy of 0.5 mm. Stem growth was recorded monthly form July 2005 to February 2006 and every two months from April 2006 to June 2008. Stem growth was expressed as percentages in relation to initial stem circumference.

Litter production and Leaf area index

Litter production was measured using 75 leaf litter traps (5 litter traps per plot) from July 2006 to July 2008. One litter trap was located near each corner and one in the center of the plot. The leaf- litter traps had a square opening of 50 x 50 cm and were placed at 40 cm above the ground. All trap contents were collected monthly, placed in a plastic bag, and transferred to IBGE's laboratory. In the laboratory, materials were oven-dried at 65°C for 96 hours until constant weight. After drying, the litter samples were separated into: 1) leaves, 2) plant reproductive structures, and 3) other materials, which included stems, twigs and pieces of bark, and then weighed. All the small particles less than 1mm were discarded.

Leaf area index (LAI) was measured in July 2004, September and October 2007 using an AccuPAR line-integrating ceptometer (Accupar*,* Decagon Devices*,* Pullman*,* WA, USA*)*. The AccuPAR calculates LAI from measurements of intercepted photosynthetically active radiation. All measurements were performed only during clear sky days within one hour of solar noon. We subsampled LAI at 13 locations within each plot on each sample date.

Statistical analyses

We tested the differences among treatments in terms of soil water content, litter decomposition rates, soil nutrient, aluminum and carbon contents and soil pH using one-way analysis of variance (ANOVA). To test the effect of litter addition and removal on soil respiration and tree growth we used mixed-effect models in R, version 2.6.2 (R Development Core Team 2008) with the package "nlme" version 3.1-86 (Pinheiro et al., 2000). When we had two consecutive days of measurements for the same plot, two models with temporal pseudo-replication were tested; both models had treatment as a fixed factor and day as an intercept. Model 1 had subplot nested within treatment plot and model 2 had plot-subplot concatenated. We used the Aikake's information Criterion (AIC) as a measure of model fit to select the model with greater explanatory power of the two models.

To analyze tree growth, three models with different fixed-effects structures were tested. Model 1 had treatment as a main effect, model 2 had treatment as a main effect and initial circumference as a covariate as well as initial circumference by treatment interaction, and model 3 had treatment as main effect and initial circumference as covariate. All the models had plot as a random factor. Aikake's information Criterion was used as a measure of model fit.

Results

A total of 748 individuals representing 53 species, 42 genera and 25 plant families were inventoried in our study area. Our six focal tree species represented 46% of all stems greater than 5 cm in diameter (Figure 2.1). Forty seven species accounted for the remaining 54% of all woody stems. This area is a typical cerrado *sensu stricto* physiognomy**;** a savanna with relatively high tree density and few herbaceous plants (Goodland 1971 and Goodland and Pollard 1973). According to Alvaro de Oliveria (IBGE 1995) soils in this part of the reserve are classified as red latosols.

Soil water content and temperature

Soil water content in the upper 5 cm soil layer of the litter removal plots was significantly lower ($p < 0.05$) compared to natural litter and double litter plots (Fig. 2.2). Soil water content did not differ significantly among treatments at 30 or 60 cm depth. Average and maximum daily soil temperatures were lower in double litter compared with litter removal plots, particularly in upper soil layers during the dry season (Fig. 2.3). At 30 cm deep, soil temperatures in the litter removal plots were approximately 2 ^{o}C higher compared to double litter plots.

Rate of litter decomposition and soil nutrients

The percent of leaf mass remaining in decomposition bags decreased exponentially with time (Fig. 2.4). Leaves of *S. macrocarpa* decomposed faster than leaves of

S. paniculatum and *O. hexasperma*. Decomposition rates tended to be lower in the removal treatment, compared to the other treatments particularly for *S. paniculatum* leaves ($p<0.05$).

Total carbon, pH and nutrient availability in the first 5 cm of soil were not significantly different among plots before litter manipulation began on July 2004 (Fig. 2.5). After four years of litter manipulation Ca and Mn levels were significantly higher ($p< 0.05$) in double litter compared to natural litter and litter removal plots. Magnesium, carbon and nitrogen tended to be higher ($p=0.06$, 0.07 and 0.08 respectively) in the addition treatment compared to the natural litter and litter removal treatments. On the other hand, pH was marginally lower ($p= 0.06$), in the double litter treatment compared to the natural litter and removal treatments by July 2008 (Fig. 2.5). Aluminum availability did not differ among treatments.

Soil respiration

Soil respiration was higher in the double litter plots compared to litter removal and natural litter plots (Fig. 2.6). That difference was significantly higher ($p<0.001$) in August 2006, November 2006 and October 2007, but only marginally significant ($p=0.08$) in August 2007. Based on model selection, plots and subplots were treated separately as random factors only for the data collected in November 2006. For the remaining three data sets the analysis was carried out at the subplot level. The respiration rates were higher during the wet season than during the dry season (Fig. 2.6), possibly reflecting in part the higher activity of the decomposing organisms and shallow roots.

Stem growth

Cumulative stem growth for the six most abundant species, four evergreen (*M. pohliana*, *S. macrocarpa*, *O. hexasperma* and *S. paniculatum*) and two deciduous (*Q. grandifloria* and *C. brasiliense*), in the removal, natural litter and litter addition plots are shown in Figure 2.7. Accumulative stem growth on May 2008 was significantly higher for *S. paniculatum* in the double litter plots (p=0.01) than trees in natural litter and the removal plots, even after accounting for the interaction and main effects of initial circumference. There were no significant differences in accumulative stem growth for the other five species among treatments.

Litter production and Leaf area index

The amount of litterfall in the three litter treatments exhibited seasonal changes from July 2006 until July 2008. Leaf fall was highest at the end of the dry seasons (July to September, Fig. 2.8 A). Litter fall was equal among litter treatments. The branches, twigs, and reproductive structures components of litter fall did not show consistent seasonal changes (Fig. 2.8 B, C). Leaf area index was not affected by the litter treatments.

Discussion

Our study area represents a cerrado *sensu stricto* that occurs on deep and well drained red latosols (Oliveria (IBGE 1995)). According to Haridasan (1992) cerrado *sensu stricto* is the most extensive physiognomy in the cerrado region of central Brazil. It used to occupy more than 65% of the cerrado region which extends over 180 million hectares. According to this author cerrado *sensu stricto* seems to be the result of the dystrophic soils and its interaction with climate and intermittent fires.

The manipulation of litter influenced a soil properties and processes but had a smaller effect on tree growth in five of the six species investigated. Litter addition significantly decreased soil temperature and increased soil gravimetric water content in the uppermost soil layers. These changes in soil temperature and water content likely enhanced the activity of decomposing organisms and superficial root systems, which was reflected by higher soil respiration rates in the double litter plots, particularly during the wet season. Litter addition also increased litter decomposition rates of the three focal species. It is possible that mineralization of nutrients in the double litter plots as a result of faster litter decomposition, increased the uptake of nutrients by the vegetation.

Soil water content and temperature

The litter layer acts as an interface between the soil surface and the atmosphere, providing some protection to the soil surface by intercepting rain (Benkobi et al., 1993), solar radiation and buffering the soil surface against large temperature fluctuations (Ponge et al., 1993). Litter's buffering effect is particularly important in savannas because canopy interception of rain and shading by trees is relatively low compared to tropical rain forests. Depending on the type of savanna, sometimes less than 40% of the ground is covered by trees (e.g. *campo sujo*). At the end of the dry season most herbaceous vegetation dies-back, thereby exposing a high percentage of the soil surface. At this time the buffering effect of litter becomes even more important for maintaining ecosystem functions.

In this study, litter removal resulted in a substantial increase in soil temperature and a decrease of soil water content. Inconsistent results have been shown by several studies regarding the effects of litter manipulation on soil water content and soil temperature in other ecosystems (Sayer 2006). For example, it was observed that litter removal increases water content immediately after precipitation and decreases it during dry periods (e.g. Lunt 1951, Ginter et al., 1979). Consistent with Gill (1969) and Poser (1990) results, we found little effect on soil water content in the double litter treatment. Litter layer buffers fluctuation in soil water content by reducing evaporation from the soil surface and intercepting incoming solar radiation. Diurnal temperature fluctuations are also buffered by the presence of litter cover (Sayer 2006). In our study, the presence of a thick layer of litter buffered maximum soil temperatures in the first centimeter of the soil profile by approximatelly10^{o}C in the double litter plots, compared to the removal plots.

Rate of litter decomposition

Litter decomposition had a tendency to be faster in the double litter plots than in the removal plots, but the differences were statistically significant only for *S. paniculatum*. In our double litter plots, it was likely that more decomposing organisms and a relatively buffered microenvironment helped to enhance decomposition rates. Some studies have found that litter removal decreases active microbial biomass (e.g. Anderson and Domsch 1978; Peng et al., 2003; Nilson et al 1999), but others showed no decrease in microbial biomass with litter removal (Nadelhoffer et al., 2004). Inconsistent results regarding the microbial biomass may be due to the fact that decomposition rates depend not only on decomposing microorganisms but also on litter quality and environmental conditions during the decomposition process. Leaf decomposition rates differed across species and contrary to expectation *S. macrocarpa* had the fastest rate of decomposition, even though it had the highest LMA. Decomposition is not only related to toughness of the leaf but also to nutrient content and secondary compounds such as lignin and tannins (e.g. Perez-Harguindeguy et al., 2000). Unless additional information on leaf nutrients and secondary compounds in senescent leaves are obtained, it will be difficult to explain the inverse relationship between LMA and decomposition rates as observed in this study.

Soil respiration

Since litter removal decreases the amount of fresh decaying organic matter in the soil surface it affects microbial communities which may result in a decrease in soil respiration (e.g. Bowden et al., 1993; Li et al., 2004). Most studies have found that litter removal decreases soil respiration from 7-60% depending on the vegetation type and the duration of litter removal (Sayer 2006). In our study, the effect of litter removal on soil respiration was strongly seasonal. During the dry season, when soil water content in the upper soil layer was low (soil water potential can drop to -3.0 MPa during the dry season; Bucci et al., 2006), the effects of litter removal were relatively small. In contrast during the wet season the effects of litter removal were substantially larger with soil respiration rates decreasing by approximately 20% compared to the double litter treatment.

Soil Nutrients

The increase of both leaf decomposition rates and the amount of litter in the double litter plots resulted in a substantial increment of soil nutrient concentrations compared to the litter removal plots. It is interesting to compare the results of this experiment in which the amount of litter was manipulated over time with the results of concurrent studies investigating spatial variability of nutrient concentration along topographic and tree density gradients in the same area. Savannas of central Brazil exhibit variations in tree density usually associated with slight topographic gradients of several hundred meters in length and less than 100 in elevation. Along these gradients, vegetation varies from open savannas with relatively few small trees in the lower portions of the topographic gradients to closed savannas or woodlands with a relatively high density of taller trees in the upper portions of the gradient (Hoffmann et al., 2005). We did not find variation in soil nutrient availability along these topographic/tree density gradients at the IBGE's Ecological Reserve (R. Villalobos-Vega, unpublished information). Other studies have shown inconsistent changes in nutrient concentrations along these topographic/physiognomic gradients (e.g. Askew et al., 1970; Gibbs et al., 1983; Ribeiro 1983; Haridasan 1992; Bucci et al., 2006). The reasons for not finding consistent differences in soil nutrient availability along these gradients may reside in the nature of the carbon and nutrient cycling of the oligotrophic cerrado soils. Leaves of deciduous and many evergreen tree species senesce and are shed during the dry season, when soil water content in the upper soil layers is low and consequently decomposition rates are also low. Litter decomposes faster, and mineralized nutrients are rapidly absorbed by roots at the onset of the rainy season (Garolfo 2001). Even though litterfall increases along the tree density gradient, differences in litter production across savanna physiognomies are not as large as the differences caused by the experimental manipulation of litter in this study. We have previously found that litter accumulated at the end of the dry season ranged from 103 g m^{-2} in open savannas to 282 g m^{-2} in closed savannas (R. Villalobos-Vega, unpublished information). In contrast the average difference in the amount of litter between litter addition and removal plots in this study was approximately 440 g m^{-2}, which was substantially larger than differences observed along the topographic/physiognomic gradients. Therefore, it appears that nutrient cycling in the cerrado ecosystem is in a closed loop with most of the nutrients released by decomposition and mineralization being absorbed and utilized by plants such that nutrient leakage is minimized (Sarmiento 1984). At a soil depth of 50 cm nutrient availability is extremely low, and only traces of nutrients are found in the water table between 1-12 m below soil surface depending on the topographic position and season (R. Villalobos-Vega, unpublished information). In natural litter plots the amount of soil nutrients in the upper soil layers remained fairly constant during the four years of our study. In double litter plots the litter accumulation increased the amount of nutrients released resulting in a higher nutrient availability in the upper soil layers. Such an increase in soil fertility suggests that additional nutrients were not utilized immediately by the plants. A new equilibrium point in the nutrient circulation pathway may be reached once new growth take place as a consequence of higher soil fertility.

Stem growth

Among the six tree species studied, stem growth was significantly higher for only one species, *S. paniculatum,* growing in the double litter plots compared to removal and natural litter, even after accounting for interaction with initial circumference. It is a fast growing pioneer species (Pires and Marcati 2005; Felfili et al., 2004) with shallow root systems (Jackson et al., 1999; Scholz et al., 2002) which have associations with mycorrhizal fungi and *Rhizobium* (nitrogen fixing bacteria) (Quintanilha de Albuquerque and Dias 1999; Franco et al., 1996). Such associations would enable this species to quickly absorb nutrients released by the decomposing litter in the litter addition plots, competing successfully with herbaceous plants in their ability to exploit limiting resources. Despite being adapted to chronic nutrient limitations, *S. paniculatum* appears to be able to exploit increases in nutrient availability by allocating resources to stem growth. It is possible that the other species do not have sufficiently shallow roots to absorb upper soil nutrients or that they allocate the newly acquired nutrients to leaf or root growth instead of stem growth or reproduction. Longer treatment periods probably would have enhanced stem growth in some of the other species.

Conclusions

The removal as well as the addition of litter significantly affected several ecosystem-level processes and properties such as soil temperature, soil water content and availability of nutrients and ecosystem processes such as litter decomposition rates and soil respiration. Nutrient uptake by roots, tree growth, litter production and soil nutrient availability are in steady state equilibrium in natural communities (natural litter plots). Such equilibrium is important for nutrient conservation and to minimize nutrient leakage in a highly nutrient limited ecosystem. Altering the amount of litter on the savanna floor, one component of this interlocked system, resulted in a substantial changes of soil temperature and respiration, stem growth of *S. paniculatum* and the decomposition rates for one of three studied species. After three years of continuous litter manipulation the addition of litter significantly increased organic soil carbon as well as soil nutrient availability, including nitrogen and phosphorus (two of the most limiting nutrients in the cerrado). Opposite trends were found for the removal treatment.

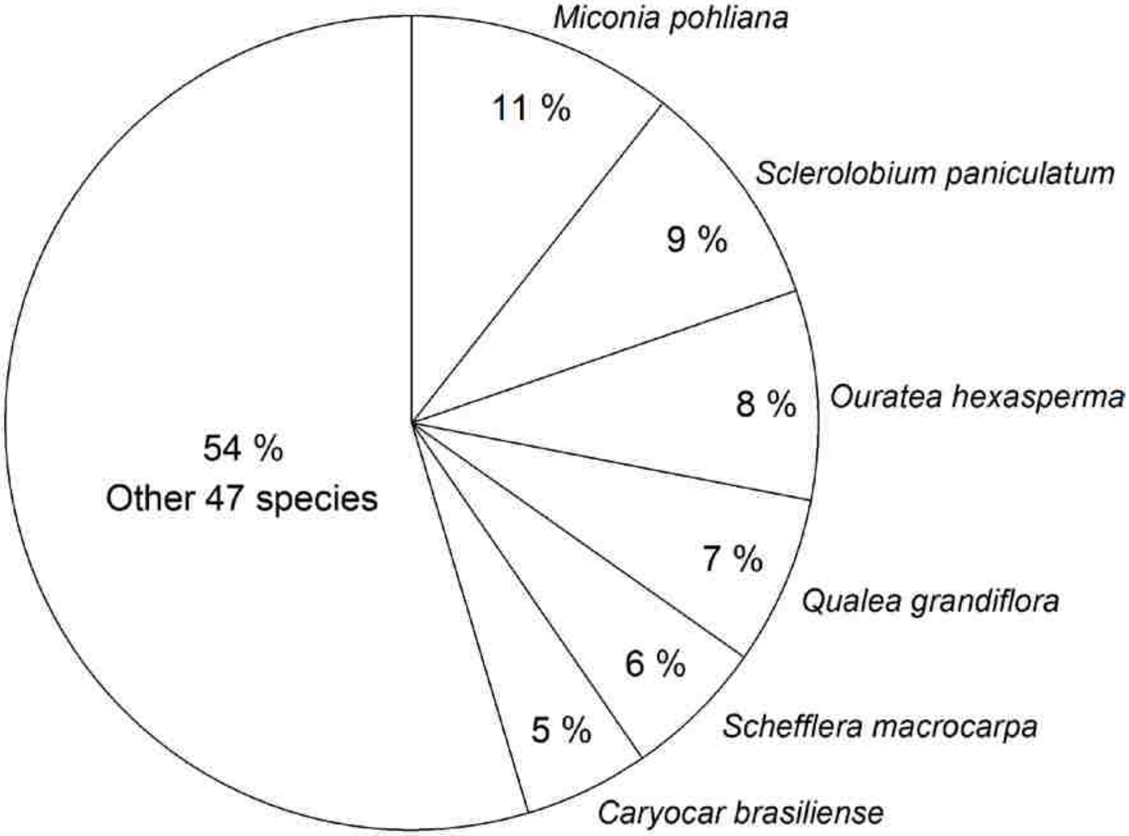

Figure 2.1. Relative abundance of tree species in the experimental plots. The six most common species (46 % of all individuals) were chosen for nutrient analysis and stem growth measurements. Only trees larger than 5 cm diameter at 50 cm above the soil surface were recorded.

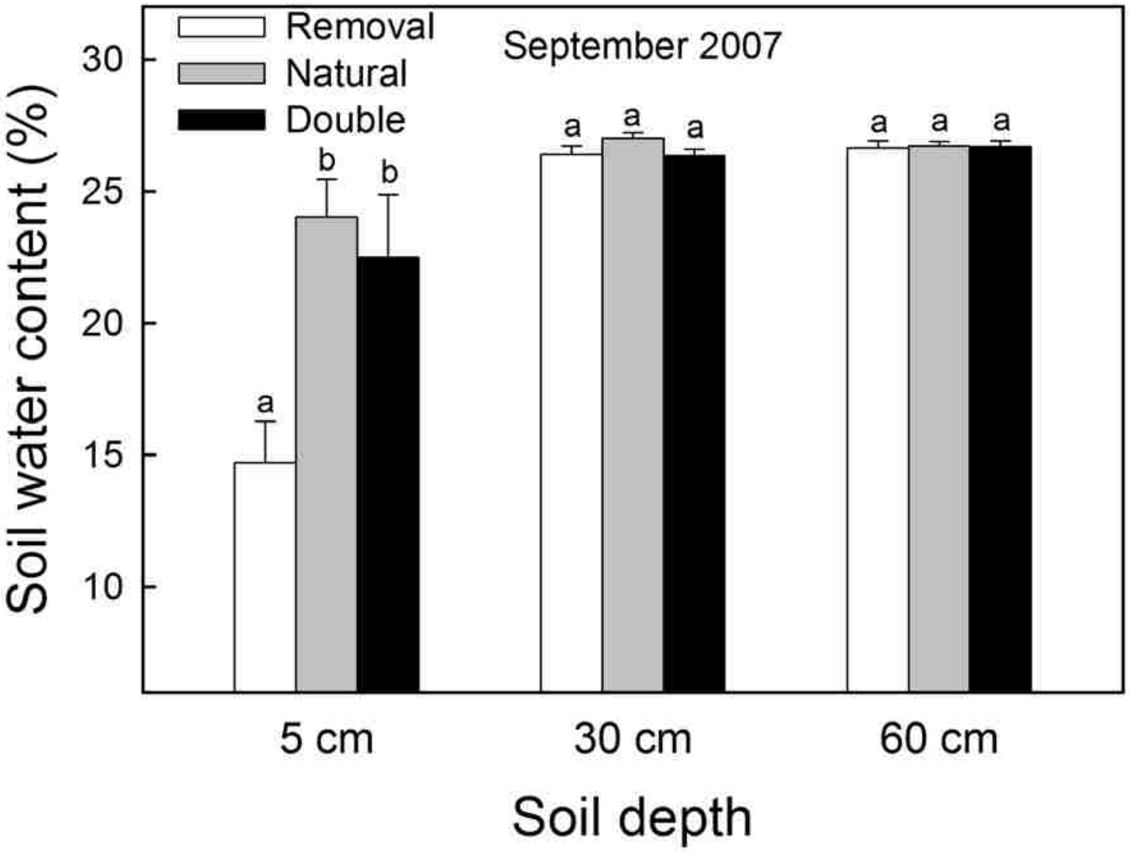

Figure 2.2. Soil gravimetric water content in the experimental plots: removal, natural and double litter. Three soil samples were collected on September 17, 2007 at different depths (5, 30 and 60 cm) in all treatment plots. Bars are averages + 1SE . Bars marked with the same letter are not significantly different as determined by Tukey's pairwise comparison ($\alpha = 0.05$).

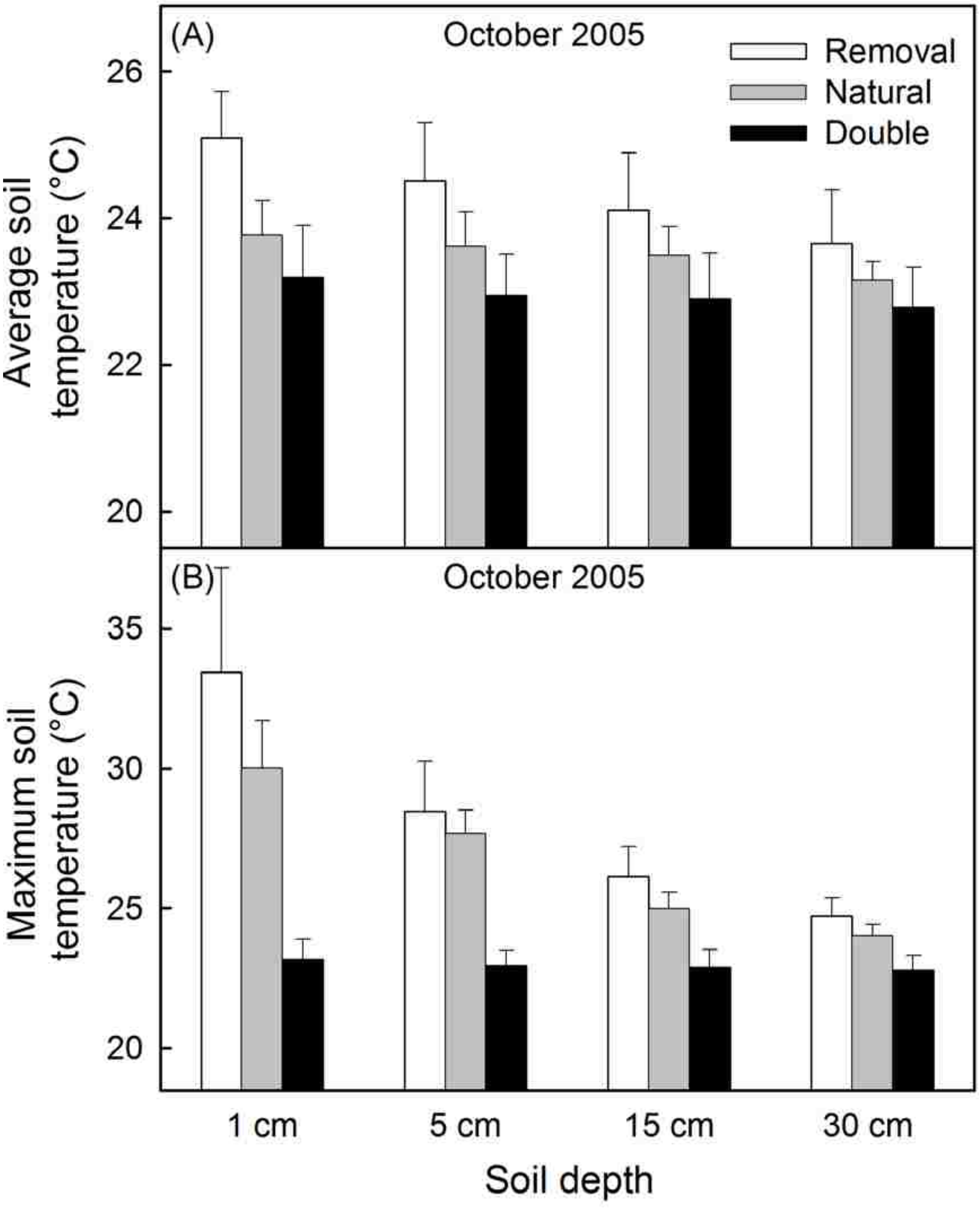

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Figure 2.3. Average and maximum soil temperatures at different depths (1, 5, 15 and 30 cm) in the experimental plots (n=3 per depth): removal, natural and double litter, measured from October 18 to 21, 2005, in the middle of the dry season. Only one plot per treatment was used. Bars are averages + 1 SD.

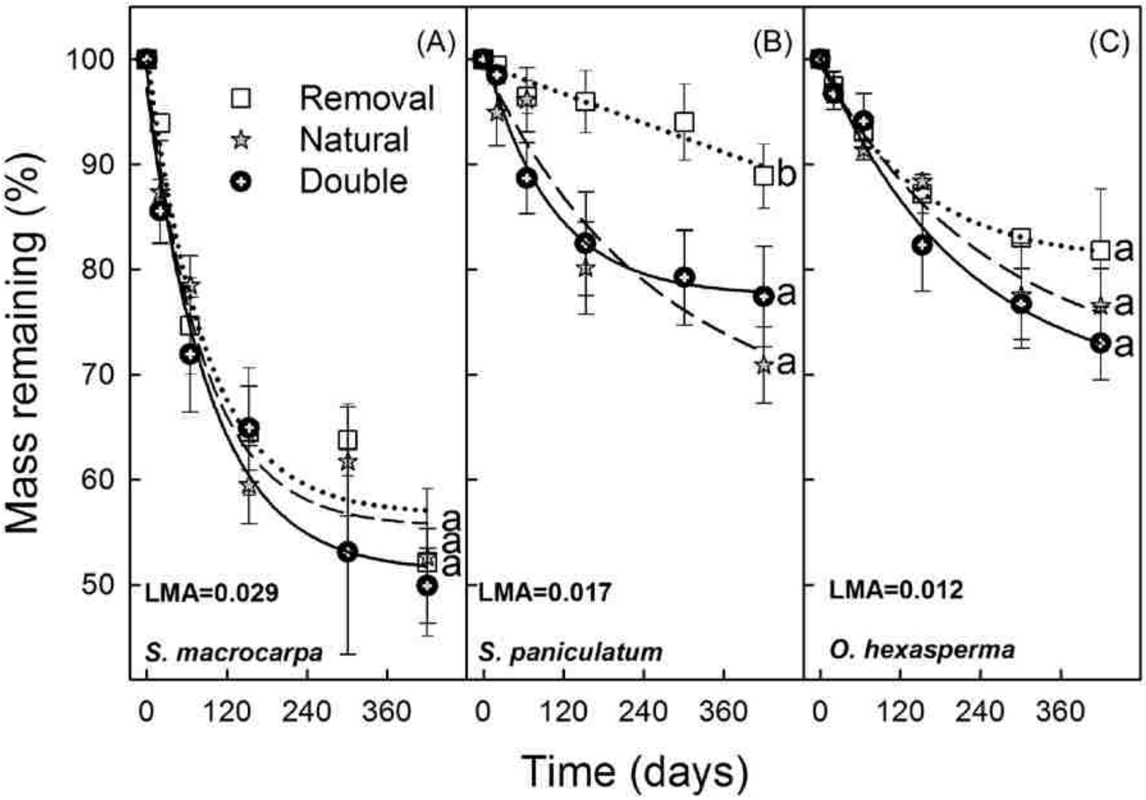

Figure 2.4. Decomposition rates (% of mass remaining) of *Schefflera macrocarpa*, *Sclerolobium paniculatum* and *Ouratea hexasperma* litter in the experimental plots (removal, natural and double litter). Values are averages ± 1SE (n=4 per treatment). The initial biomass of litter was measured on November 2006. An exponential decay function was fitted to the data with the exception of *S. paniculatum* litter in the removal treatment where a linear regression was used. Average leaf mass per area (LMA) in g cm^{-2} for leaves of each species is indicated. End values marked with the same letter are not significantly different as determined by pairwise t test comparison ($\alpha = 0.05$). Holm adjustment method was used to control for the family-wise error rate.

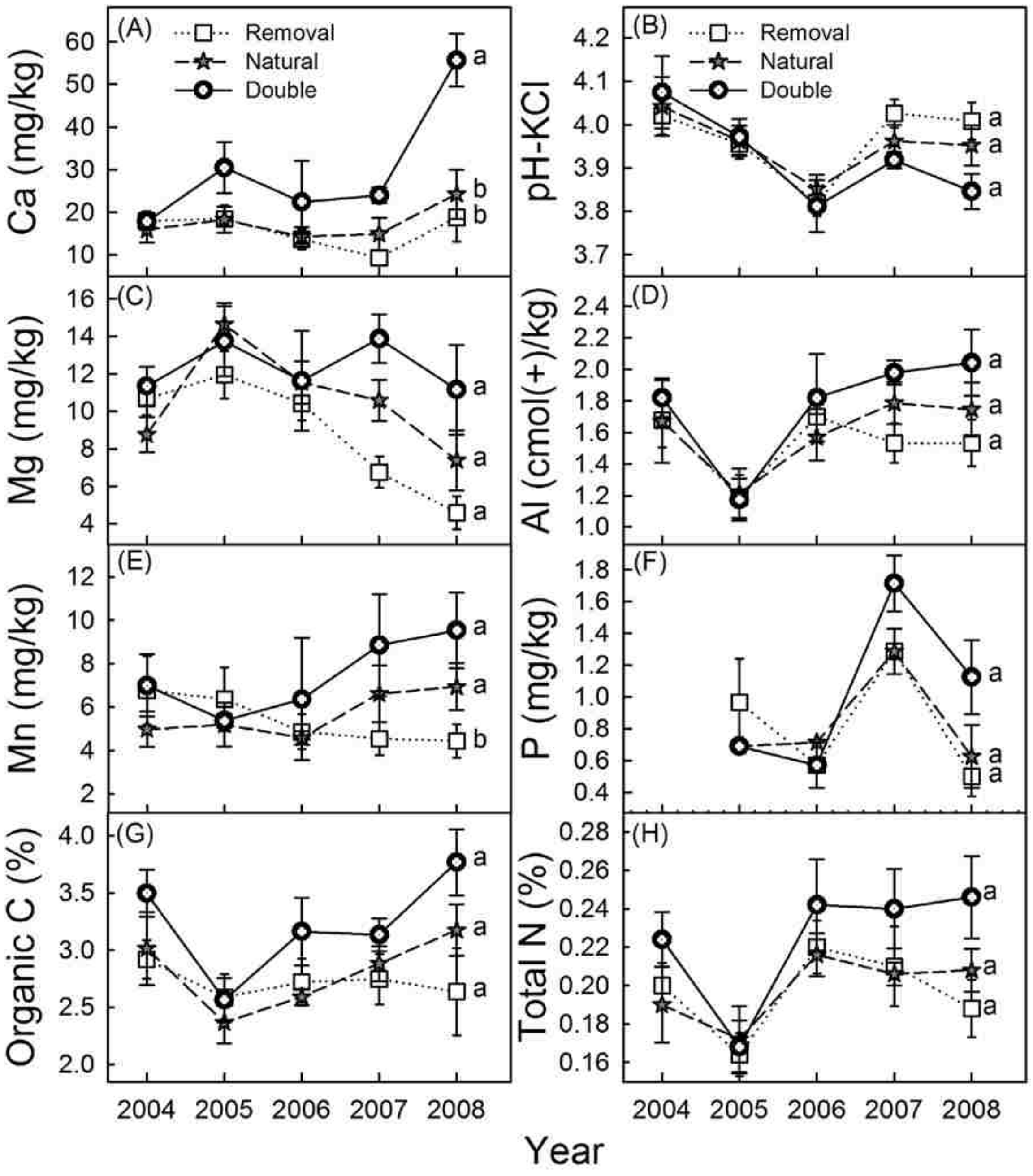

Figure 2.5. Total carbon, pH and soil nutrient availability for the first 5 cm of soil in the experimental plots (removal, natural and double litter). Results are shown for the initial conditions (July 2004) and during four years of treatment, from July 2005 until July 2008. Values are averages ± 1SE (n= 5 per treatment). Values for 2008 with the same letter are not significantly different as determined by pairwise t test comparison ($\alpha = 0.05$). Holm adjustment method was used to control for the family-wise error rate.

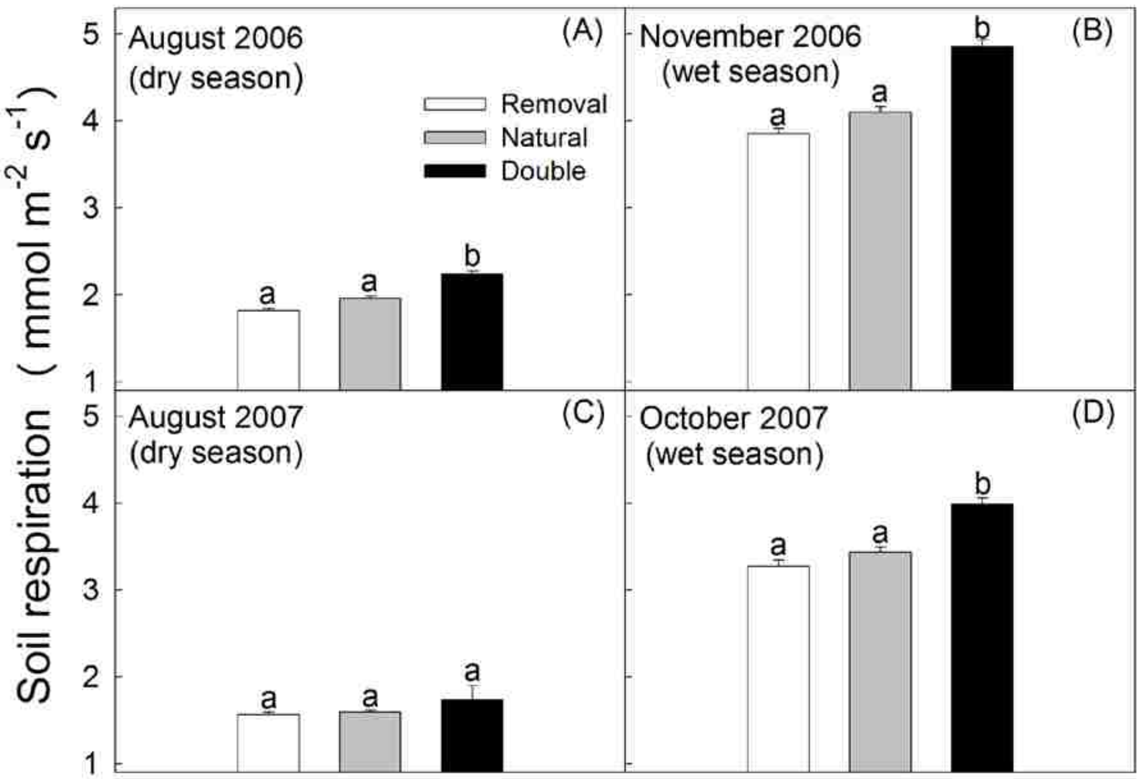

Figure 2.6. Soil respiration measured in all experimental plots (removal, natural and double litter) at the end of the dry season (August 2006 and 2007) and during the wet season (November 2006 and October 2007). Bars are averages + 1SE (n=20 per treatment). Bars marked with the same letter are not significantly different as determined according to the treatment contrast analysis (α = 0.05).

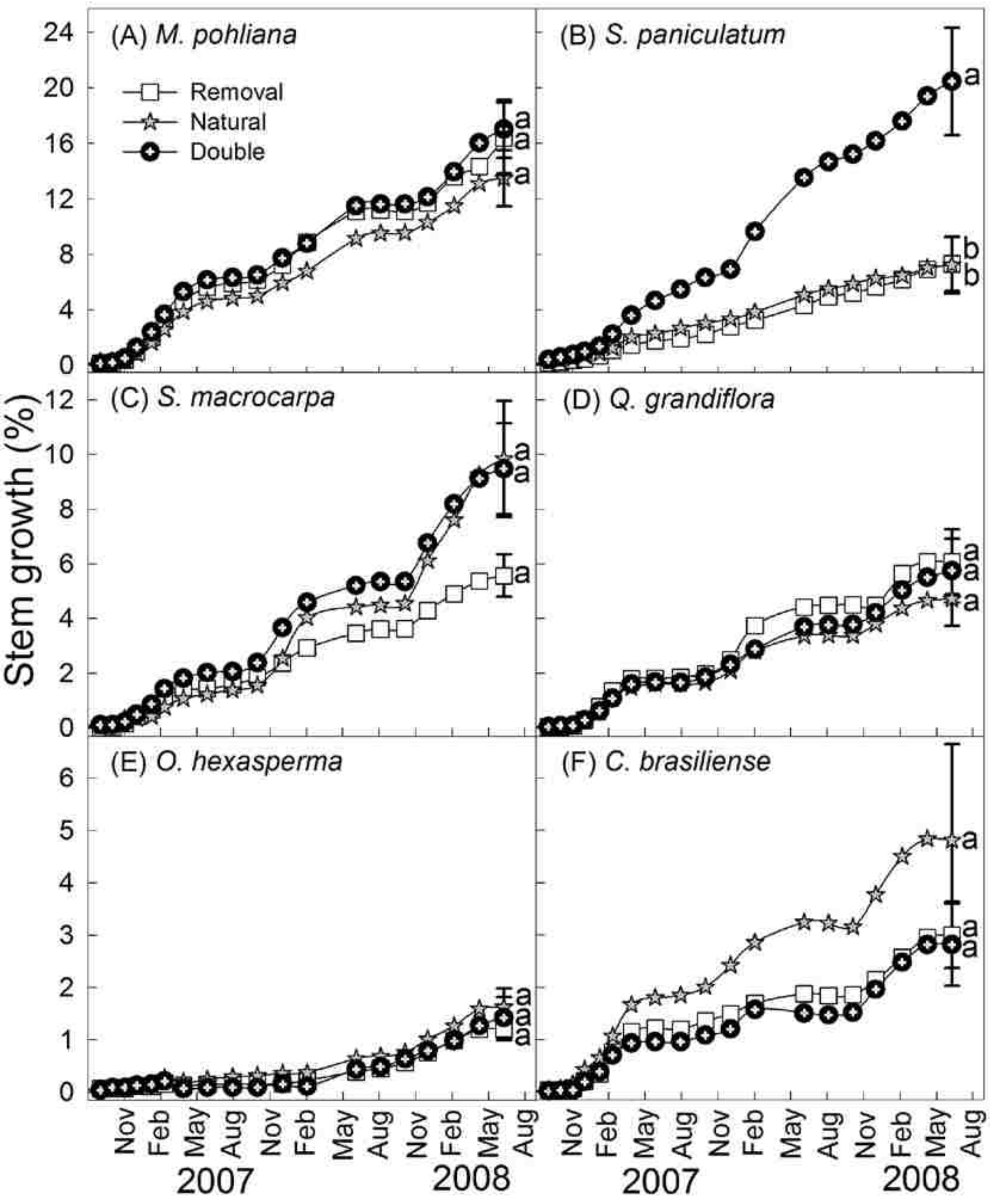

Figure 2.7. Accumulative stem growth (percentage growth normalized to the initial stem circumference) of six dominant woody species, from August 2006 until May 2008 in removal, natural and double litter plots for 4 evergreen (*Miconia pohliana*, *Schefflera macrocarpa*, *Ouratea hexasperma* and *Sclerolobium paniculatum*) and 2 deciduous (*Qualea grandifloria* and *Cariocar brasiliense*) tree species. Values represent stem growth averages of 5 to 14 individuals depending on species and treatments. Lines with the same letter are not significantly different as determined according to the treatment contrast analysis (α = 0.05). Error bars (± 1SE) were included only for the last date of measurements.

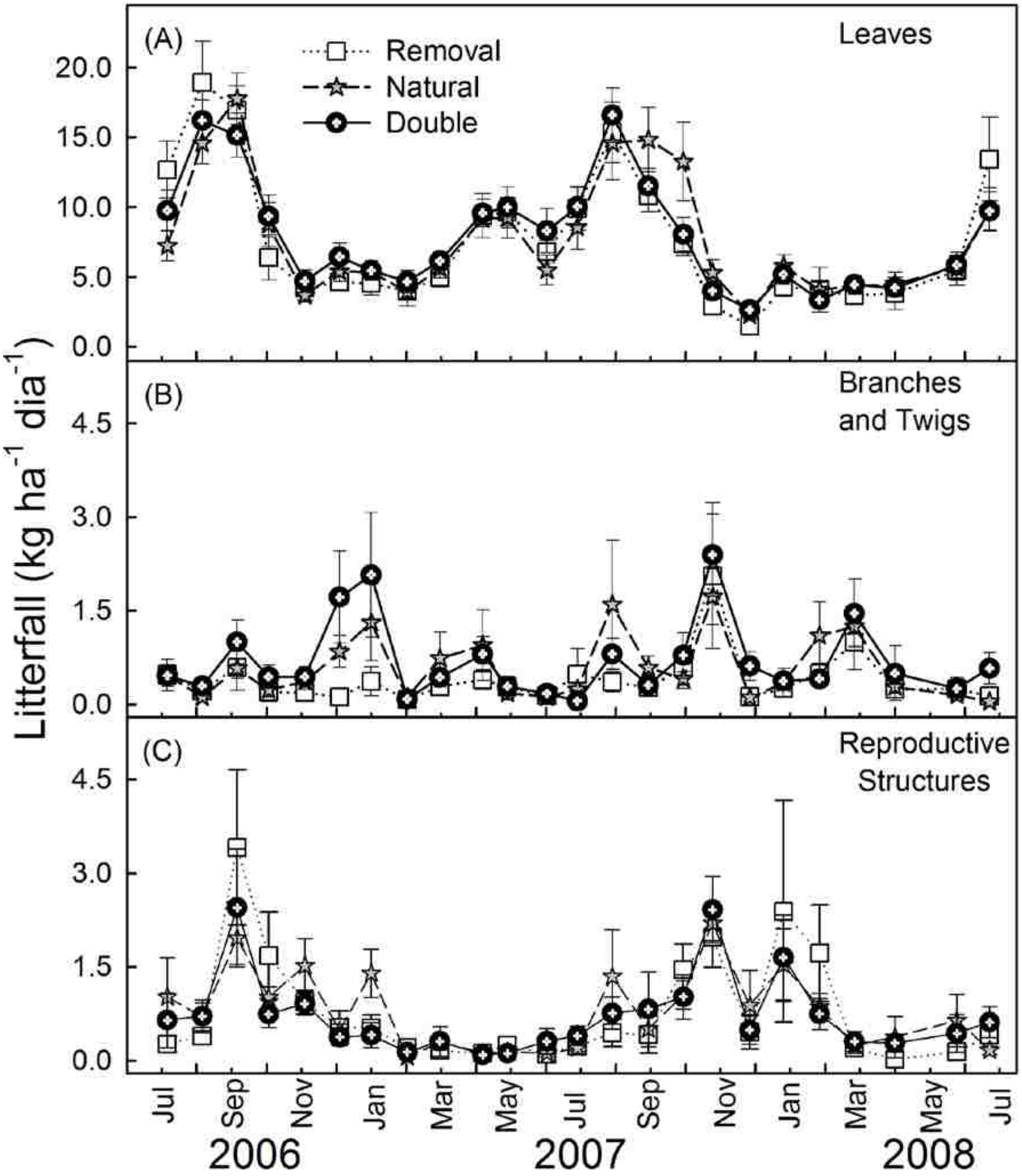

Figure 2.8. Litter fall in the removal, natural and double litter plots from July 2006 until July 2008. Litter was subdivided into (A) leaves, (B) branches and twigs, and (C) reproductive parts (e.g. flowers and fruits). Values are averages ± 1SE (n= 25 per treatment).

Chapter 3

Spatial and temporal variations in water table depth as determinants of savanna ecosystem structure and function

Summary

Savannas of central Brazil (cerrado) exhibit variations in tree density associated with shallow topographic gradients of several hundred meters in length, from open savannas with relatively few trees in the lower portions of the slopes to closed savannas with a relatively high density of taller trees in the upper slopes. Determinants of variations in tree density along the topographic gradient have been controversial and several hypotheses have been suggested to explain this pattern of physiognomic variation across the cerrado landscape. Because ecosystem processes in the cerrado are intrinsically coupled to the hydrological cycle, we studied the effect of water table depth and its temporal variation on spatial patterns of vegetation distribution and related ecosystem processes. Diurnal and seasonal changes in water table depth were monitored along two topographic gradients in a cerrado landscape of the Brazilian plateau. Woody species composition, growth rates of four tree species, litter production, soil nutrients, and nutrient resorption efficiency were measured along the topographic gradients where diurnal and seasonal changes in water table depth was continuously monitored for over a year. Seasonal changes in water table depth were strongly influenced by the seasonal pattern of precipitation. The water table decreased consistently during the dry season

(May through September). After the first rains of the wet season, in October, the water table rose first in the lower portions of both gradients and remained near the soil surface (between 0.2 and 2 m) until the end of the wet season. In contrast, in the upper part of the gradients, the water level rose after a lag of several months, and remained between 6 and 12 m below the soil surface until the end of the wet season and the beginning of the dry season. Other environmental factors, such as the concentrations of several soil nutrients (e.g. P) did not change substantially along the topographic gradients. The highest water table depth attained during the year was an overriding factor controlling density and diversity of woody species. A positive linear relationship was observed between tree abundance and minimum water table depth, with lower tree abundance in sites where the water table was near the soil surface. Minimum water table depth also explained a substantial percentage of stem growth variations in 3 out of the 4 tree species studied, as well as N and P leaf resorption efficiency of *Qualea parviflora*, one of the dominant woody cerrado species.

Background

Ecosystem processes are intrinsically coupled to the hydrological cycle, and in particular to the amount and seasonal variation in precipitation, soil moisture, and water table depth (Hutjes et al., 1998; Rodriguez-Iturbe et al., 1999; Arora 2002). Understanding plant responses to the environment requires recognition of the complex hydrologic controls that operate in different portions of heterogeneous landscapes. For example, topography influences soil moisture, the amount of incoming solar radiation as well as the distance to underground water. The effect of topography on ecosystem structure tends to be striking in regions with strong seasonal variations in precipitation. In semi-arid and arid environments, for example, underground water may enhance plant performance by increasing soil water availability when the water table is close to the upper soil layers. On the other hand, if the water table is too close to the surface, waterlogging may be detrimental to plant growth (Lenssen 2003; Visser and Voesenek 2004; Jackson and Colmer 2005; Mendoza et al., 2005). Water table depth may also influence several ecosystem level processes such as litter production, soil nutrient availability and resorption efficiency of plants.

Savannas of central Brazil (cerrado) exhibit consistent differences in tree cover along shallow elevation gradients (Goodland 1971; Eiten 1972; Lopes and Cox 1977). These topographic gradients characterize the cerrado landscape. Vegetation varies from open savannas with relatively few small trees in the lower portions of the topographic gradient (campo sujo) to closed savannas or woodlands with a relatively high density of taller trees in the upper portions of the gradient (cerradão). Herbaceous plant abundance follows the opposite trend with continuous coverage in open savannas to very low coverage in closed savannas and woodlands. Several hypotheses have been put forth to explain this important pattern of physiognomic variation across the cerrado landscape. Goodland (1971) suggested that Al concentration was an important determinant of physiognomic variation because its concentration increases toward the lower end of the topographic gradient where trees are shorter and savannas are open. Soil fertility and soil moisture have also been suggested as controlling factors of tree density and height along the topographic gradient (Goodland and Pollard 1973; Oliveira-Filho et al., 1989;

Ruggiero et al., 2006; Bucci et al., 2008). Fire frequency is one of the more frequently cited factors shaping savanna physiognomies, with high fire frequency resulting in low abundance of woody plants (Rawitscher 1948; Goodland 1971; Moreira 2000). Although fire undoubtedly has important environmental effects on cerrado vegetation, fire alone cannot explain the consistent changes in tree density along topographic gradients.

In spite of the consensus that water table plays an important role in determining variations in cerrado physiognomies, a long term quantitative study of cerrado topographic gradient has never been done. Consequently, it is difficult to assess the effect of water table dynamics and soil waterlogging on spatial patters of vegetation distribution and ecosystem level processes in the cerrado. The main objective of this study was to determine seasonal changes in water table depth in relation to topography, tree density, canopy height, tree growth, and soil nutrient availability in representative cerrado gradients. The following predictions were tested: (a) Soil nutrient availability is higher, water table is deeper and toxicity of Al and Fe are less in the upper portions of the topographic gradient compared to the lower portions. (b) Tree growth rates are higher in the upper portions than tree growth rates in the lower portions of the gradient. A cause-effect relationship is assumed to exist with tree growth being influenced by nutrient availability, underground water sources, and high concentration of available Al and Fe in the soil. These predictions were addressed by doing a survey of woody vegetation and savanna structure characterization at different locations along topographic gradients, and by measuring diurnal and seasonal changes in water table depth, as well as growth rates of four tree species, nutrient resorption efficiency of selected tree species, total litter production and soil nutrient concentration along the gradients at each sampling location.

Materials and Methods

Site description

The study was carried out at the Instituto Brasileiro de Geografia e Estatistica (IBGE) Ecological Reserve, a field experimental station located 33 km south of Brasilia, Brazil (lat. 15^o 56', long 47^o 53' W, alt. 1100 m. The IBGE includes areas of all major physiognomies of cerrado vegetation from open to closed savannas, and evergreen gallery forest restricted to flood plains of small rivers and streams. Annual precipitation in the reserve ranges from 880 to 2150 mm with a mean of 1500 mm (www.recor.org.br). There is a pronounced dry season from May through September with the months of June, July, and August being nearly rainless. Mean annual temperature averages 22^{o}C. Maximum and diurnal air temperature differences can be as large as 20^{o}C during a typical dry season day.

Two transects were established along a topographic- tree density gradient at the IBGE reserve (Fig. 3.1). The four criteria for choosing the transects were: 1) the absence of fire for at least 10 years, 2) transects perpendicular to contour lines, 3) change in tree density consistent with topographic changes from closed savannas in the upper parts to open savannas in the lower parts of the gradient, and 4) presence of at least 3 physiognomies (as described by Goodland 1971 and Goodland and Pollard 1973). The physiognomies included in this study were campo sujo, campo cerrado and cerrado *sensu stricto*. Campo sujo is an open savanna with scattered small trees and shrubs over a continuous herbaceous layer, campo cerrado is an open savanna with a denser woody layer and a continuous herbaceous layer; and cerrado *sensu stricto* is a closed savanna with a relatively high tree density and some herbaceous plants. Wells were drilled at five sites along each gradient.

Plant survey and target species

To characterize savanna composition and structure along both transects, two plots of 14 m X 14 m were established on both sides of each well and perpendicular to the topographic gradient. All trees with a minimum stem diameter of 1cm at 50 cm above ground level, and height ≥ 1 m were included in the survey. Height measurements were taken for each individual, but stem diameter was recorded only for trees with stems larger than 3 cm.

Four species were chosen for detailed studies within a radius of 30 m around each well along the density gradient: *Qualea parviflora* (Vochysiaceae), *Eriotheca pubescens* (Bombacaceae), *Schefflera macrocarpa* (Araliaceae) and *Styrax ferrugineus* (Styracaceae). These species were chosen because they were found along both transects in all ten locations.

Seasonal changes in water table depth

To monitor diurnal and seasonal changes in water table depth, five wells (11 cm in diameter) were drilled to a depth reaching the water table in each transect spanning the three physiognomies. An additional well was drilled to measure local atmospheric pressure variation. Drilling was done from January to March 2007. Measurements of barometric pressure of this well were used to perform a correction routine which eliminates the noise caused by diurnal changes in barometric pressure on the water table measurements.

Borings were done using a portable drilling machine, and then a 6 cm diameter PVC pipe was place inside the wells. Each pipe was capped at the bottom and sawed slots were made in the tube walls to allow water to flow across the well. Once the pipes were installed, small quartz fragments were placed around the sawed slots. To avoid infiltration along the pipe, a layer of bentonite was dropped on top of the quartz fragments. Soil was then placed on top of the bentonite until almost reaching the ground surface. Finally, the upper 30 cm of the well was filled with concrete and the remaining 1 m of the PVC pipe protruding above the soil was also protected with concrete. Automatic pressure recording piezometers (leveloggers, Solinst Canada Ltd) were placed in each well to monitor groundwater levels. Water level was recorded every 15 minutes and data were retrieved every two months.

Growth rates of tree species along the topographic gradients

To measure tree growth, dendrometers were installed in the main stem of the four target species that span the entire gradient. Between 7 and 9 individuals per species per site were included. Growth increments were measured monthly from October 2007 to August 2008, and growth rates calculated as a percentage of initial stem circumference. Band-dendrometers (Series 5, low tension, from Forestry Suppliers Inc., Jackson, Miss.) were used with *Qualea parviflora*, and homemade dendrometer bands were used with the other three species: *Eriotheca pubescens*, *Schefflera macrocarpa* and *Styrax ferrugineus*.

Band-dendrometers had a scale housing bolted to the tree with one end of the metal band fixed to the stem. The other end was attached to a constant tension spring (1.22 N). An adjustable Vernier scale provided a 0.1 mm resolution for stem expansion measurements. Homemade dendrometer bands consisted of thin straps of metal placed around a tree, with one end passing through a collar (which is attached to the other end) and then connected back to itself with a spring, as described by Cattelino et al. (1986). Three months after dendrometer installation (to allow stem-dendrometer adjustment) a permanent mark was made on the metal band next to the collar. As the trees grow, the mark moves away from the collar and the spring is stretched keeping the dendrometer tight. A metric tape was used to measure initial stem diameter with an accuracy of 0.5 mm.

Litter production

The amount of litter along the gradients was measured inside circular areas of 1200 m^2 around each well. A 0.25 cm^2 square frame made of wire was thrown five times at random inside each 1200 m^2 area. All the litter within the frame was collected, placed in paper bags, and oven dried at 65°C for 48 hours. The dry mass of litter per unit area (g m^{-2}) was calculated. The collection of litter was performed at the end of the dry season (last week of August or beginning of September), when litter accumulation is maximum.

Soil and groundwater analysis

In order to determine differences in soil nutrient concentration along the topographic gradients, three soil samples per site were collected at different depths (5, 10, 25 at 50 cm) in each transect. Soil samples were collected down to a depth of only 50 cm since nutrient concentrations tend to be very low below 50 cm depth. Samples were collected using an auger, placed in plastic bags and transported to the laboratory for analysis. Soil pH, organic carbon and total nitrogen content and available nutrient concentration were determined. Soil pH was measured in 1:2.5 soil-water suspension and in 1M KCl, Exchangeable Ca, Mg and Al were determined in soil extracts of 1 M KCl and exchangeable K and available P, Fe, Mn, Zn and Cu in Mehlich's extract of a diacid mixture of 0.05 M HCl and 0.0125 M H_2SO4. The cations in soil extracts were determined by atomic absorption spectrophotometry and P by colorimetry (Allen 1989). Total N in soil was determined by Kjeldahl digestion and distillation. Soil organic carbon was determined by the method of Walkley and Black (Allen 1989).

Concentrations of elements in groundwater were determined along the gradients. Water from each well was sampled at both maximum and minimum water table depths. Water samples were placed in vials and taken to EMBRAPA for determine concentration determination of 22 different elements.

Leaf Nitrogen and Phosphorus resorption

Mature, fully expanded and sun exposed leaves (5–15) of *Qualea parviflora* were collected from the upper crown of each tree (n=7), one month after the beginning of the rainy season (September-October). Attached senesced leaves (5–15, yellow and ready to drop) were collected at the end of the dry season (end of August –September) by gently shaking the trees. In the laboratory, leaf area was measured and then leaves were oven dried at 65°C for 3 days to obtain a dry mass. Leaf mass per unit leaf area (LMA) was then calculated. The leaves were cleaned with distilled water and dried in a force-convection oven at 70 °C. Wet digestion using a mixture of sulfuric, nitric and perchloric acids (1:10:2) was employed for the chemical analysis. Phosphorous was determined colorimetrically (Allen 1989), and nitrogen was determined by Kjeldahl digestion and distillation. Nutrient resorption efficiency (RE) was estimated on a leaf area basis. In order to accomplish this, the nutrient concentration (N or P) was converted to foliar content by multiplying LMA (g cm^{-2}) by concentration (mg g^{-1}) to yield nutrient content per unit area. Resorption (%) was calculated as the nutrient content of mature leaves minus that of senesced leaves, divided by the nutrient content of mature leaves. Calculations based on leaf areas are better than calculations based on mass because leaf LMA may increase in senesced leaves compared to mature ones (Rentería 2005). This phenomenon can occur as a result of the accumulation of carbon compounds in senesced leaves.

Data analysis

Non-metric multi-dimensional scaling (MDS) ordination was used to examine patterns in species composition. Ordinations for the vegetation of woody species were performed with PRIMER v5 (K R Clarke & R N Gorley) using all taxa found during species surveys. The purpose of the ordinations is to represent the sites as points in a two dimensional space such that the relative distances among points are in the same rank order as the relative dissimilarities of the sites (as calculated by Bray-Curtis coefficients between every pair of the 10 sites, after square root transformation of the original species abundances of every entry in the matrix). The stress value of the ordination indicates how faithfully the high-dimensional relationships among the sites are represented in a 2-dimensional ordination plot.

Linear regressions were fitted to relationships between minimum water table depth and number of trees per hectare for trees taller than 2 m, and number of trees per hectare for trees with stem diameters larger than 6 cm. An e*xponential rise* to an *asymptotic maximum* was used to describe the relationship between minimum water table depth and number of species.

Results

Wells (1 to 5) along Transect 1 were located between 1125 and 1078 m a.s.l. while wells (6 to 10) along Transect 2 were located between 1142 and 1105 m (Table 3.1). The average slope was 5.8% along Transect 1 and 2.7% along Transect 2 (Table 3.1, Fig. 3.5). In both transects there were wells located within relatively closed savannas (cerrado *sensu stricto*) and in open savannas (*campo sujo*) (Table 3.1). The soil type in the lowest part of each gradient was either Yellow Latosol (YL) or Petric Plinthosol (PP), while the soil class in the highest portion of the gradient was Red Latosol (RL).

The number of species and the total number of trees larger than 1 cm in stem diameter and taller than 1m tended to decrease from the upper to the lower elevation sites (Fig. 3.2A, B). This trend was more consistent in transect 1 compared to transect 2. The

Shannon index of species diversity tended to decrease from the upper to the lower sites in Transect 1, but remained relatively constant along Transect 2 (Fig. 3.2C).

Smaller trees were not included in figure 3.3 because they may not have root systems as deep as their larger counterparts and as a consequence they could be less susceptible to water table changes. Tree density of the largest individuals in each site (trees with stem diameters between 6 and 9 cm or larger than 9 cm, and heights between 2 and 3 m or higher than 3 m) decreased from upper to lower elevations in both transects (Fig. 3.3). Trees taller than 3 m in site number 5 did not fit the pattern of decreasing height with elevation because of the presence of a single species, *Baccharis Salzmanii*, a shrub that grows particularly well in this site (77% of all individuals recorded). The trend was the same but not as distinct when trees in other two diameter classes (<3 and 3 to 6 cm) or small trees (height <2 m) were included in the analysis (data not shown). Also notice that the total number of individuals in top panels (A and B) is different from those in the bottom panels (C and D) because there were more individuals taller than 2 m than trees with stems diameters larger than 6 cm.

Seasonal changes in water table depth were strongly influenced by the seasonal pattern in precipitation (Fig. 3.4). At the end of the 2007 rainy season (April) water table levels were relatively close to the soil surface in well 4 of Transect 1 and in wells 9 and 10 of Transect 2. The water table depth decreased consistently during the 2007 dry season in all the wells (May through September). Near the end of October, shortly after the beginning of the wet season, the water table increased first slowly and two months later relatively rapidly in the lower part of the gradient (wells 4 and 5) of transect 1, and remained close to the soil surface (e.g. between 0.2 to 2m depth) until the end of the wet season. The water table rose rapidly in the lower part of the gradient of transect 2 (wells 9 and 10) at the end of the November-December period, but the water table in the upper portions of both gradients (e.g. wells 1 and 7) responded to the rainfall after a lag of several months. Figure 3.5 shows the maximum and minimum depths attained by the water table in each well along both transects during the study period. Transect 1 was shorter and steeper compared to Transect 2, while the elevational difference between the lower and uppermost part of both transects were similar (about 50 m) (Fig. 3.5).

Sites 1 to 5 (Transect 1) are located on the right side of the non-metric multi-dimensional scaling ordination space while sites 6 - 10 (Transect 2) are located on the left side (Fig. 3.6). This pattern is consistent with differences in elevation as well as differences in minimum water table depth between both transects (average elevation was lower and water table closer to the soil surface in Transect 1 compared to Transect 2). There was a positive linear correlation between total number of trees per ha and minimum distance to the water table when using all trees taller than 2 m in height from both transects (R^2= 0.52) (Fig. 3.7A). A better predictive power was obtained when trees with diameters larger than 6 cm, instead of trees taller than 2 m, was used in the correlation analysis (R^2= 0.84, Fig. 3.7C). An exponential regression was found to fit the number of woody species versus minimum water table depth (Fig. 3.7E). Sites with water tables close to the soil surface had less than 50% of species compared to sites with relatively deep water tables. The correlations were not significant when maximum distance to water table was used instead of minimum distance to water table (Fig. 3.7B, D and F).

Growth rates for all four tree species were very slow during the end of the 2007 dry season (October and November) but increased after December 2007 during the rainy season (Fig. 3.8). Growth rates remained high through April 2008 for all species. Before the end of the wet season, growth rates decreased again and remained constant throughout the entire 2008 dry season (Fig. 3.8). For three of the four species studied, a significant linear relationship was observed between annual growth rate and minimum water table depth per site (Fig. 3.9). The relationships were positive for *E. pubescences* and negative for *Q. parviflora* and *S. ferrugineous*. No significant relationship between growth and water table was observed for *S. macrocarpa*.

Most nutrients decreased in concentration abruptly with increasing soil depth regardless of topographic position along the gradients (results not shown). At about 50 cm depth concentration of most nutrients were very close to zero. Averages of the four soil layers sampled across the first 50 cm of the soil are depicted in figure 3.10. Nutrient concentrations in the upper 50 cm of the soil profile exhibited small but consistent changes along the topographic gradient, particularly in soils along transect 1 (Fig. 3.10). For example, C, N and pH tended to increase with decreasing elevation but Al content tended to decrease with decreasing elevation. The remaining nutrients analyzed did not show a clear pattern of variation along the gradients.

Water table samples showed trace amounts of the 22 elements tested for, including NO_3^-, F^-, B, Cu, Al, Mg, Mn, P, Si and Zn (results not shown). Higher levels were detected for potassium (0.231 to 0271 mgL^{-1}), NO_3^- (0 to 0.275 mgL^{-1}), Fe (0.073 to 0.165 mgL^{-1}), and Na (1.277 to 1.314 mgL^{-1}), though no consistent variations along both transects were observed according to the site's topographic position.

Leaf nitrogen and phosphorus resorption efficiency of *Qualea parviflora* increased from upper to lower portions of transect 1 (Fig. 3.11). For example, resorption efficiency was 0.30 mg/g in trees growing at the highest site (site 1) and increased to 0.45 mg/g in trees growing at the lowest site (Site 5). A negative linear relationship was fitted to resorption efficiency versus water table depth in trees growing along transect 1, suggesting that resorption efficiency in *Q. parviflora* leaves during senescence is higher in sites where the water table depth is close to the soil surface (Fig. 3.12). No such trend was observed in *Q. parviflora* trees growing along transect 2.

Discussion

Water table depth

Seasonal changes in water table depth along both transects were strongly influenced by the seasonal pattern in precipitation. At the beginning of the wet season, the water table started to rise first at sites in the lower portions of both gradients and remained near the soil surface (e.g. between 0.2 and 2m depth) until the end of the wet season, when it started to fall again. In the upper sites, the water table started to rise several months after the onset of the rainy period. In some wells, it took up to five months for the water table to respond to the precipitation events that occurred at the beginning of the wet season. This delay in response could be due to a combination of factors. Infiltration rates are very slow at the beginning of the wet season, when soil water content is still very low (Bucci et al., 2008; Scholz et al., 2008). In addition, water uptake by herbaceous vegetation and shallow roots systems of woody plants increases at the beginning of the wet (growing) season, when water becomes readily available for plants, resulting in less water available to recharge the water table. Lastly, the distance from the soil surface to the water table was large in the upper sites, sometimes larger than 10 m. Contribution of runoff from the upper part of the landscape to the water table level in lower sites is negligible since soils are very well drained and there is no evidence of erosion caused by runoff.

The results of this study suggest that the highest water table level attained during the year is an overriding factor controlling tree density and species diversity along topographic gradients in the cerrado. A strong positive linear relationship was observed between tree abundance and minimum water table depth, with low tree abundance observed in sites where the distance to the water table was relatively small. The correlation between maximum water table and tree abundance was not as high as minimum water table depth suggesting that factors related to anaerobic conditions are functionally related to savanna physiognomy variation. If trees with stems larger than 6 cm are used in the regression analysis with minimum water table depth, then only 25 % of the trees growing in the upper parts of the gradient grow in the lower elevation sites, where water table depth is close to the soil surface. Even though the correlation between these two variables is not necessarily indicative of a cause-effect relationship, it is possible that the minimum water table depth can play an important role in determining tree density and diversity along the topographic and diversity gradients. If the water table is close to the rooting zone, drainage during the rainy season is impeded and anaerobic conditions may constrain root functioning and growth, and perhaps inhibit seedling establishment.

Roots systems of woody plants are usually dimorphic with shallow and deep roots (Jackson et al., 1999; Scholz et al., 2002; Goldstein et al., 2008). Shallow roots have better chances of avoiding water saturated conditions but deeper roots have to face anaerobic conditions when the water table is close to the soil surface. Deciduous and brevideciduous cerrado trees have dimorphic roots which are involved in lifting water from deeper soil layers, whereas evergreen cerrado trees do not have extensive shallow roots and apparently do not hydraulically lift water (Scholz et al., 2008). It is to be expected that evergreen and deciduous trees, with different root distributions within the soil will respond differentially to waterlogging.

The presence of a saturated soil layer could be of importance for understanding changes in tree density, tree hight, stem diameter, and changes in species composition along the topographic gradients in the cerrado. Joly and Crowford (1983) demonstrated the inability of cerrado tree roots to tolerate waterlogged soils. Several mechanisms by which flooding creates anoxic conditions for roots and affects plant performance have been suggested (e.g. Waldren et al., 1987; Visser et al., 2003; Visser and Voesenek 2004; Jackson and Colmer 2005; Mendoza et al., 2005). Roots with aerobic metabolism depend on oxygen diffusion from the bulk soil for adequate physiological functioning. These roots may stop growing and eventually die if they are exposed to saturating conditions for a relatively long period of time.

Besides oxygen deficiency, waterlogging caused by high water table may also result in other negative effects on plant performance. Increases in levels of ethylene as a consequence of waterlogging can further inhibit root growth. Waterlogging can also facilitate the accumulation of products such as Mn^{2+}, Fe^{2+}, S^{2-} and H_2S, resulting from the anaerobic metabolism of soil microorganisms. These substances can reach toxic levels and become detrimental for plants. Certain wetland species are able to restrict uptake of Mn^{2+} and Fe^{2+} from waterlogged soils; but such capacity is generally absent in species restricted to well drained habitats (Davies 1984; Wheeler et al., 1985; Snowden 1995). In our study site, Mn^{2+} concentrations in the soil increased in the lower portions of both gradients, with Mn^{2+} levels in lower portions reaching twice the concentration in the upper parts (Fig. 3.10). In contrast, Fe^{2+} showed no pattern of variation along the topographic gradient. *Qualea parviflora* senescent leaves, on the other hand, exhibited a gradual and consistent increase of Fe^{2+} concentration from the upper to the lower portions of both gradients (from 149.7 to 203.7 mg kg^{-1} in Transect 1 and from 171.5 to 319.9 mg kg^{-1} in Transect 2).

Soil nutrients and toxicity

Factors responsible for the consistent changes in tree density in cerrado vegetation are still debated (Hoffman et al., 2005). One factor, the short supply of almost all plant nutrients, in particular low N and P levels (Goodland and Pollard 1973; Haridasan 2001; Bucci et al., 2006; Bustamante et al., 2006; Kozovits et al., 2007), may be limiting tree growth and preventing the development of a multi-layered forest in Neotropical savannas (Sarmiento 1984). Aluminum content and its related toxicity have been considered historically to be an important controlling factor of tree density (Goodland 1971). Other elements that are potentially toxic in high concentrations are Mn^{2+} and Fe^{2+} (Wheeler et al., 1985; Snowden 1995; Haridasan 2008). According to Haridasan (2008), Mn^{2+} and

Fe^{2+} in cerrado soils are toxic when pH is below 5.6 and 4 respectively. Our results indicate that Mn^{2+} but not Fe^{2+} may be marginally toxic in the lower portions of the gradients (pH 5.4 to 5.7).

Nitrogen and carbon concentrations increased from the upper portions to the lower portions of both gradients. The same trend was observed for soil pH in Transect 1. Some authors found consistent variations in soil nutrient content along topographic gradients in the cerrado, (Moreira 2000; Ruggiero et al., 2002), however other authors did not (e.g.De Oliveira-Filho et al., 1989). Soil N appears to be a limiting nutrient for cerrado tree growth. Long term fertilization with N resulted in substantial increases in stem diameter growth and in total leaf surface area of cerrado tress (Bucci et al., 2006).

Leaves of many deciduous and evergreen tree species senesce and drop during the dry season. Because of low water content in the upper soil layers during this period (Bucci et al., 2008; Scholz et al., 2008), organic matter decomposition mainly occurs after the first large rain events at the beginning of the wet season. Litter is rapidly decomposed and mineralized nutrients are quickly absorbed by roots or immobilized by microbial biomass (Garofalo 2001). We observed that the underground water sources contained insignificant quantities of nutrients, suggesting that most of the nutrients are absorbed and utilized by plants and that the plants controlling the nutrient circulation are very efficient in avoiding nutrient leakage outside the system. Because of the tight nutrient circulation in the different cerrado physiognomies, large changes in soil nutrient concentration along the gradients are not expected to be found, despite large differences in aboveground biomass and consequently in total ecosystem nutrients.

Growth rates and nutrient resorption efficiency

In three of the four species studied, a significant linear relationship was observed between growth rate and minimum water table at each site. The relationship was positive for *E. pubescences*, indicating that growth rates increase with increasing distance to the water table, and negative for *Q. parviflora* and *S. ferrugineous*, indicating that proximity to the water table promotes growth. The relationship between minimum distance to the water table and stem growth was not statistically significant for *S. macrocarpa*. The different responses of radial growth to distance to water table depth could reflect intrinsic differences between these species in waterlogging tolerance, such as root system architecture, maximum root depth and/or physiological mechanisms conferring the roots some degree of tolerance to anoxic conditions. Other factors could also affect growth, including light levels and competition between grasses and woody species.

There was a significant correlation between resorption efficiency of nitrogen and phosphorus in *Q. parviflora* leaves and minimum water table depth in Transect 1, but not in Transect 2. This difference between transects reflects the fact that water table is shallower in Transect 1; where the negative effect of waterlogging is stronger. Waterlogging may impair nutrient uptake; therefore, it is expected that trees such as *Q. parviflora* increase resorption efficiency in sites where minimum water table depth is close to the soil surface during relatively long periods of time, compared to better drained sites, where minimum water table depth is deeper.

The two transects used in this study shared more similarities than differences. Transect 1 represents the lower portion of a topographic gradient while transect 2 represents the uppermost portion of a topographic gradient. As a consequence, the water table was shallower in Transect1 compared to Transect 2, where soils are deeper and better drained. This difference between transects could explain why variables such as growth and leaf nutrient resorption showed a stronger correlation with minimum water table depth in Transect 1 compared to Transect 2. It also explains why we were able to pool data obtained in both transects and fit relationships using minimum water table depth as a predictor of the savanna composition and structure, as if both transects were parts of an extended gradient.

Conclusions

There are different types of gradients in the cerrado landscape based on topography, fire frequency, soil characteristics and tree density. When the gradient studied encompasses a wide variation of savanna types from woodlands in the upper portions of the gradient to open savannas in the lower potions, and fire is excluded, water table dynamics become an important factor controlling tree species density, richness and diversity. It is quite possible that the controversy about the controlling factors of this pattern of physiognomic variation across the cerrado landscape is biased by the characteristics and extension of a particular gradient studied. If the depth of the water table is not an overriding factor in the gradient studied (e.g. when it is far from the soil surface), then other factors such as soil nutrients may become prominent. The ordination analysis with vegetation composition from both transects suggested that each transect in this study can be considered components of a longer tree density/topographic gradient. Results of this study have shown that ecosystem processes in Neotropical savannas are strongly coupled to the hydrological cycle. Minimum water table depth explained changes in tree density along the topographic gradient and to a lesser extent the variation of stem growth in 3 of the 4 tree species studied as well as N and P resorption efficiency in *Q. parvifloria* leaves.

Table 3.1: Localization of physiognomies, Elevation and slope angle of sampling sites and wells along the two transects in the IBGE Reserve as well as soil type according to Alvaro de Oliveria (IBGE 1995): Red Latosols (RL), Red Yellow Latosols (RYL) , Yellow Latosols (YL) and Petric Plinthosolos (PP).

Transect	Site/Well	Elevation (m)	Slope %	Physiognomy	Soil
1	1	1125	4.34	Cerrado *sensu stricto*	RL
1	2	1118	6.49	*Campo cerrado*	RYL
1	3	1104	5.31	*Campo cerrado*	YL
1	4	1092	5.13	*Campo sujo*	PP
1	5	1078	7.73	*Campo sujo*	YL
2	6	1142	1.70	Cerrad*o sensu stricto*	RL
2	7	1128	2.81	Cerrad*o sensu stricto*	RL
2	8	1114	3.00	*Campo Cerrado*	RYL
2	9	1109	2.71	*Campo Cerrado*	YL
2	10	1105	3.34	*Campo sujo*	PP

Figure 3.1. Location of transect 1 (T1) and transect 2 (T2) at the Instituto Brasileiro de Geografia e Estatistica (IBGE) Ecological Reserve.

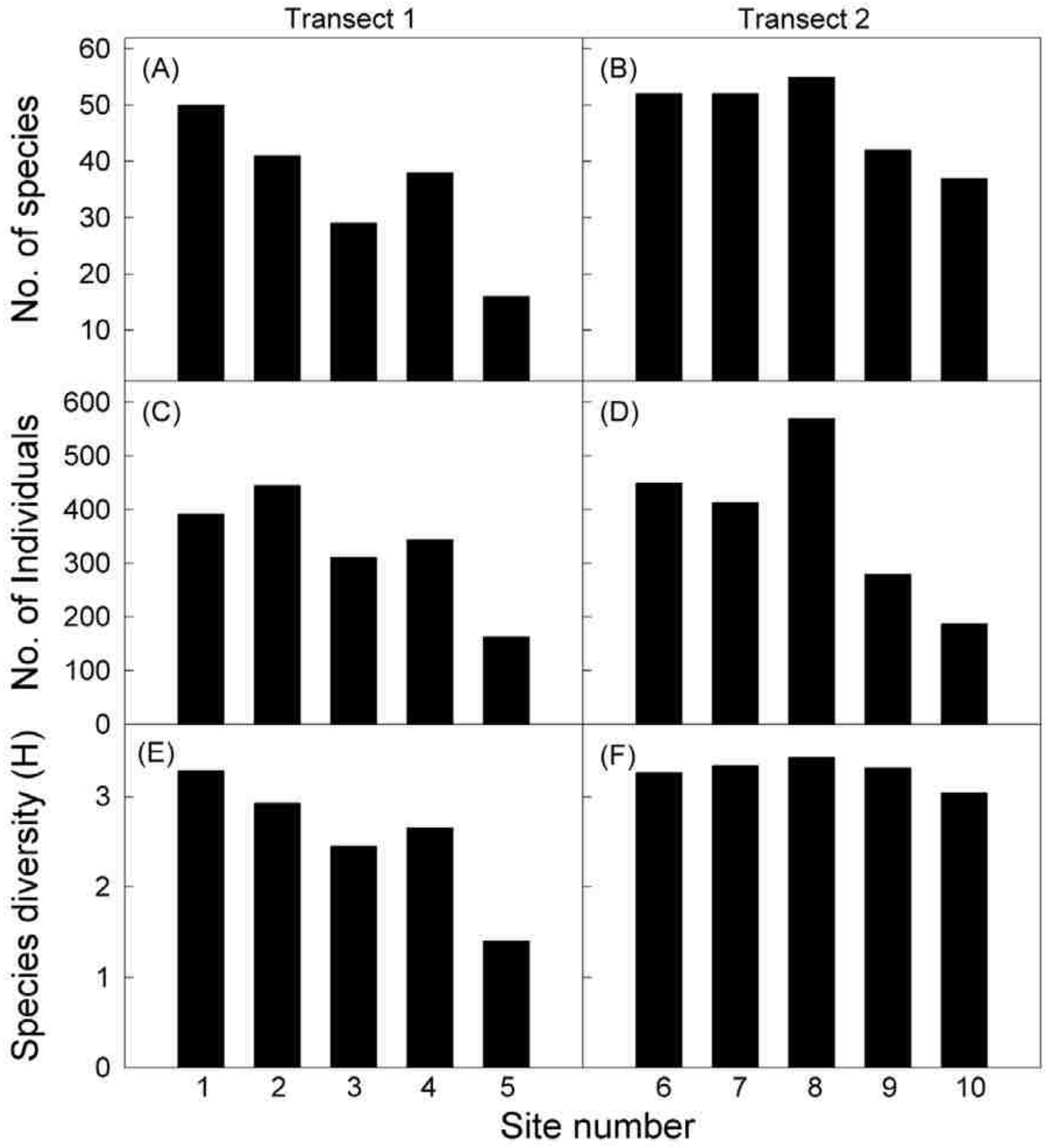

Figure 3.2. Variation in species richness, tree density and species diversity (Shannon index, H) along two transects at the IBGE Reserve. At each site (Table 3.1), two 196 m^2 plots located on both sides of each well and perpendicular to the slope, were sample for all trees larger than 1 cm stem diameter.

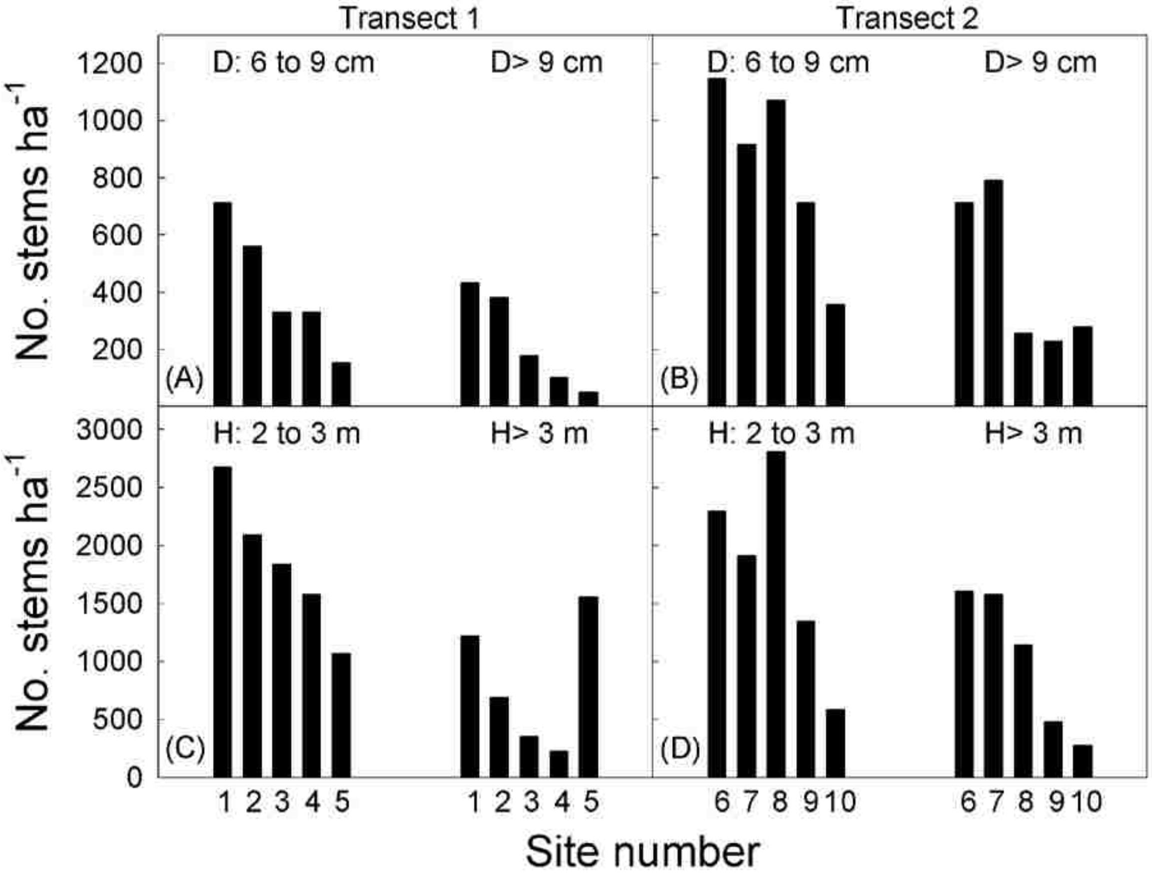

Figure 3.3. Density of trees in different classes of stem diameter (D) and height (H) along two transects at the IBGE Reserve. Site details in Table 3.1.

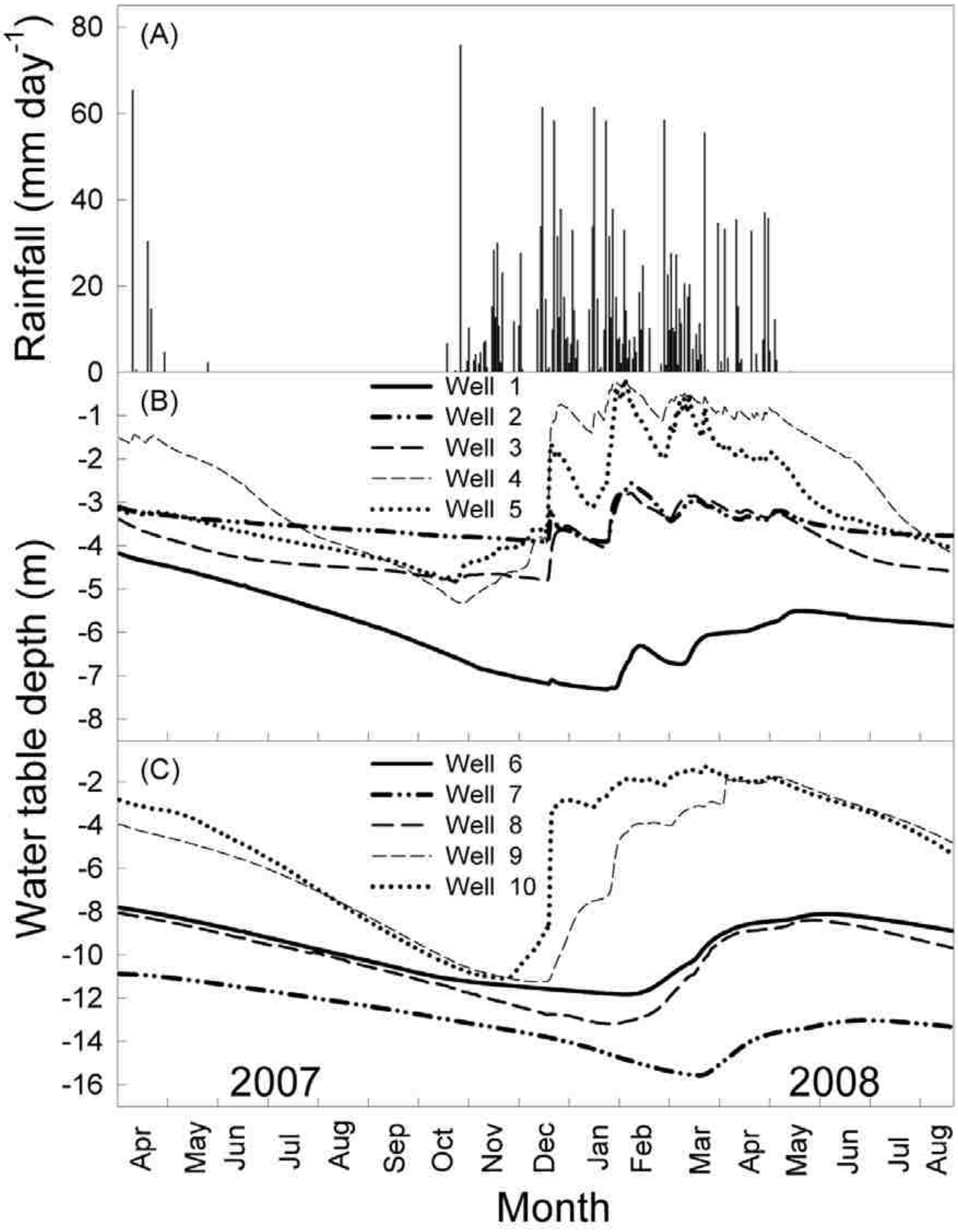

Figure 3.4. Precipitation and water table depth at different sites along the two transects, from April 2007 to August 2008, at the IBGE Reserve: amount of daily rainfall (A), and water table depth for transect 1 (B) and transect 2 (C). Site details of transects in Table 3.1.

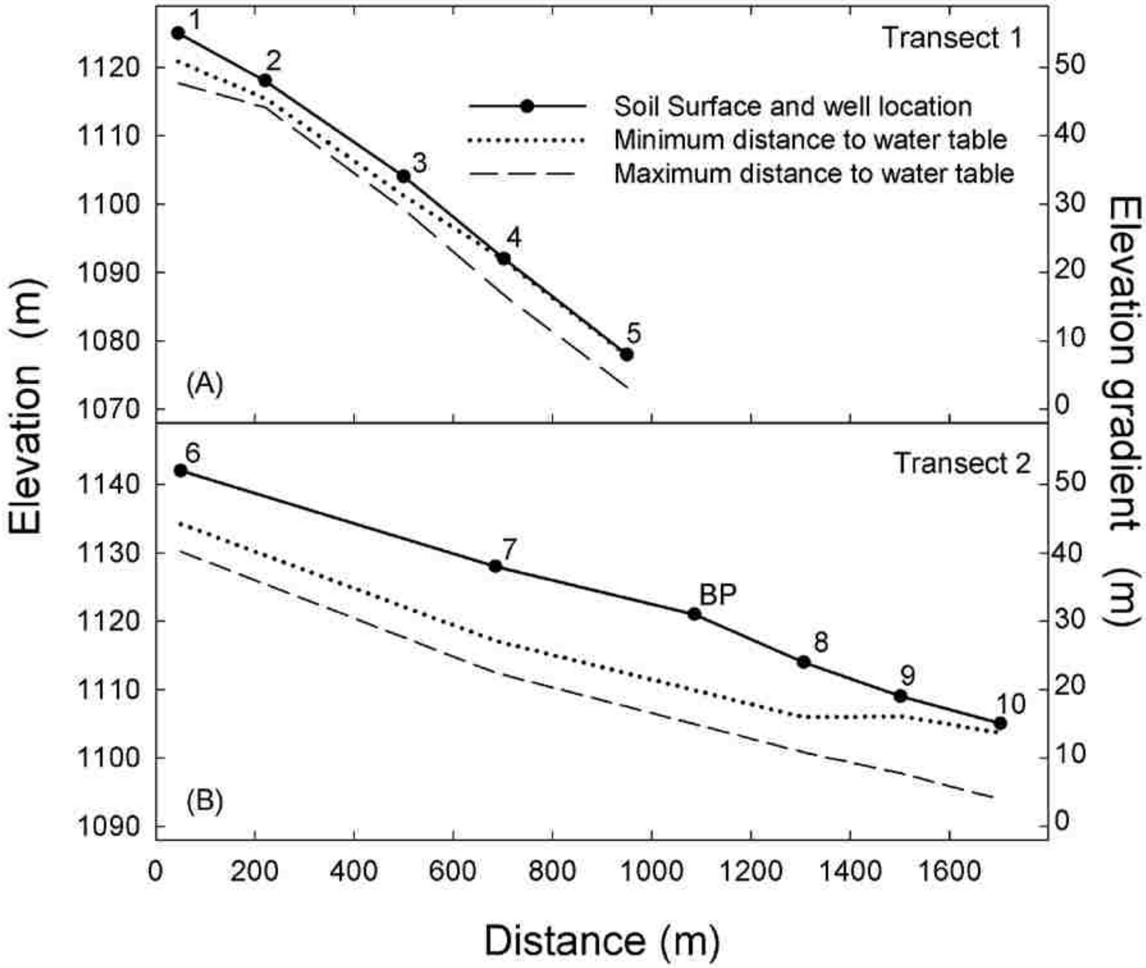

Figure 3.5. Maximum (dotted line) and minimum (dashed line) elevations of water table in each well during the study period (April 2007 to August 2008) along the two transects as a function of distance from the first well. The continuous line indicates the soil surface. The letters BP in transect 2 shows the location of the well that was only used for barometric pressure measurements.

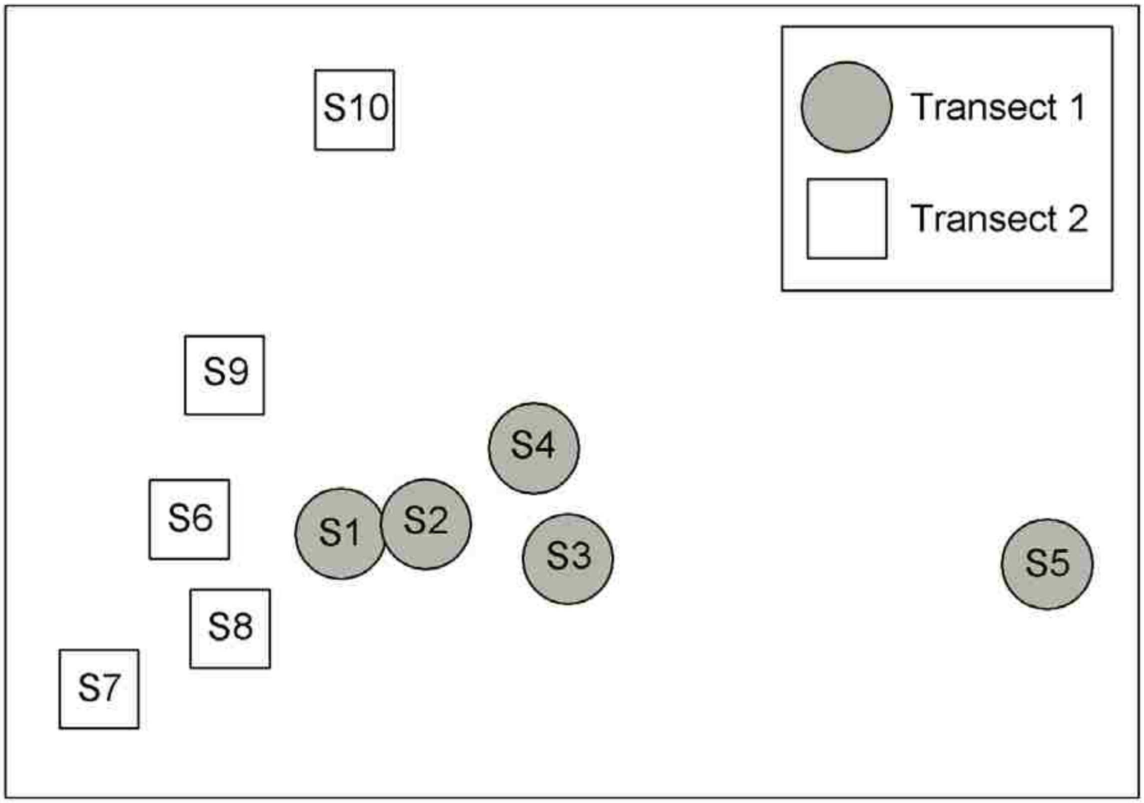

Figure 3.6. Two dimensional representation of the ordination analysis of sites along the two transects (stress level: 0.05) using relative abundance of all trees larger than 2 cm in diameter. The abbreviations S1 to S10 indentifies site number. See information of sites in Table 3.1.

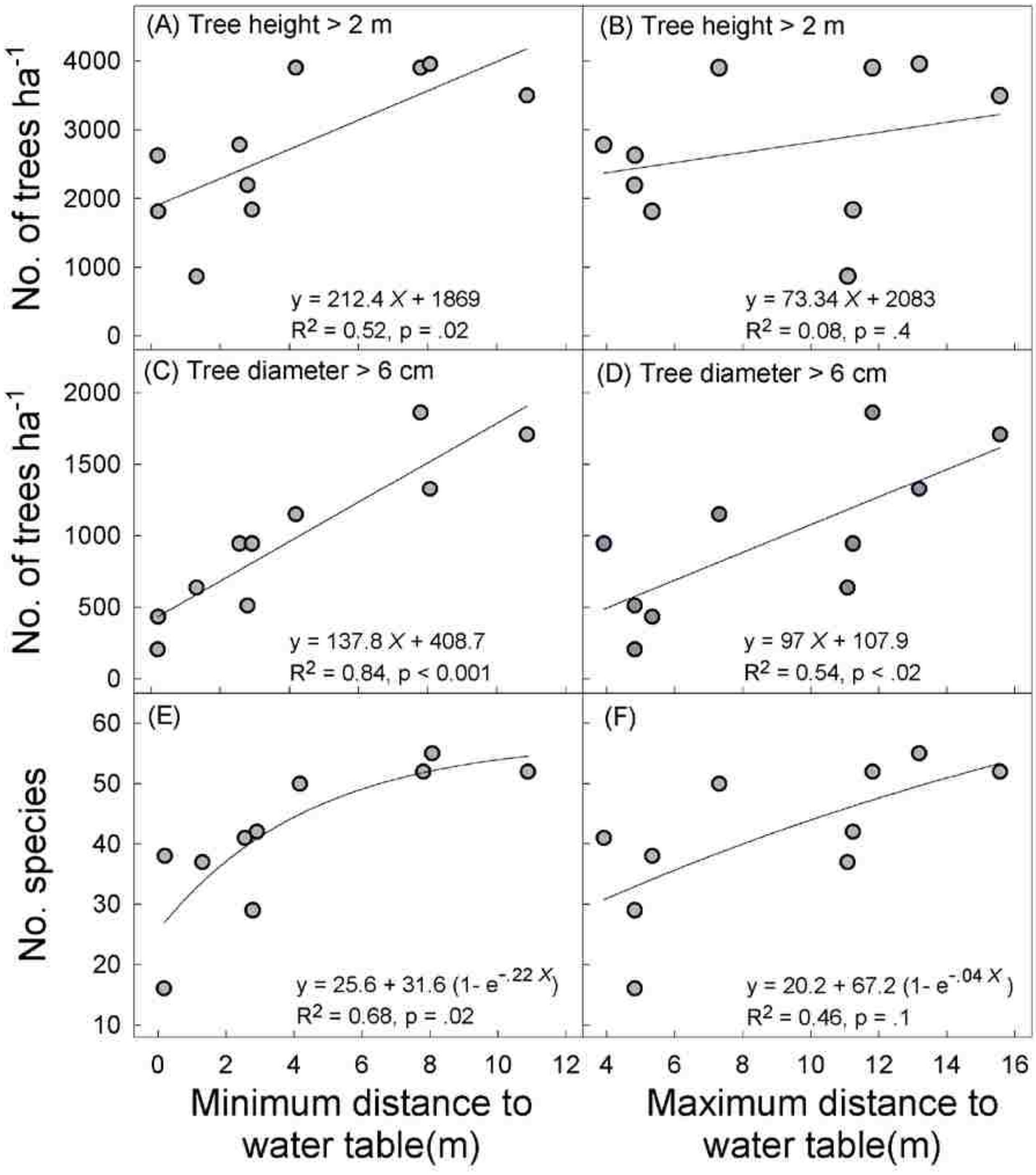

Figure 3.7. Density of trees and species richness as a function of minimum and maximum water table depth: (A and B) trees larger than 6 cm in diameter, (C and D) trees taller than 2 m, (E and F) number of species.

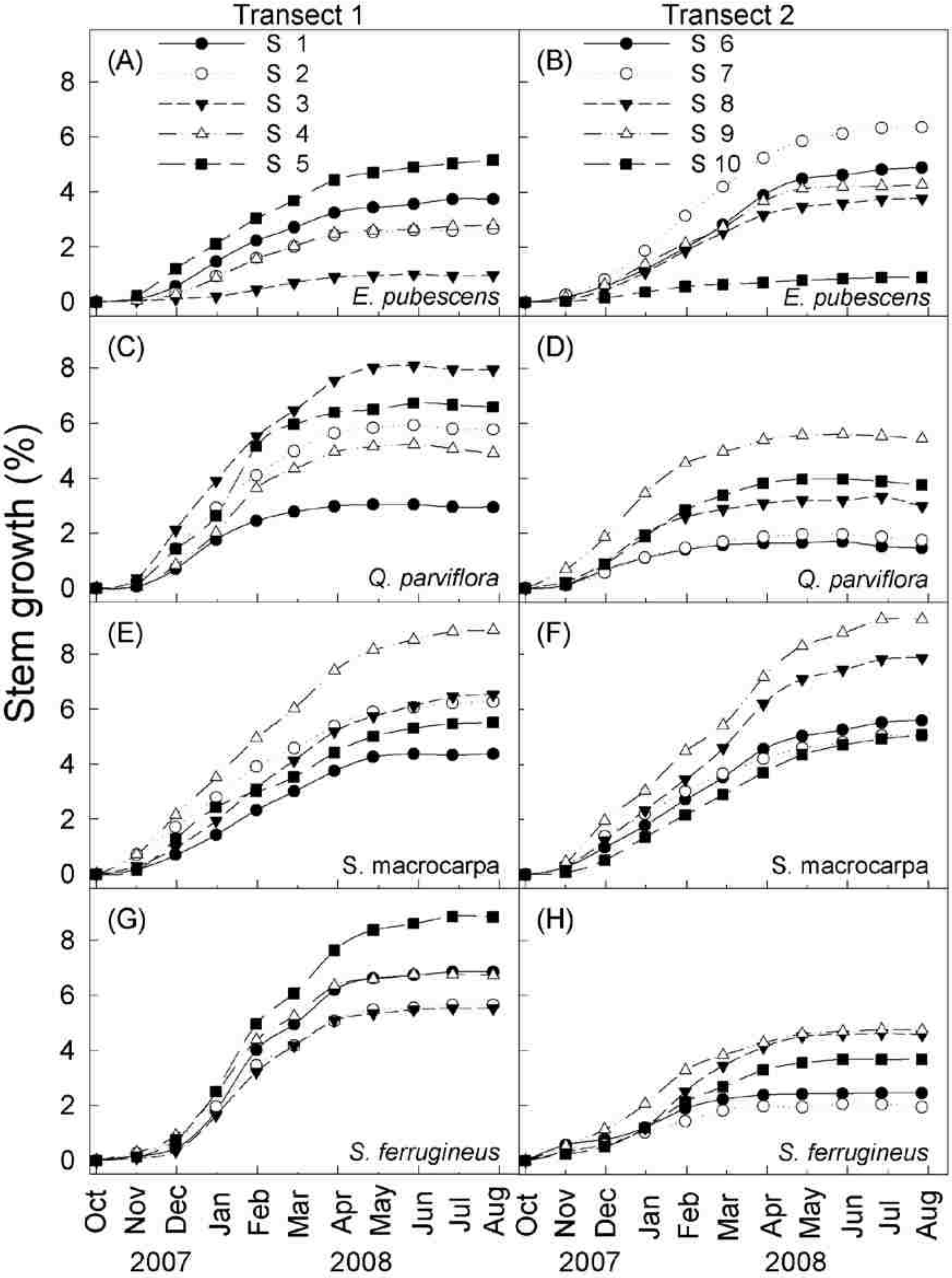

Figure 3.8. Cumulative increase (%) in stem diameter of four cerrado tree species growing close to each well along transects 1 and 2 from October 2007 until August 2008.

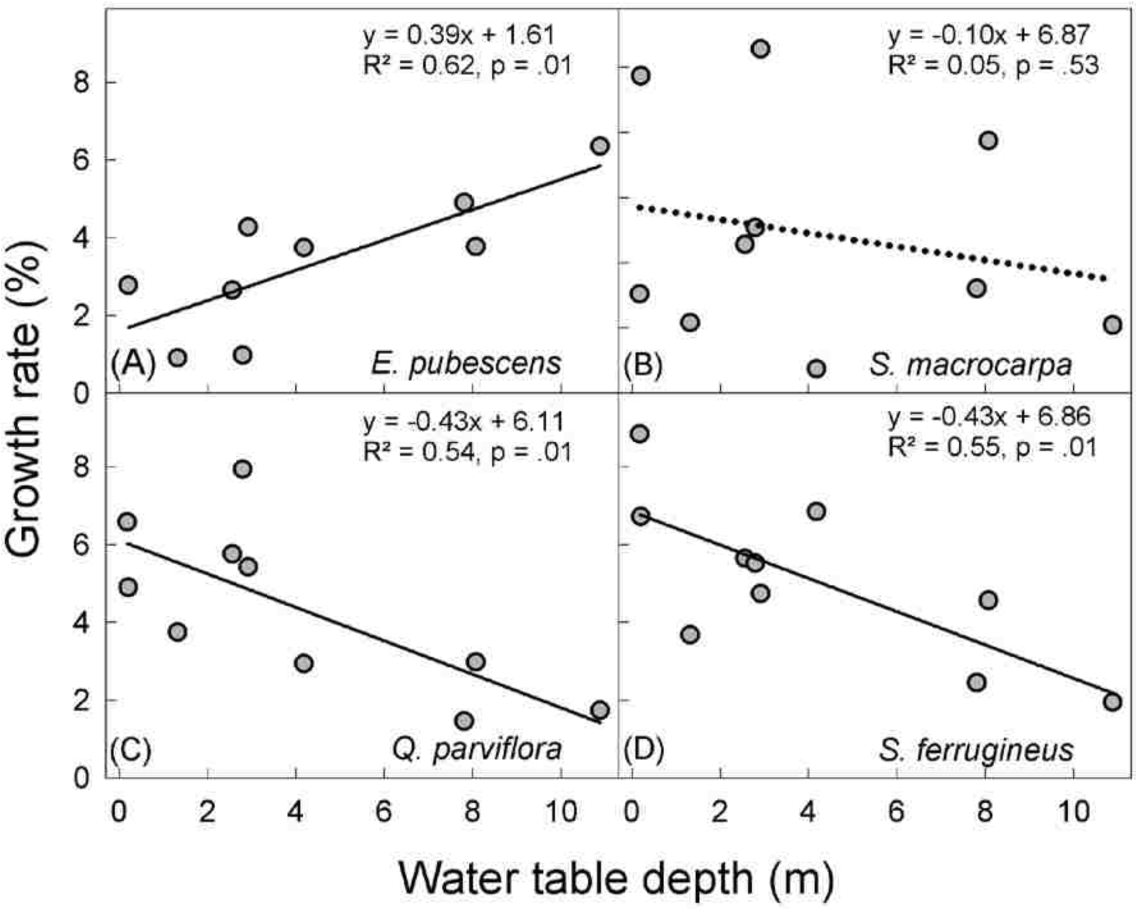

Figure 3.9. Relationship between growth rate of different cerrado tree species and minimum water table depth. The relationships were statistically significant for *E. pubescences*, *Q. parviflora* and *S. ferrugineous*.

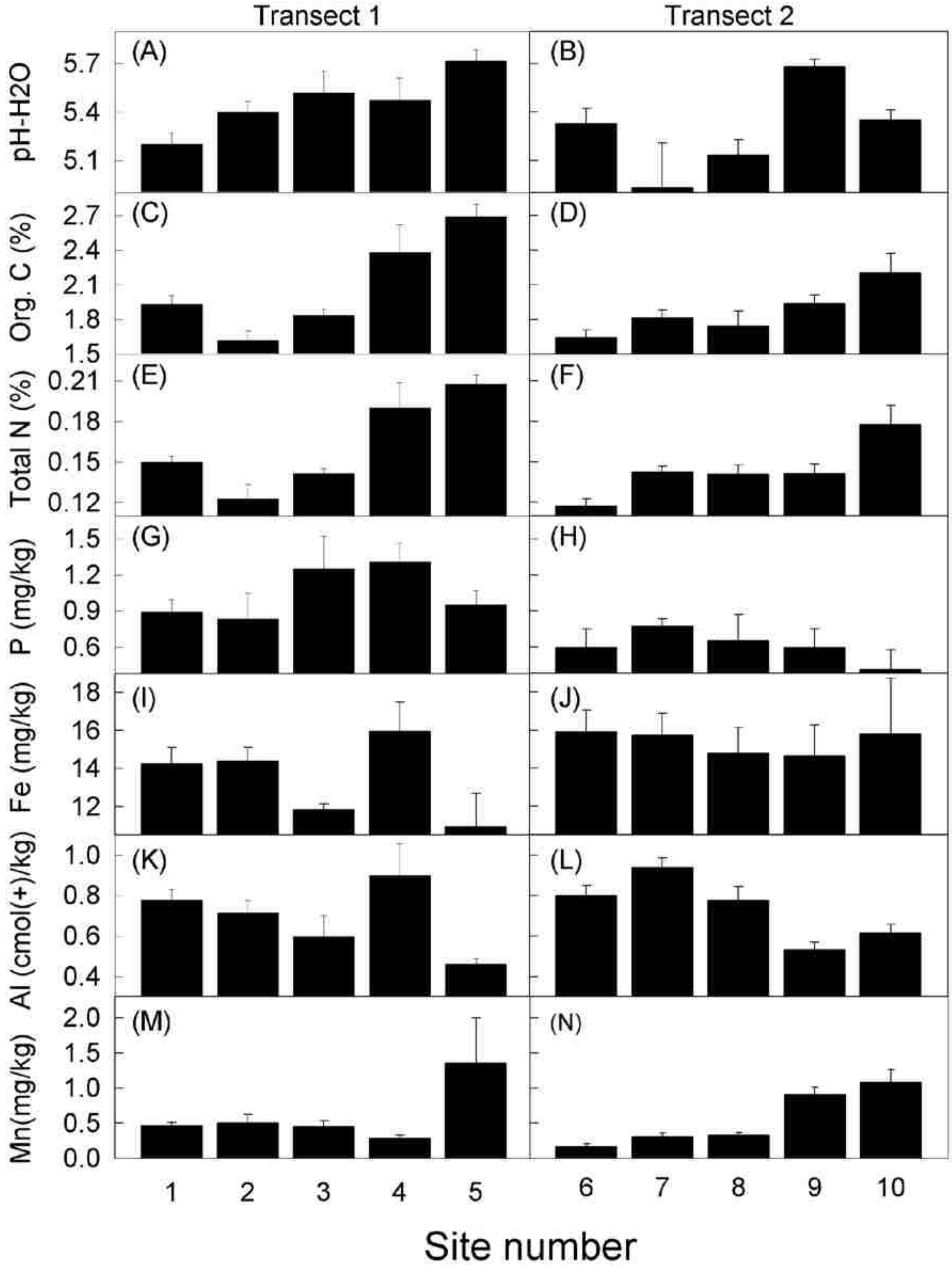

Figure 3.10. Average nutrient concentrations and pH in the upper 50 cm of soil at each site along transects 1 and 2.

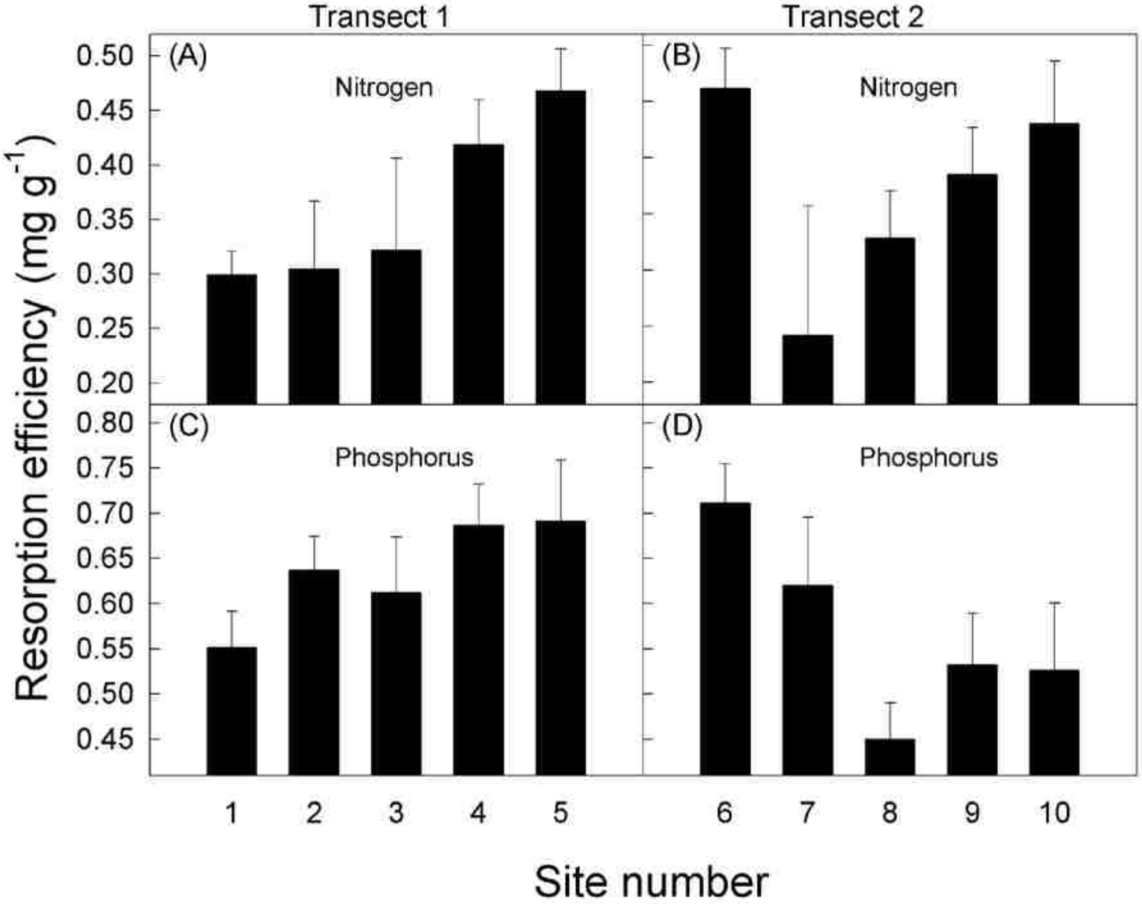

Figure 3.11. Nitrogen and P resoprtion efficiency in *Qualea parviflora* trees growing along transects 1 and 2.

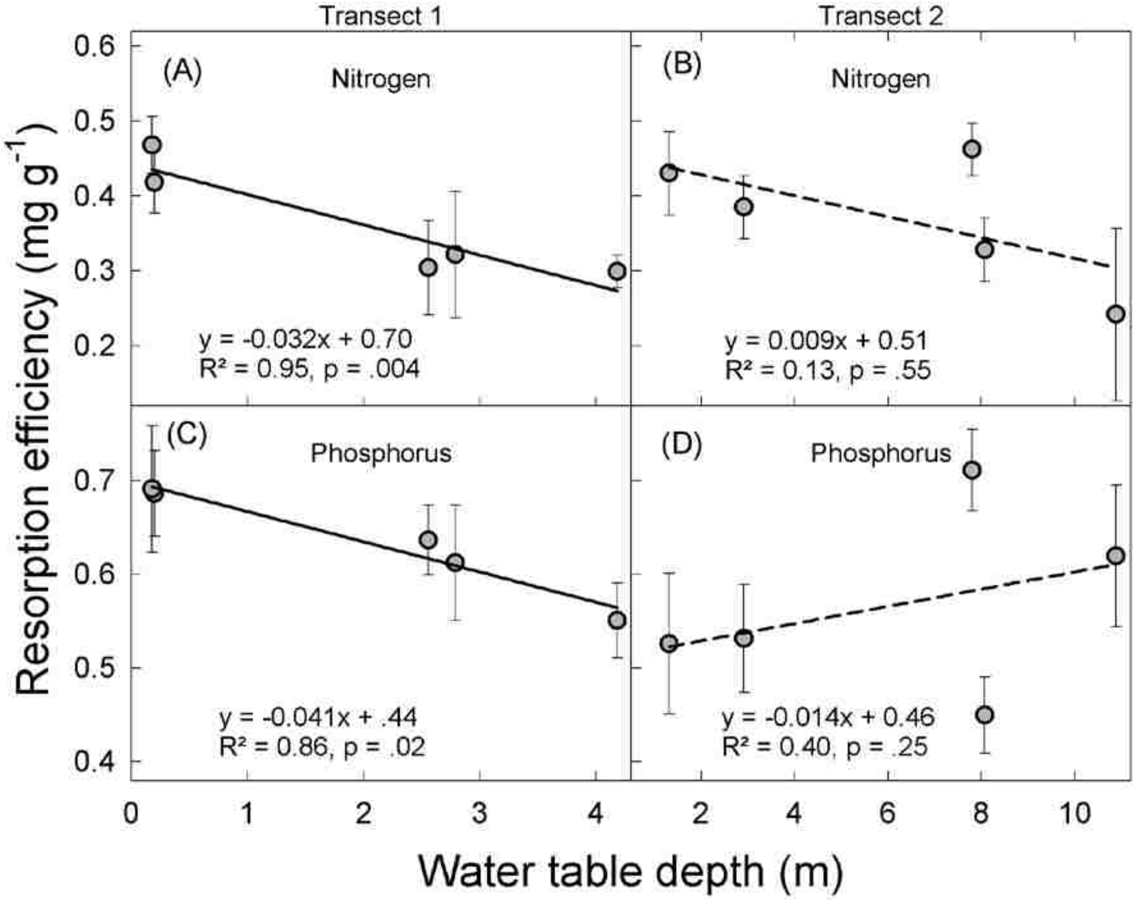

Figure 3.12. Resorption efficiency versus minimum water table depth in *Qualea parviflora* trees growing along transects 1 and 2.

Chapter 4

Water table dynamics in a heterogeneous wetland: diurnal and seasonal fluctuations in relation to rainfall, transpiration and evaporation

Summary

The Everglades, one of the largest wetlands in North America, is a slow-moving system of rivers, flowing at about 0.40 km per day. The water table in the Everglades fluctuates diurnally and seasonally close to the soil surface. Some parts of the wetlands remain underwater for most of the year but Hardwood Hammock forests are rarely flooded, even though the water table can get as close as 40 cm to the soil surface in some areas during the rainy season and may drop nearly to 2 m during the dry season. Seasonal and diurnal changes in water table depth were monitored for 2 years with barometric pressure corrected transducers located in wells, one inside a Hammock forest and one in an adjacent small lake. Another pressure transducer was located in a stand dominated by an exotic-invasive woody species (*Schinus terebinthifolius* and *Ardisia elliptica*) nearby the studied Hammock Site. Sap flow was measured during a few consecutive days in several individuals of the most common species in the Hammock forest and in the exotic dominated stand (*Schinus* site). Daily average sap flows per tree, sapwood cross-sectional area and stem diameter of all trees in each site were used to scale up tree water utilization to stand level transpiration. We decomposed time series of water table depth data (six consecutive days during rainless periods) using time series analysis to separate

seasonal trends from diurnal fluctuations. Diurnal fluctuations in water table levels were relatively larger in the wet season, when the water table was close to the soil surface, than in the dry season, when water table levels were at a substantially far from the soil surface. The total quantity of groundwater withdrawn by evapotranspiration per day was calculated for the Hammocks and *Schinus* sites during the wet and dry seasons. Sap flow and groundwater estimates of stand level transpiration agreed within 40 to 70% in the Hammock forest and only within 13 to 18% for the *Schinus* site. This study shows that fluctuations in water table depth can be used as a surrogate of stand level transpiration rates, particularly during the dry season when groundwater is the main source of water for trees. Lateral movement of groundwater along vegetation stands and the surrounding open bodies of water (e.g. lakes), however, may affect evapotranspiration estimates. Heterogeneity of the landscape, stand size and resistance to lateral water flow are some of the factors that should be taken into account when diurnal fluctuations in water table depth are used to estimate stand level evapotranspiration.

Background

Evapotranspiration is the main pathway of water input from terrestrial and wetland ecosystems into the atmosphere. Evapotranspiration estimates in wetland ecosystems are particularly challenging because of their transitional nature between terrestrial and aquatic systems. One of the main determinants of ecological and hydrological process in wetlands is the presence of a shallow groundwater. Groundwater commonly refers to the subsurface water that fully saturates pores or cracks in soils and rocks. Groundwater in wetlands is replenished by precipitation and soil infiltration as well as by laterally moving water.

The Everglades, one of the largest wetlands in North America, is a slow-moving system of rivers flowing southwest into the Atlantic and the Gulf of Mexico at about 0.40 km per day. The flat topography and low elevation of the Everglades results in a laterally-dominated flow system and a shallow water table. The water table is the level at which the groundwater pressure is equal to atmospheric pressure and can be visualized as the surface of the groundwater. Large portions of the landscape in the Everglades are under water during the rainy season, but as the dry season advances, high areas start drying out as the water retreats to lower sites. A variety of plant physiognomies can be found in the Everglades depending mostly on very small changes in elevation. Examples of these physiognomies are cypress, mangrove forests, pinelands, hardwood hammocks, and marshes that differ by few centimeters in elevation (White 1994; Wetzel et al., 2005). The hardwood Hammocks, patches of semi-deciduous broad-leaf forest containing a mixture of tropical and temperate trees, always remain above the groundwater but have a water table very close the soil surface during the rainy season (20 to 40 cm deep). The water table in the Hammock forest can drop to two or three meters below the soil surface during the driest period of the year. The soils in Hardwood Hammocks, underlain by limestone rocks, are only about 10-30 cm on average (Saha et al., 2009). Underneath the root net and organic layer, there is a substrate of calcareous material or limestone. These calcareous rocks are porous and contain internal channels and fractures that can be used by roots to penetrate and access the groundwater during the dry season. Little is known about Hammock trees water sources and how these may change with water levels throughout the year (but see Saha et al., 2009; 2010). This information is important for understanding patterns of water uptake and the hydrological balance of the hardwood Hammocks.

Ewe et al. (1999) pointed out the importance of understanding patterns of water uptake by different native plant communities (e.g. Hammocks and Pinelands), and its relevance to the fate of those communities in response to management plans involving drainage or rehydration of the Everglades ecosystem. However, understanding patterns of water uptake by invasive plant communities is as important as understanding patterns of water uptake by the natural communities. Invasion by non-native plant species is a well known problem throughout south Florida and it is particularly relevant in preserved natural areas, where large extents of land are completely covered by *Melaleuca quinquenervia* (Cav.) S.T. Blake (paper-bark tree) and *Schinus terebinthifolius* Raddi (Brazilian-pepper). These two species are highly invasive, representing a serious challenge for eradication purposes and management of natural areas. Knowing patterns of water uptake and water use of this exotic species and their effects on local hydrological processes, in relation to natural plant communities, is important for management and conservation.

The great heterogeneity of the Everglades (e.g. lakes, swamps and different vegetation types including invasive species) and the lateral movement of surface water and groundwater may affect estimates of upward vertical fluxes of water vapor (transpiration and evaporation). While evapotranspiration estimates for the Everglades have been obtained using mathematical models and through lysimeters in the field

(Abtew 1996; 2005) and by Bowen ratio and eddy covariance methods (German 2000), there have been no field based estimates in woody vegetation in the Everglades. Indeed there is a paucity of studies on woody vegetation evapotranspiration in wetlands, in general. Consequently, methods to estimate evapotranspiration based on diurnal water table fluctuations and methods based on individual trees sap flow measurements were compared. Estimates of total stand level transpiration based on measurements of sap flux density (J_S) of individual trees are potentially influenced by baseline errors in J_S measurements, systematic spatial variation in J_S within stems and a lag between water uptake and transpiration caused by stem capacitance (stem water storage) (Ewers and Oren 2000; Meinzer et al., 2003). The scaling up of sap flow measurements from individual trees to the stand can be straightforward as long as most of the trees are included in the measurements. Fluctuations in the groundwater level have also been used to estimate total evapotranspiration which includes transpiration by trees. This approach may overcome the problem of scaling up water utilization from individual trees to whole stands because changes in groundwater levels represent an integration of the ground water utilization by all individual trees in a particular stand. White (1932) developed a method based on diurnal water table fluctuations to estimate evapotranspiration from shallow unconfined aquifers. One of the potential problems of this method, however, is the magnitude of the diurnal changes in groundwater level fluctuations, in particular, when they are too small.

The objectives of this study were 1) to compare stand evapotranspiration estimates based on individual tree sap flow and on diurnal oscillations in the water table, 2) to examine if the diurnal oscillations in water table depth in a Hammock forest are determined by transpiration water loss, 3) to determine to what extent the tree species in Hammock forests are using underground water during the wet and dry seasons, and 4) to compare groundwater utilization between a Hammock Forest and an adjacent stand dominated by *Schinus terebinthifolius*, an invasive species. In addition, water level variation in an adjacent lake was monitored to determine potential driving forces of groundwater recharge in both the Hammock and the *Schinus* sites.

Materials and Methods

Site description and species studied

Field work was performed at the Everglades National Park, near the south entrance of the Park in Homestead (lat 25°23’ 09”, long 80° 37’ 20”), Florida, U.S.A. This area is located on the Miami Rock Ridge, part of the Atlantic coastal ridge, which is a mid-Pleistocene marine limestone deposit along the SE coast of Florida. The Everglades National Park is characterized by hot, wet summers and warm, dry winters, with lowest average monthly temperature of 12°C. About 80% of the rainfall occurs from May to October and the mean annual temperature is about 27 °C. Mean annual rainfall is 1470 mm, although this amount can vary widely when hurricanes impact the region.

The study area comprises a mosaic of vegetation types (Fig. 4.1) with a Hammock Forest stand (Hammock site), which has a pineland to the northwest, a large area dominated by *Schinus terebinthifolius* (Anacardiaceae) to the south and southwest, and a seasonally flooded sawgrass area to the east and northeast. The invasive forest stand

(*Schinus* site) is located in an old abandoned agricultural land. There is also a lake (Hidden Lake) to the southeast next to the Hammock and a couple of small ponds inside the forest. Fifteen plots of 20 x 20 meter were randomly established in two areas parallel to a dirt road that crosses the Hammock forest and six additional 10 x 10 m plots were randomly established at the adjacent *Schinus* site. An inventory of all woody species within each plot with diameters larger than five centimeters (at 30 cm above the ground) was conducted in both sites.

Monitoring diurnal water table levels

To monitor diurnal and seasonal changes of water table depth as well as seasonal and diurnal changes of water level, four wells were drilled in the study area including the Hidden Lake. One well was drilled in the Hammock site, the second in the *Schinus* site and the third well was located in the Hidden Lake to monitor water levels. A fourth well was drilled in the Hammock site to measure local atmospheric pressure variation (barometric pressure). Barometric pressure was used to correct water table measurements.

Wells were made using a portable perforating machine that extracts limestone cores of approximately 11 centimeters in diameter. PVC pipes (6 cm in diameter) were placed inside each well and each pipe was capped at the bottom and sawed slots were made in the tube walls to allow water movement across the well. Once the pipes were installed, small quartz material was placed around the sawed slots section up to the soil surface. Perforations were made in April (2004) when the water table depth was lowest.

Automatic pressure recording piezometers (Barologgers, Solinst Ltd, Canada) were placed in each well to monitor water levels. Water level was recorded every 10 minutes and data were retrieved every month.

Evapotranspiration using diurnal patters of water table

The method developed by White (1932) was used to estimate the total quantity of ground water withdrawn by evapotranspiration during a day. The total ground water discharge during a 24-h period was calculated as

$$Q_{ET}= S_y(24h \pm s) \tag{4.1}$$

where Q_{ET} is the total ground water discharge or evapotranspiration, S_y is the specific yield near the water table, h is the hourly rate of rise of the water table from midnight to 8:00 AM (when evapotranspiration was negligible), and s is the net fall or rise of the water table during the 24h-period. Specific yield is the volume of water release per unit water table fluctuation (Nachabe 2002). We have used an average specific yield obtained from studies done in the limestone outcrops of the Everglades (Bolter et al. 2001).

The primary assumptions of the White (1932) method are (1) ET is negligible during the nighttime period, (2) the rate of water table increase (h) remains constant throughout the day, (3) the decrease of water level is mainly due to the water uptake by plants and by evaporation from the soil surface, (4) that the incoming and outgoing lateral water movement remain constant throughout the day, and (5) the water table is always below the ground surface during the study period.

Transpiration using the heat dissipation method

Whole-plant sap flow was measured in 32 trees during several consecutive days using the heat dissipation method (Granier 1985; 1987). Three to five individuals of the most common species were monitored at each time. Whole-plant sap flow in the *Schinus* site was measured in only16 trees, and because of its low tree diversity only two species were monitored (*S. terebinthifolius* and *Lysiloma latisiliquum* Benth.). Briefly, a pair of 20 mm long, 2 mm diameter probes was inserted into the sapwood in the main stem of each tree. The upper (downstream) probe contains a copper-constantan thermocouple and a heating element of constantan, which is continuously heated at a constant power by the Joule effect, the unheated upstream probe serves as a temperature reference. Temperature differences between the upstream and downstream probes were measure every 60 s, and 10 min averages were recorded with a data loggers (CR 10X, Campbell Scientific).

Sap flux density was calculated from the temperature difference between the two probes using the empirical calibration developed by Granier (1985; 1987) and re-validated by (Clearwater et al., 1999). Mass flow of sap per individual was obtained by multiplying flux density by sapwood cross-sectional area. The relationship between sapwood cross-sectional area and stem diameter was obtained by injecting dye on the main stem of several individuals of most common species representing a wide range of diameters. After two hours, a core was obtained using an increment borer right above the dye injection point. The area of conducting tissue was determined from the pattern of staining as the dye moves along the transpiration stream.

Mass flow of sap per individual was scaled to obtain tree transpiration at the stand level (E, mm day $^{-1}$) according to the following equation (Bucci et al., 2008):

$$\mathrm{E} = \left(\frac{F}{BA_i}\right) BA_T \tag{4.2}$$

where F is the average daily sap flow per tree (kg day^{-1}) obtained from at least 3 to 4 days of measurements per month, BA_i is the mean basal area per tree (cm^2), and BA_T is the total basal area per unit of ground (cm^2 m^{-2}).

Data analyses

Because the diurnal fluctuations of the water table were relatively small, time series analysis of the water level data was necessary to unveil the diurnal changes and to remove noise due to measurement errors and to environmental changes that are not driven by water uptake from plants. Time series analysis was used to decompose time series of six days (six days of raw water table data) into three components: diurnal fluctuations, the overall trend and the remainder. Only six day periods without sudden fluctuations in water level, (due to important rainfall events or the opening and closing of canal gates) were chosen for the analysis to meet the assumption of constant incoming and outgoing water flow. After the time series analysis was performed, a moving average was fitted to the diurnal component of the analysis to better visualize the diurnal water table fluctuations. Both the time series analyses and the moving average were carried out with R, version 2.6.2 “ts” library in package stats (R Development Core Team 2008). A previous analysis had been done to determine the number of days that each time series should contain. Using several days (e.g. 12 days) the magnitude of diurnal variations were too small and oversimplified. Using only a few days (e.g. 3 days) resulted in too much noise, reflecting fluctuations in environmental factors, and too few values as required by the model to find distinct diurnal patterns. The best solution for tackling the tradeoff between oversimplifications and too much detail was solved by using 6 days periods and by selecting only periods without substantial changes in trend (e.g. rainless).

Results

Species composition and relative abundance

In the Hammock site we found a total of 19 trees species but the six most abundant species were selected for the sap flow study: *Bursera simaruba* (Burseraceae)*, Metopium toxiferum* (Anacardiaceae)*, Nectandra coriacea* (Lauraceae)*, Dipholis salicifolia* (Sapotaceae)*, Simaruba glauca* (Simaroubaceae) *and Coccoloba diversifolia* (Polygonaceae) (Fig. 4.2A). In the invasive dominated forest, only 7 species were found; *Schinus terebinthifolius*, *Ardisia elliptica*, *Lysiloma latisiliquum*, *Myrsine floridana*, *Coccoloba diversifolia* and *Ilex krugiana*. In the Hammock forest, four dominant tree species make up 60% of all individuals, and in the invasive dominated forest, *S. terebinthifolius* makes up 80% of all trees (Fig. 4. 2B).

In the Hammock site there was a total of 2223 trees per hectare, total basal area per unit of ground (BAt) was 37.8 cm^2 m-^{2} and the mean basal area per tree (BAi) was 170.0 cm^2. In the *Schinus* site there was a total of 1183 trees per hectare, BAt was 23.7 cm^2 m^{-2} and BAi was 200.6 cm^2.

Seasonal and diurnal changes in water table depth

Seasonal changes in water level depth were mostly determined by the precipitation regime (Figs. 4.3A and B). Water level decreased at the end of the wet season between October and November, for each of the three years shown in Figure 4.3B. The lowest level was observed in May at the end of the dry season.

The water table level steadily decreased during rainless periods in the Hammock forest stand (Fig. 4.4 A, C and E). The rate of water table decline was about 6 cm per day in May and March (dry season) and about 8 cm per day in October (wet season). Water table depths were different for each period: Water table depth was 189 to 194 cm during the dry season (May) and only 36 to 44 cm during the wet season (October). The depth was intermediate for March (76 to 82 cm below the soil surface). Diurnal patterns of water table variations and moving averages for each study period can be seen in Figure 4.4 (B, D, and F). Only one day of diurnal variations are shown for each time series in Figure 4.4 because time series analysis predicts the average diurnal fluctuations for the six day period. Water levels increased shortly before midnight until about 11AM. During midday and afternoon periods, the water levels decreased. The daily oscillation of the water table for the dry season was 0.4 cm (Fig. 4.4B). During the peak of the wet season, diurnal fluctuations of the water table were larger than those observed during the dry season (Fig. 4.4 F). Maximum diurnal oscillation of the water table for the wet season was 1.2 cm, but the pattern of variation was similar than the one observed during the dry season; water level increased before midnight until about 10:00 AM to 11:00 AM followed by a sharp decreased (Fig. 4.4 F). The magnitude of the daily oscillations during March was intermediate between wet and dry seasons (Fig. 4. 4 D).

Similar trends and in diurnal patters of water table fluctuations were observed at the *Schinus* site (Fig. 4.5). The maximum diurnal oscillation of the water table was about 0.8 cm during the wet season but only 0.4 cm during the dry season peak with an intermediate oscillation during March. The maximum diurnal oscillation of the water table during the dry season was not as large in the *Schinus* site compared to the Hammock site. Seasonal trends during the 6 day period were also similar to the seasonal trends of the water table in the Hammock forest.

Scaling up: estimates of evapotranspiration

Figure 4.6 depicts diurnal fluctuation of the water table in the Hammock forest during the dry and wet seasons (Fig. 4.6 A, B respectively) and in the invasive dominated forest stand during the dry and wet seasons (Fig. 4.6 C, D respectively). The dashed line is the predicted water table recharge calculated using the water table rise during the nighttime period. It was obtained by fitting a linear relationship to the water table diurnal fluctuation from midnight to 8 AM (negligible transpiration according to the sap flow studies with individual trees). In both sites, the rate of water table recharge was higher (steeper slope) in the wet season than in the dry season.

Examples of diurnal variations in sap flow of selected species are shown in Figure 4.7 during the end of the wet season (Nov. 2006) and during the end of the dry season (May 2006) when water levels where high and low, respectively. Nighttime transpiration was negligible for all species in both seasons. Some trees exhibited higher rates of sap flow during the dry season (May 2006) while others exhibited higher rates of sap flow during the wet season (November 2006).

Evapotranspiration estimates at the stand level using sap flow from individual trees and diurnal fluctuations in the groundwater (White method) are summarized in Table 4.1. Sap flow and White methods agree better for the Hammock Site than for the *Schinus* site where sap flow estimates were 5 to 7 times smaller. The White method predicted relatively low stand evapotranspiration values (about 3 mm day^{-1}) during the dry season (May), and higher evapotranspiration values (about 4.8 mm day^{-1}) during the wet season (October). The White method predicted similar evapotranspiration for the *Schinus* site (higher values in the wet season compared to the dry season) (Table 4.1).

Figure 4.8 depicts daily water table level fluctuations in the Hammock site, *Schinus* site, and Hidden Lake during dry and wet seasons (Fig. 4.8 A and B respectively). Water table in the Hammock and *Schinus* sites exhibited a synchronized fluctuation pattern during the dry season (Fig. 4.3A). Water table level in both sites decreased around 10AM and the recharge started at 7PM. The water level of the lake followed a similar fluctuation pattern but it was not synchronized with the water table depth fluctuations in Hammock and *Schinus* sites; there was a lag of approximately 3 hours for both discharge and recharge. During the wet season there was more asynchrony among the Hammock Site, the *Schinus* site and the lake (Fig. 4.8B). The water table depth for Hammock and *Schinus* sites decreased at the same time, between 10AM and 11AM. The water table in the *Schinus* site reached its lowest level approximately 3 hours later than the Hammock site, and at this point both sites and the lake began to recharge, but the water table at the Hammock increased faster than that of the *Schinus* site and the lake. Water level at the lake reached a minimum value around 6PM and remained fairly constant for about 4 hours. In general, the amplitude of water table fluctuations was larger during the wet season than in the dry season.

Discussion

Water table fluctuations and tree water uptake

Diurnal oscillations in water table depth were partially determined by transpiration water loss. The water table level exhibited diurnal fluctuations in Hammock and *Schinus* sites decreasing at midmorning (consistent with water utilization by plants and evaporation from the soil surface) and increasing at night, first slowly and then fast after midnight. Water table increase was the result of water table recharge from the slow lateral moving water. The water table depth was one of the determinants of the magnitude in diurnal fluctuations of the groundwater. When the water table was relatively far from the ground surface, the magnitude of water table fluctuations in the Hammock and *Schinus* sites were similar but smaller in the dry than in the wet season. When the water table was close to the soil surface, the magnitude of the fluctuations was large for both vegetation types, but it was even larger for the Hammock site than for the Schinus site. These findings suggest consumption of underground water by trees during both the dry and wet seasons, and also the existence of local patters of lateral flow driven by differences in water consumption among vegetation types (Hammock versus *Schinus* sites).

Our findings partially agree with a recent study of water source utilization in hardwood hammocks of the Everglades using the natural abundance of ^{18}O from the soil water, the groundwater, and the tree stem sapwood (Saha et al., 2009). The authors concluded that hammock trees in the wet season relied on soil water, while in the dry season they relied on groundwater. It is quite possible that during the dry season nearly all the water transpired by trees was derived from the groundwater. It is not known if during the dry season deep roots that tap groundwater during the dry season (low water table) were already there or if they grow as water table depth increases. Saha et al. (2009) suggested that, as water table depth increases, anoxic conditions in the soil decreases, permitting re-growth of roots downwards. Our results indicate, on the other hand, that at least some roots are capable of tolerating anoxic conditions and that deep roots may have been present already at depth. If those deep roots are present but non-active during the wet season, the only requirement to become functional (as the water table goes down) would be to re-grow fine roots, as suggested by Saha et al. (2010). If this is the case, downward root growth may not be necessary for all species as the dry season progresses Rapid root growth to keep up with the rate of falling water table at the onset of the dry season may constrain plant survival because not all roots may find cracks and existing holes in the limestone substrate.

It is commonly accepted that hardwood hammock plants are intolerant to flooding and to the anoxic conditions resulting from water persistence (Snyder et al., 1990), but this may be an oversimplified view of waterlogging tolerance by Hammock trees. In order to understand our results we need to consider the complex nature of the limestone (the substrate where Hardwood Hammocks are established). The limestone is a very heterogeneous multidimensional substrate with fractures, pores and holes of different sizes and depths. Soil and organic material are mostly concentrated in the top 20 cm of the ground surface, but it can also accumulate in small depressions at different depths. The heterogeneity in micro-topography may influence lateral and vertical root distribution. As a consequence, roots are more commonly but not necessarily restricted to the soil surface. Even though we did not conduct a quantitative study of root distribution, all fallen trees in the area (due to the effect frequent hurricanes) show large and shallow root mats (Saha et al., 2010 and personal observation). Some roots may be able to grow deep exploring new sources of water and nutrients whenever they find the right micro site. How deep they would grow will depend on species-specific waterlogging tolerance.

Hammock trees are not as tolerant to flooding as other plant communities located at lower elevations within the Everglades. The lower a plant community is along elevation gradients, the better adapted those plants should be to cope with potential waterlogging and seasonal changes in water table level. The degree of tolerance should vary from species to species and to a lesser degree from individual to individual. Consequently, root depth should also vary according to the waterlogging tolerance capacity of each individual and the availability of micro sites.

Hammock forest could be conceived as systems with a non-uniform root distribution, with high density of roots in the most superficial layers of the profile and low density in the deep layers. This pattern of root distribution agrees with the pattern of nutrient abundance, since soil water has more nutrients than groundwater (Saha et al., 2009). During the dry season deep roots are likely to take advantage of deep, but readily available water. Then when water table level rises (as the rainy season progresses) more roots have access to shallow underground water. Based on the relatively large fluctuations of water table level during the wet season (Fig. 4.4 E and F) we hypothesized the existence of a critical point or threshold of maximum underground water utilization by Hammock trees. This threshold occurred during the highest peak of the wet season, when water table was close to the soil surface, allowing Hammock trees to utilize a greater proportion of underground water without the potential deleterious effects of waterlogging. Furthermore, during the wet season (high water table) stand level transpiration is expected to be higher, because during this season, higher radiation and greater availability of water enhance growth and photosynthesis.

The magnitude of diurnal water table fluctuations from dry to the wet season reflects the degree of water utilization related to the seasonal pattern of precipitation and to the vertical root density gradient. Our findings do not necessarily contradict results from other studies (e.g. Ish-Shalom et al., 1992; Ross et al., 1993; Snyder et al., 1990) showing that during the wet season a large proportion of water uptake is obtained from the top layers of the soil. During the wet season, the Hammock forest stand uses a larger amount of groundwater compared to the dry season (Fig. 4.4). However, the amount of groundwater may be relatively small compared to the amount of groundwater withdrawn from the top layers of the soil profile, where most nutrients and roots are concentrated. In fact, Saha et al. (2009) found that during the wet season plant stem water composition was 60 to 80% rain water and 20 to 40% ground water.

An alternative explanation for the large water table level fluctuation during the wet season is the possibility of an indirect effect of plant water uptake from the soil surface. Plants take water from the vadose zone (also called unsaturated zone), which refers to all the material between the soil surface and the zone of saturation (or phreatic zone). The amount of water in the vadose zone controls the transpiration of the plants. When the water table gets as close to the soil surface as it does in our study area (during the wet season), it is possible to see larger groundwater level fluctuations due to an increase in water uptake from the upper soil layers. Soil moisture always has a close hydraulic connection with the groundwater table through the capillary fringe and also via the active hydraulic gradient created by roots absorbing water. Therefore, it directly and indirectly affects the water balance of the groundwater systems. It has been shown that moisture extraction from the vadose zone can depress the groundwater table due to a reverse hydraulic gradient (Gribovski et al., 2008). When the capillary fringe extends to the ground surface or just below, direct evaporation from the water table can produce similar diurnal patterns (White 1932).

Patterns of lateral flow and hydrological feedbacks

During the wet season, the diurnal fluctuations of the lake's water level (Fig. 4.8B) paralleled those of the water table depth in both the Hammock and *Schinus* sites; however there was a lag in the morning with the water table level in the Hammock site decreasing a few hours before and deeper than the water table in the *Schinus* site and the lake's water level. When the water table decreases, a hydraulic head is created, developing a driving force that allows the water, mainly from the lake, to move laterally into Hammock and then to *Schinus* site. Feedbacks between different landscape units also have implications related to changes in land use due to agriculture or by invasion of exotic species. These feedbacks are not as strong during the dry season (Fig. 4.8A), and that may be due to an increase in resistance to lateral flow when the water level is very low. In fact, Nachabe (2002) suggested that specific yield of shallow water table environments cannot be constant but should vary with depth.

The rapid increase of water table level in both vegetation types after midnight (Figs. 4.8A and B) coincided with the rapid increase in the level of the lake. The recharge occurred when trees were no longer transpiring. The lateral movement of water between different vegetation units or between the surrounding small lakes and the vegetation may affect ET estimates. It is not known how important this effect is on ET estimates for a particular vegetation stand but the more homogeneous the landscape is and the larger the size of the vegetated sites are, the better the ET estimates should be. Heterogeneity of the landscape, stand size and resistance to lateral water flow are some of the factors that should be taken into account when using White's method to estimate stand level evapotranspiration.

Evapotranspiration estimates

Our ET estimates with White's method for both the Hammock and the *Schinus* sites ranged from 2.86 to 5.48 mm per day. This range is within the range measured using a variety of techniques in different places. For example, Nachabe et al. (2005) measured 1.5 to 6.3 mm day^{-1} for a low-lying forest in central Florida (very close to our estimates). Hill and Neary (2007) on the other hand, obtained what they considered high estimates for wetlands (from 4.1 to 18.8 mm day^{-1}) using water level fluctuations in sinkholes. For a stand with trees, shrubs and grasses, Bauer et al. (2004) calculated an ET's of 0.06 to 4.3 mm day^{-1}, and Butler et al. (2007) found 2.9 to 9.3 mm day^{-1} (also for mix vegetation), which is within the ranges observed by Goodrich et al. (2000) (4 to 8 mm day^{-1}). Gribovszki et al. (2008) reported 3.2 to 10.5 mm day^{-1} and Lautz (2008) 0.5 to 4.6 mm day^{-1}, both for riparian zones. Gazal et al. (2006) found ET's from 2 to 7 mm day^{-1} for a semiarid cottonwood forest, while Hughes et al. (2001) observed ET's ranging from 2 to 6 mm day^{-1} for a temperate salt marsh.

Estimates of stand level transpiration using the sap flow measurements (heat dissipation method) and diurnal fluctuations of the water table level (White method) did agree within 40 to 70% for the Hammock forest and only 13 to 18% for the *Schinus* site. It is possible that estimates of water consumption using the White method overestimates evapotranspiration for the *Shinus* site. The distance of the well located in the *Schinus* site is approximately 100 meters form the *Schinus*-Hammock border. The interactions and feedbacks observed among the Hidden Lake, Hammock and *Schinus* sites (Fig. 4.8) indicate the presence of a continuous water table and low resistance to lateral flow, which makes possible that water consumption by Hammock trees affects water table fluctuations in nearby areas. Low estimates of transpiration in *Schinus* Site are consistent with the lower number of trees per unit area in the *Schinus* site (1183 trees ha^{-1}) versus the Hammock site (2223 trees ha^{-1}) and with the total basal area per unit of ground 37.8 cm^{2} m^{-2} and 23.7 cm^{2} m^{-2} for Hammock and *Schinus* sites, respectively.

In order to validate our calculations of stand level transpiration with sap flow measurements we used an alternative scaling up method, fitting a linear relationship between sap flow data and basal area per tree (of all trees measured). With this method, if the correlation coefficient of the relationship is high, the basal area can be considered a good predictor of sap flow per tree, regardless of species identity. Stand transpiration for each site was then obtained by multiplying the basal area of each tree per site times the predicted sap flow using the linear scaling relationship, and then summing all sap flows. Our estimates using this alternative method were almost identical to those obtained with equation 4.2. For example, for the same 6 days period in May 2006 we estimated 2.19 mm day^{-1} using equation 4.2 and 2.03 mm day^{-1} using a linear relationship between sap flow and basal area per tree. The heat dissipation method is an energy and time consuming method that requires frequent visits to the study site to keep the system working properly. The White method represents a reliable alternative to estimate stand level transpiration that is easier to operate.

This study shows that groundwater estimates of water utilization in the Everglades can be used as a surrogate of stand level transpiration rates, particularly during the dry season when groundwater is the main source of water for trees. Heterogeneity of the landscape, stand size and resistance to lateral water flow are some of the factors that should be taken into account when diurnal variations in groundwater are used to estimate stand level evapotranspiration. Since water flowing in the Everglades is artificially managed by canals and gates, it is important to choose data sets for periods without sudden changes in water level. This will also prevent the violation of the White method assumption of constant incoming and outgoing lateral water movement, which could be also violated by important rainy events.

Conclusions

This study shows that: (1) groundwater is used by hammocks and Schinus vegetation in both wet and dry season. (2) The amount of water withdrawn from the groundwater was larger during the wet season than during the dry season, which is consistent with the root distribution pattern of trees as well as the greater photosynthesis due to high radiation in wet season (the season for growth and biomass accumulation). (3) Diurnal oscillations of the water table depth reflect patterns of water loss due to tree transpiration. The water table decreased following the increase in transpiration (sap flow) by trees and increase later in the evening following a decrease in transpiration. (4) Since a fraction of the root system access the water table during both the wet and dry seasons, it is possible that roots of at least some species can tolerate anoxic conditions to some degree. (5) In both study sites, the White method for assessing stand level transpiration can be used as a surrogate for water uptake and whole forest evapotranspiration, particularly during the dry season, when underground water is the main water source for the woody plants. Care should be taken, however, when the size of the stand is relatively small. (6) The agreement between sap flow and White methods was adequate for the Hammock site but the agreement was not adequate for the *Schinus* site. A better agreement between these two methods would be possible if most of the stems sap flow were monitored and included in the scaling up estimates. (7) There are hydrological feedbacks between different vegetation types and nearby bodies of water, with the potential of influencing the overall regional ecosystem dynamics. Changes in land use either by conversion into agriculture of by the invasion of exotic species have the potential of altering regional ecosystem dynamics.

Table 4.1. Daily evapotranspiration and transpiration estimates for the Hammock site and for the *Schinus* site in mm day^{-1} during the dry season (May), wet season (October) and transition wet-dry season (February/March). Evapotranspiration and transpiration were calculated for different periods using White and heat dissipation methods respectively.

Site	**Month**	**White's method Evapotranspiration (mm day^{-1})**	**Heat dissipation method Transpiration (mm day^{-1})**
Hammock	May	3.04	2.19
	February/March	4.21	1.87
	October	4.83	2.08
Schinus	May	2.86	0.53
	February/March	3.62	0.48
	October	5.48	**no data**

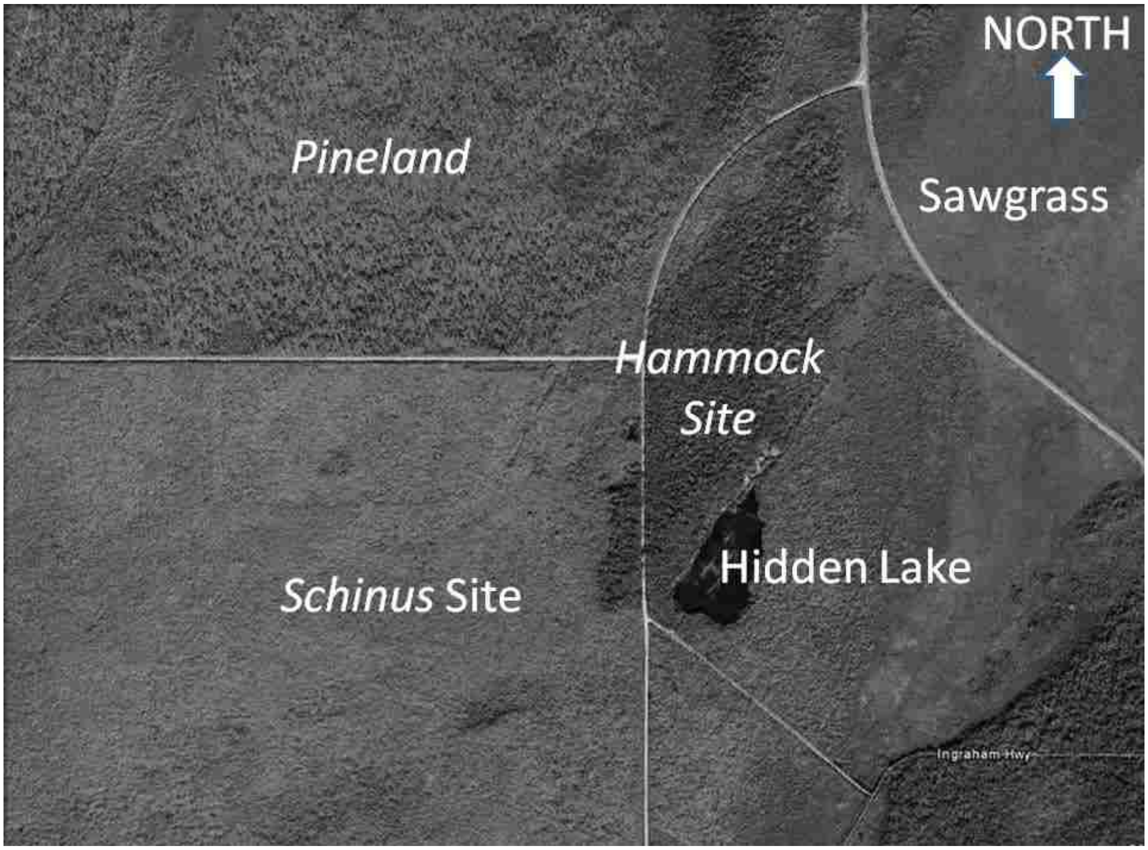

Figure 4.1. Study area and location of different vegetation types, including Hammock, *Schinus* sites and Hidden Lake at The Everglades National Park, Homestead, Florida, U.S.A.

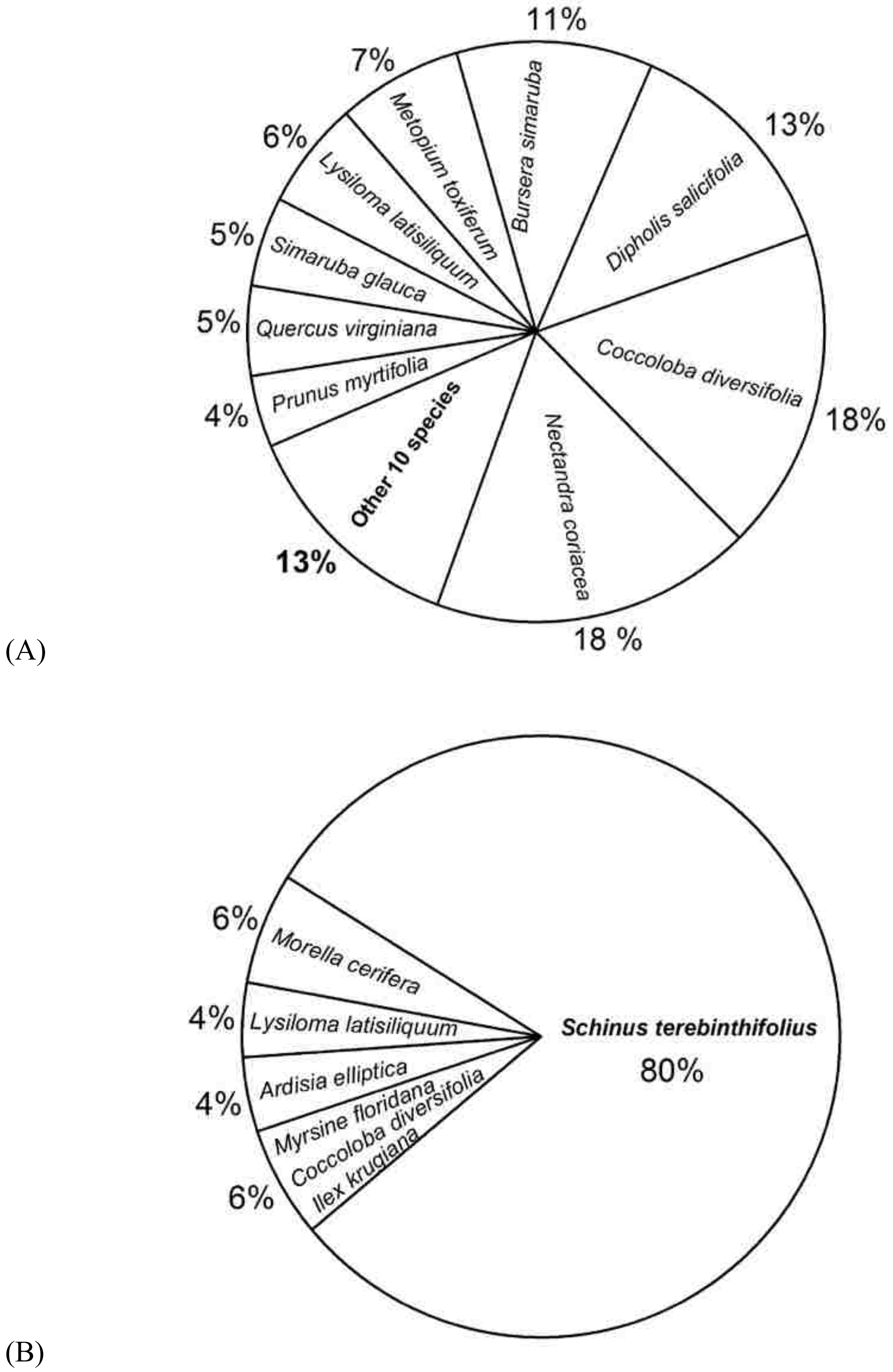

Figure 4. 2. Relative abundance (%) of the dominant species in the Hammock site (A) and *Schinus* site (B). Results were obtained from a complete inventory of trees with diameters larger than 5 cm at 50 cm height.

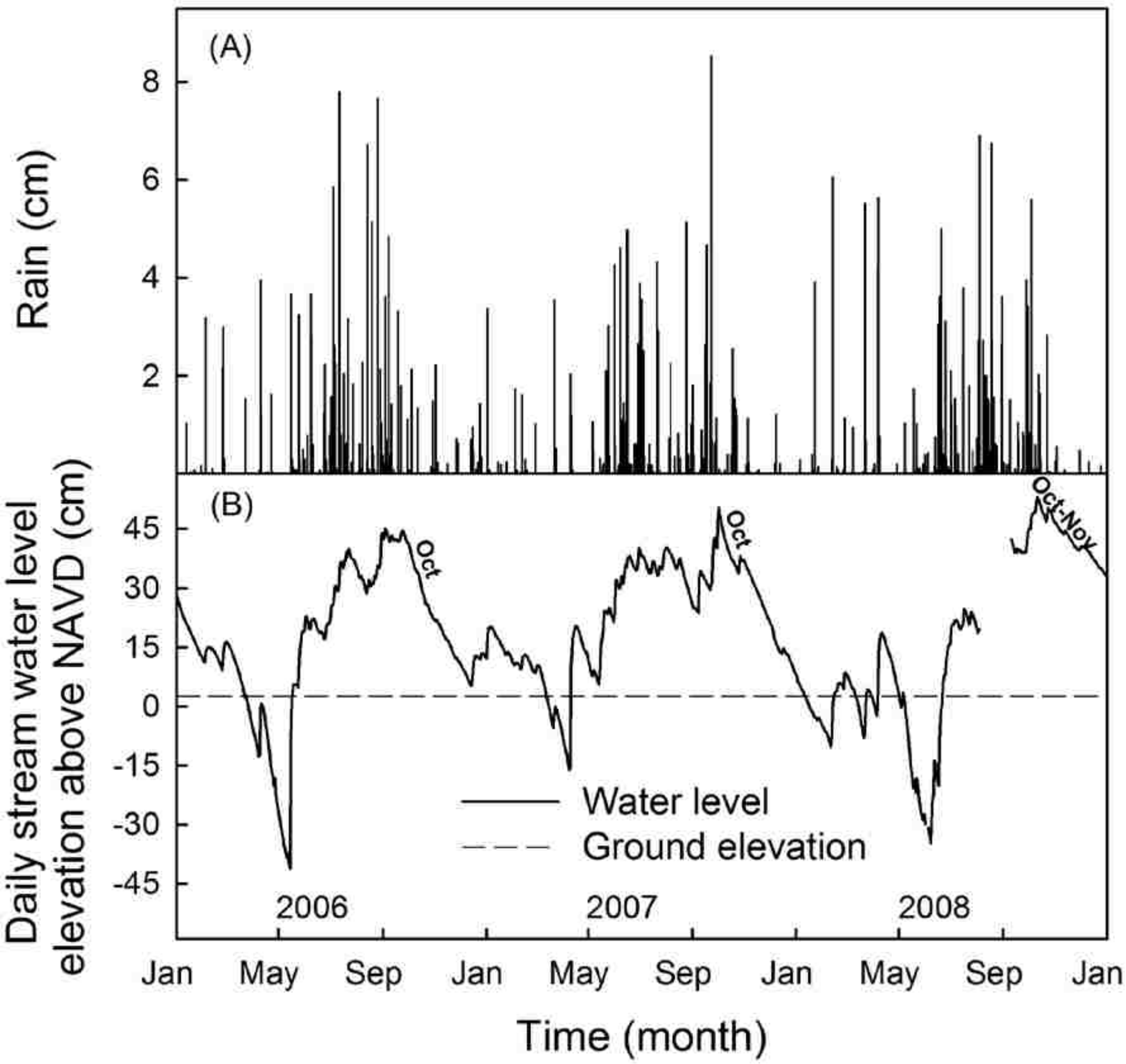

Figure 4.3. Daily precipitation (A) and water level elevation in centimeters above North American Vertical Datum (NAVD 1998) (B) at site R127 ENP close to the study site (lat 25°21'11"N, long 80°36'22") (www.usgs.gov).

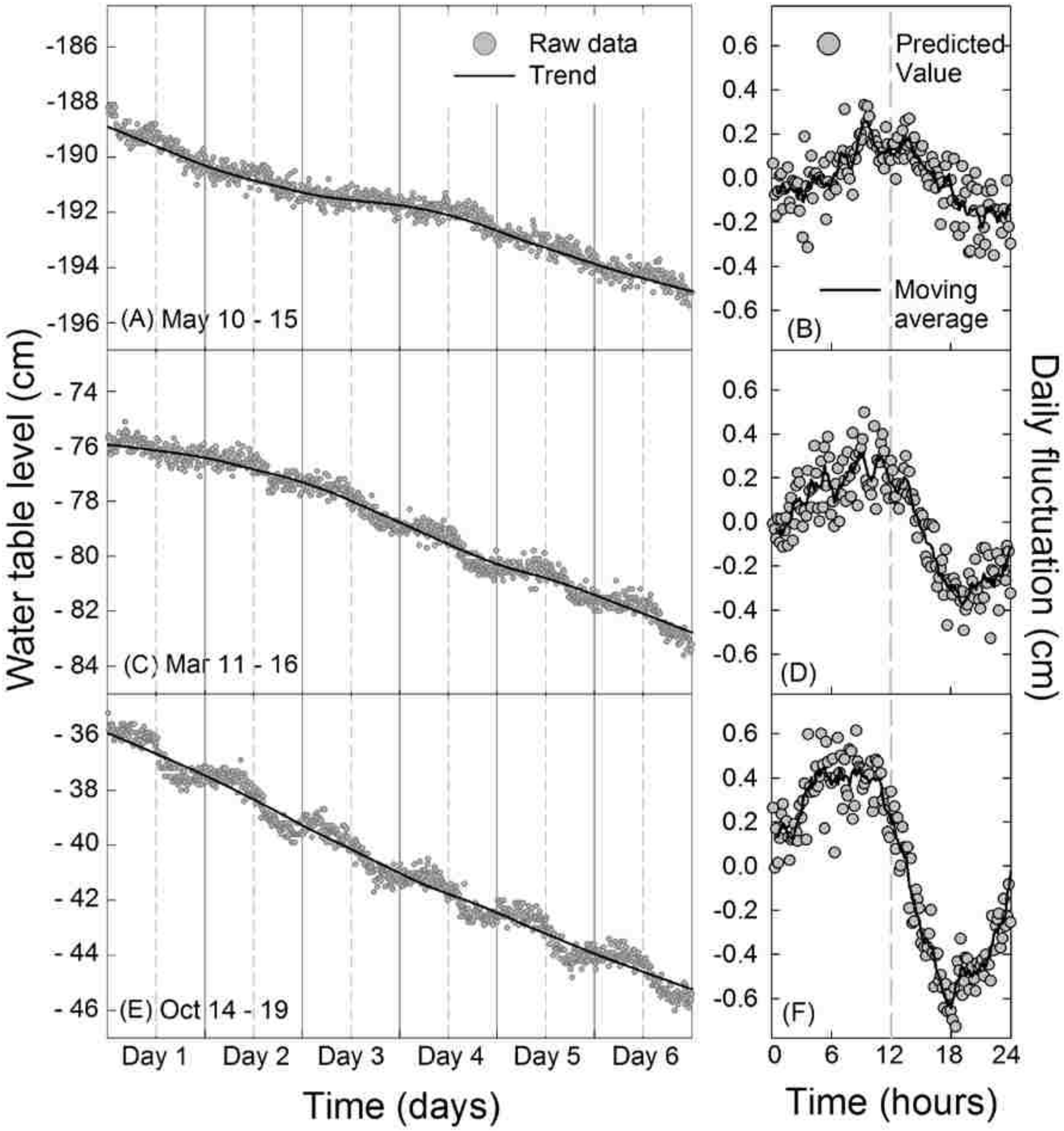

Figure 4.4. Water table level (cm) of six consecutive days in the Hammock site at different water table depths. Low water table depth (May 2006, dry season), intermediate water table depth (March 2006, transition dry-wet seasons) and shallow water table depth (October 2006, wet season). (A), (C) and (E) are overall water table trend. (B), (D) and (F) are average diurnal water table fluctuations. Vertical dash lines indicate midday.

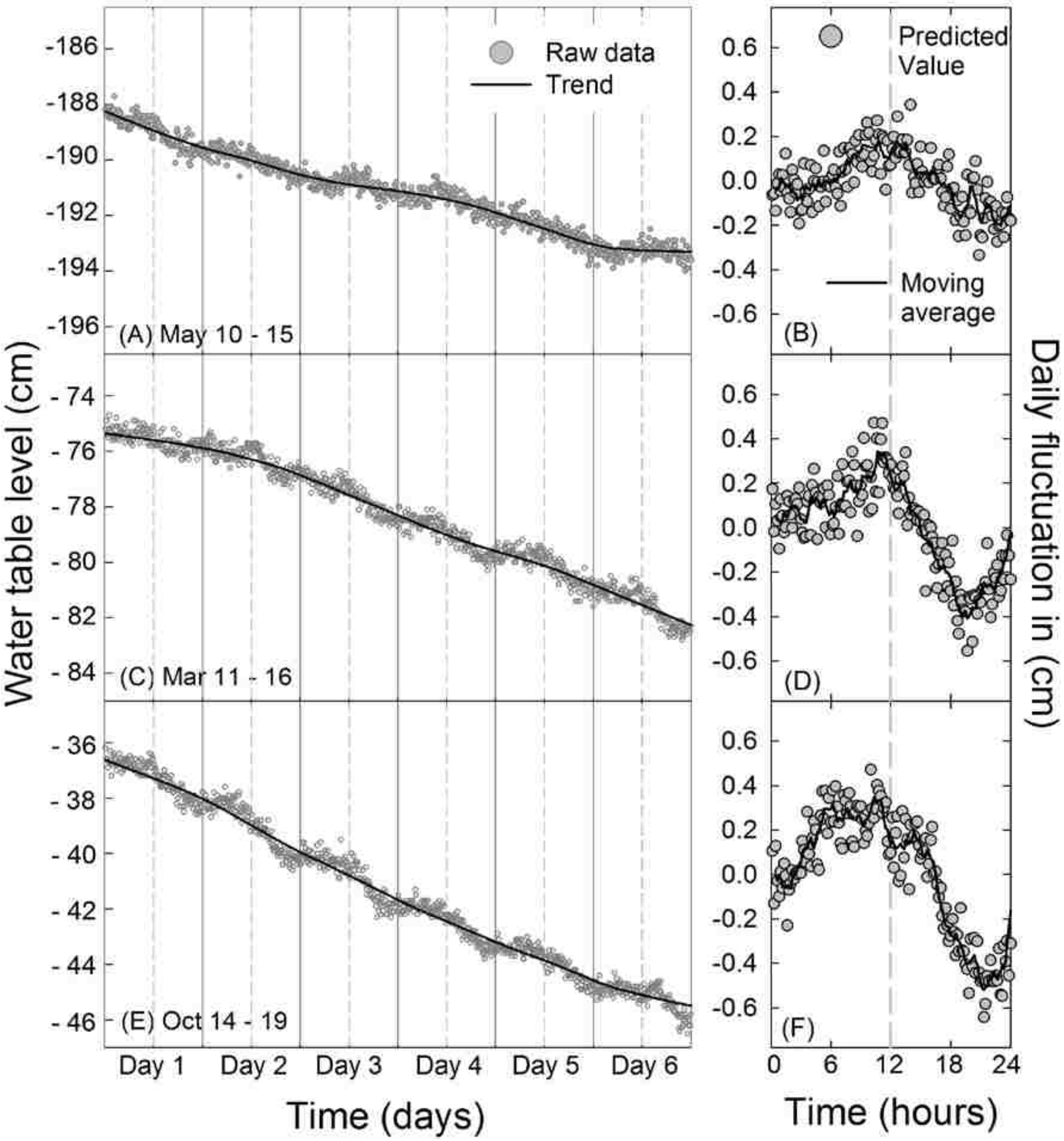

Figure 4.5. Water table level (cm) of six consecutive days in the *Schinus* site at different water table depths. Low water table depth (May 2006, dry season), intermediate water table depth (March 2006, transition dry-wet seasons) and shallow water table depth (October 2006, wet season). (A), (C) and (E) are overall water table trend. (B), (D) and (F) are average diurnal water table fluctuations. Vertical dash lines indicate midday.

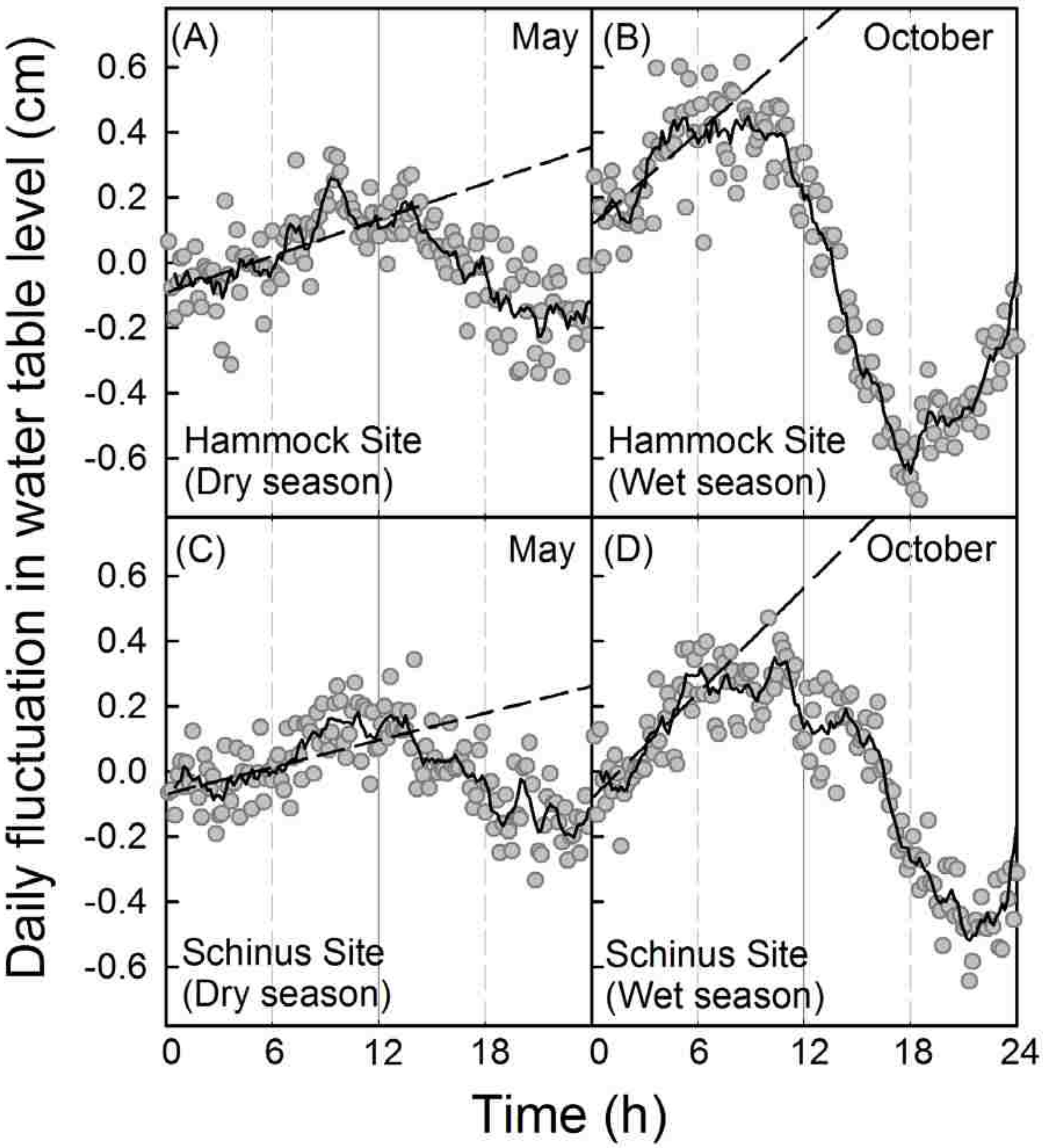

Figure 4.6. Daily fluctuation of water table depth in centimeters. Water table level fluctuation in the Hammock site, (A) dry season and (B) wet season of 2006, respectively. Water table level fluctuation in the *Schinus* site, (C) dry season and (D) wet season of 2006, respectively. The continuous dark lines indicate moving averages obtained with the water table data. Dashed dark lines indicate the recharge rate of the water table. Vertical gray lines (continuous and dashed) indicate 6 hour periods.

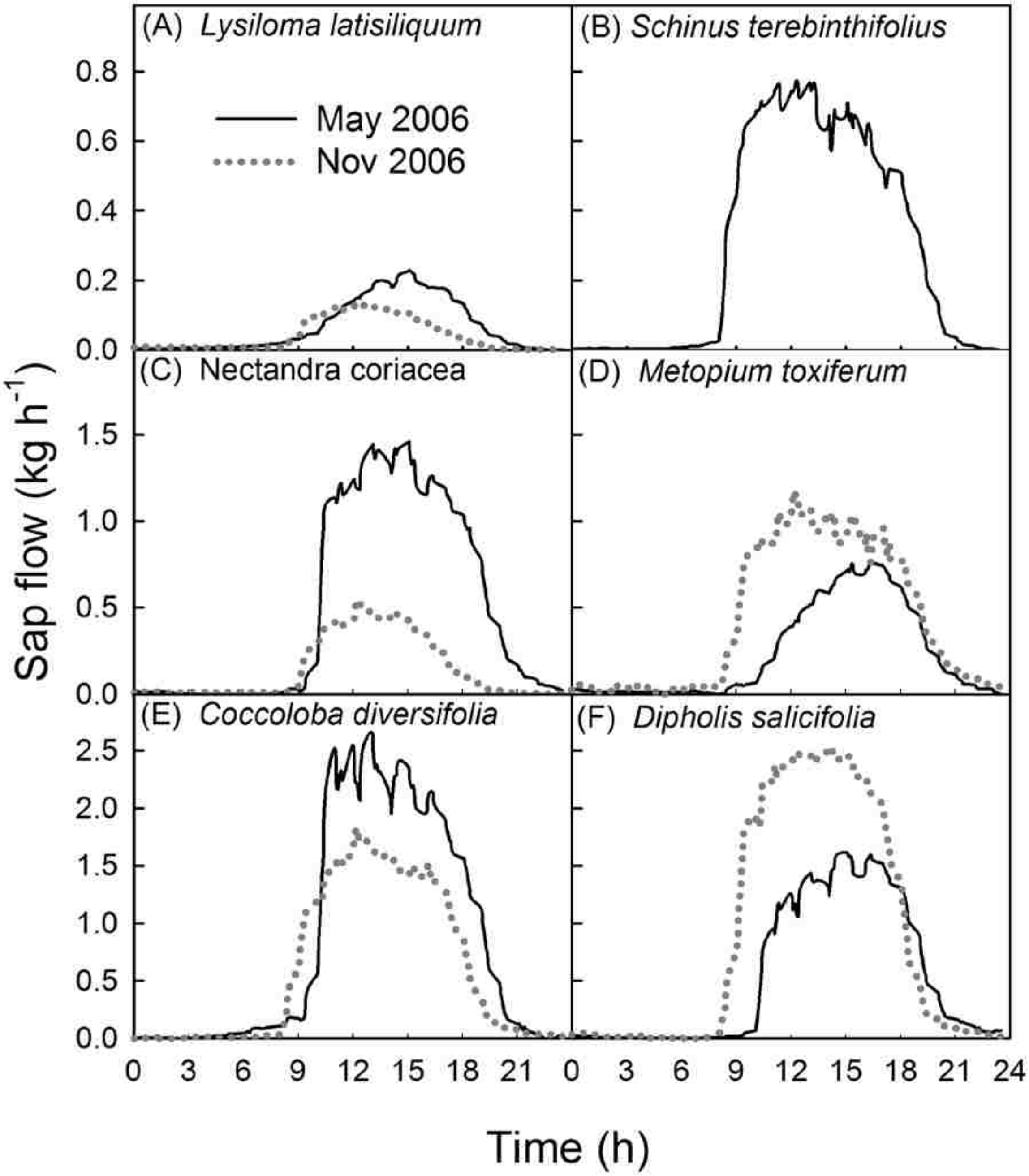

Figure 4.7. Examples of sap flow data (kg h^{-1}) of common tree species in both study sites, (A) *Lysiloma latisiliquum*, (B) *Schinus terebinthifolius*, (C) *Nectandra coriacea*, (D) *Metopium toxiferum*, E) *Coccoloba diversifolia* and (F) *Dipholis salicifolia*. Continuous and dotted lines indicate sap fluxes for the dry (May) and wet (October) seasons of 2006, respectively. There is no data for *S. terebinthifolius* during the wet season.

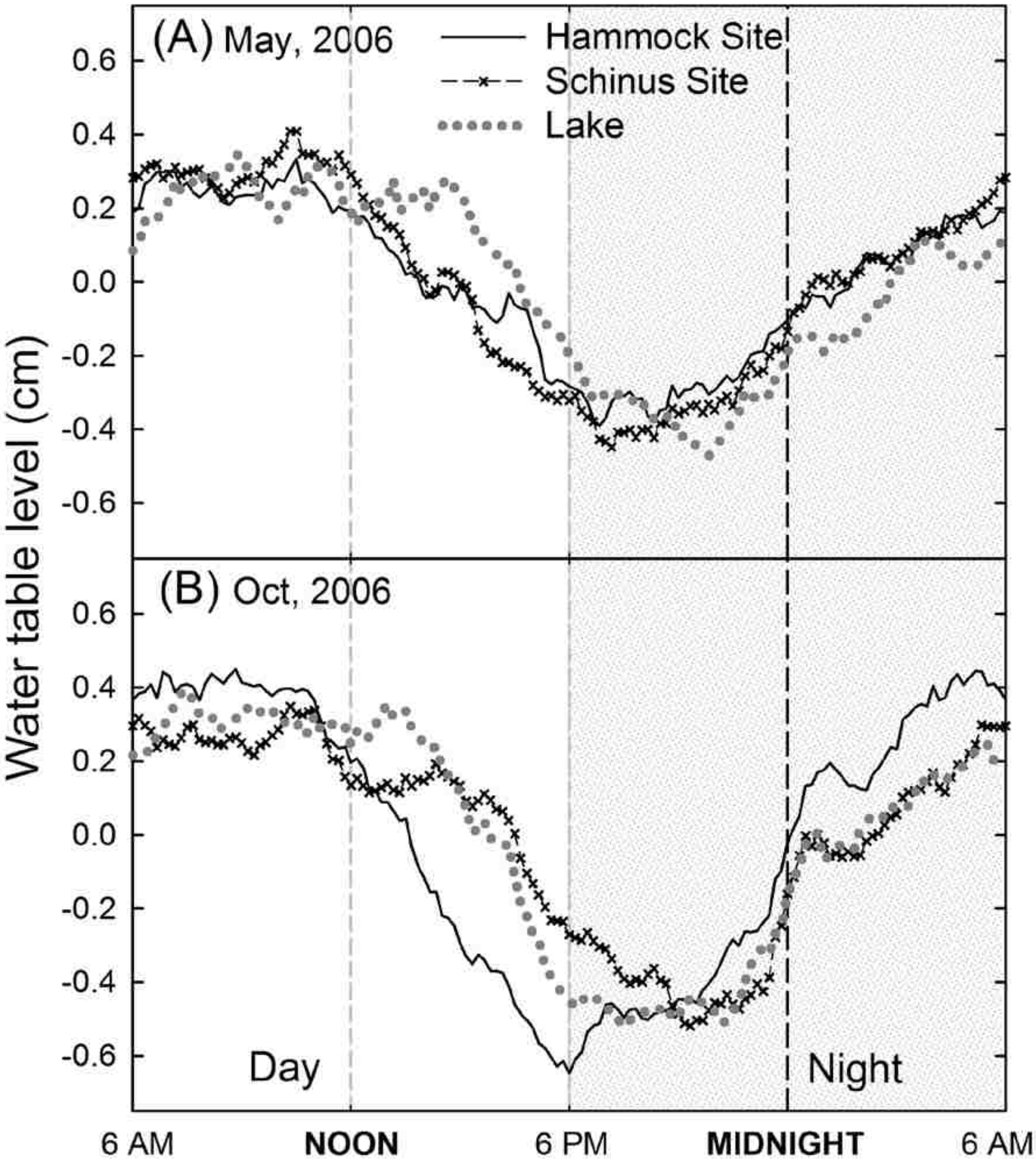

Figure 4.8. Daily water level fluctuations (cm) for Hammock site (continuous dark line), for *Schinus* site (line with x-shape symbols), and for the Hidden Lake (gray dotted line). (A) May of 2006 (dry season) and (B) October of 2006 (wet season)

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