

SUCCESSIONAL DYNAMICS AND SEEDLING REGENERATION IN AMAZONIAN  
FLOODPLAIN FORESTS

By

CHRISTINE MARIE LUCAS

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To Mimi for sharing a great love of learning; to Papa for taking me fishing and building me benches to reach things; to Mom and Dad for giving me the great gifts of love and education; and to the many teachers that opened the world to me

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## LIST OF ABBREVIATIONS

DBH	Diameter at Breast (1.3 m) Height
EMBRAPA	Empresa Brasileira de Pesquisa Agropecuaria
LBA	Large Scale Biosphere-Atmosphere Experiment in Amazonia
LMM	Linear Mixed Model
IBGE	Brazilian Institute of Geography and Statistics
IPAM	Instituto de Pesquisa Ambiental da Amazônia
INPA	Instituto Nacional de Pesquisa Amazônica
SD	Standard deviation
SE	Standard error
UFRA	Universidade Federal Rural da Amazônia
UFOPA	Universidade Federal do Oeste do Pará

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SUCCESSIONAL DYNAMICS AND SEEDLING REGENERATION IN AMAZONIAN  
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By

Christine Marie Lucas

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Amazonian floodplain forests are critical ecosystems that sustain the productivity and diversity of the world's largest and most diverse freshwater system as well as the livelihoods of millions of people. To understand how floodplain forests recover from anthropogenic disturbances in the context of severe flood stress, I tested how environmental stressors and disturbance interact to affect forest recovery at multiple scales in Eastern Amazonian floodplains.

First, I review the land-use history of Amazonian floodplains (Chapter 2). Using laboratory experiments, I tested the effects of short-term and prolonged saturation on seed germination of ten flood-tolerant species (Chapter 3). To understand factors mediating the seedlings, I tested how multiple stressors affect growth and mortality in common garden experiments (Chapter 4). To explore patterns in forest succession, I compared changes in the seedling and tree communities across gradients of livestock activity, flooding, and forest age (Chapter 5). Finally, I estimated aboveground woody biomass storage and accumulation by floodplain forests (Chapter 6).

Seeds of flood-tolerant species had diverse strategies for colonizing floodplains. Mechanical damage to planted seedlings reduced growth and survival during a critical

growth window in the low-water season. The effects of damage and flooding were independent, showing how species persist under the combined effects of multiple stressors. Light availability enhanced growth and survival of pioneers. Among trees, flood level and forest age were major drivers of dynamics of change in stand structure and species richness. Seedling species richness of seedlings in the forest was mediated by the interaction of light and flood level, showing that shade was an important limiting factor for seedling diversity. I observed no differences in tree mortality or recruitment across livestock density levels. Biomass accumulation averaged  $\sim 5 \text{ Mg ha}^{-1} \text{ y}^{-1}$  in forests 15-50 y old, and an average of 70% of biomass gained by tree growth and recruitment was lost to mortality. These results suggested that secondary floodplain forests, despite multiple land-uses, retain high rates of biomass accumulation during secondary succession. These results suggest how floodplain forests sustain high productivity and plant diversity, despite many stressors and disturbances.

## CHAPTER 1 INTRODUCTION

Riparian floodplains are among the world's most productive and diverse ecosystems. With an estimated area of 1.4% of the world's surface area (Mitsch and Gosselink 2000), floodplains are estimated to provide > 25% of terrestrial ecosystem services (*sensu* Tockner and Stanford 2002; e.g., disturbance regulation, water supply, and waste treatment). Floodplain forests are an integral component of many riparian landscapes, providing a buffer between terrestrial land-use activities and aquatic resources and offering habitats for diverse fauna. Riparian floodplain forests are among the most threatened ecosystems, with a history of 'reclamation' efforts in temperate regions and severe alteration of hydrology. The fertile soils, abundant natural resources, and access to river transport have made these environments attractive to human settlement and land-use. Floodplain forests are a clear example of 'working forests' that have developed with human land-use activities (Zarin 2004). Europe and North American floodplain forests have experienced losses reaching 80%, while tropical and subtropical floodplains currently face high rates of loss and degradation due to land-use change and alteration of hydrology (Tockner and Stanford 2002). The decline in tropical floodplain forests threatens not only the ecology of riparian systems, but also livelihoods of millions of people that depend upon floodplain forest resources.

### **Amazonian Floodplain Forests**

The Amazon River and its adjacent floodplains form the largest and most diverse freshwater system on the globe. Total land cover of floodplain forests in the Amazon Basin was estimated at 200,000 km<sup>2</sup> (Junk 1997), but a more recent estimate of floodplain and swamp forest based on remote sensing data estimates 329,000 km<sup>2</sup> or

4.2% of the total Amazon basin (Saatchi et al. 2007). Over 1000 woody species are found in Amazonian floodplain forests, with ca. 31% of these also being found in upland moist tropical forest (Wittmann et al. 2006). Floodplain forests are less diverse than upland forests, with estimates of tree diversity ranging from 53 species ha<sup>-1</sup> in the Eastern Amazon (Pires and Koury 1959) to 149 species ha<sup>-1</sup> in the Western Amazon (Balslev et al. 1987, Parolin et al. 2004b).

Amazonian floodplains constitute a heterogeneous group of forests that vary in stand structure and species composition with regards to water chemistry, soil type, hydrology, and geomorphology. Most floodplains fall into two categories distinct in water quality, soil structure, and geological history. White-water floodplains (*várzea*), comprised of nutrient-rich sediments of relatively recent deposition during the Quaternary, while black-water and clear-water floodplains (*igapó*) are nutrient-poor waters often associated with sandy soils and lower tree diversity (Prance 1979, Furch 1997). These two floodplain forest types differ in species composition (Ferreira et al. 2010), and the more productive and diverse *várzea* is considered to be of particular interest for regional diversity, natural resources, and human livelihoods for a majority of the Amazonian population (Padoch and Steward 2011).

There is broad heterogeneity among those systems considered “white-water floodplains” in the Amazon. While they share the common phenomenon of periodic flooding by sediment-rich waters, *várzea* floodplains are distinct in respect to geomorphology, hydrology, species composition, and land-use history within the Amazon Basin (Sioli 1984, Junk 1997). *Várzea* floodplains are comprised of a mosaic of environments – forests, grasslands, floating meadows, and lakes – shaped by fluvial

dynamics. In the headwaters of the Amazon, rivers are highly dynamic with high rates of sedimentation and erosion, as well as oxbow lakes that formed by sections of river cut off from the main channel (Pinedo-Vasquez 1999). The annual flooding regime in these headwater tributaries varies from polymodal to monomodal, with more rapid rates of change and abrupt fluctuations in river level than the annual floods in the Central and Lower Amazon (Junk 1997). Changes in flood level can reach up to 14 m in these tributaries (Goulding et al. 2003), but flood duration is than in the Central and Lower Amazon (1-4 mo, Nebel et al. 2001c). In the middle and lower stretches of the Amazon River (excluding the tidal estuary), the flood regime is characterized by a highly predictable monomodal flood pulse that changes in river water level gradually over a 6-month flood season (Junk 1997). There are no oxbow lakes, but rather large seasonal lakes of up to 30,000 ha (M. Crossa, personal communication, March 25, 2011) that connect with rivers during the high water season (Junk 1997). The Amazon Estuary is characterized by a tidal flood regime with daily fluctuations in river level of 2-4 m, depending on the time of year (Almeida et al. 2004). Species richness and composition vary widely among *várzea* forests of different regions and different tributaries within the Amazon Basin (Parolin et al. 2004b). Basin-wide trends in diversity suggest decreasing diversity of *várzea* forests along a West-to-East gradient (Wittmann et al. 2006). Floodplain trees have evolved a suite of physiological and phenological mechanisms for tolerating prolonged periods of waterlogging and/or submergence (Parolin et al. 2004a). Tolerance of anoxia is particularly important at the seedling phase, as seedlings may be submerged for up to 210 days (Parolin 2002). In no other place in the world are tree seedlings known to tolerate such prolonged periods of submergence.

The *várzea* of the Santarém region is distinguished by extensive areas of grasslands and floating meadows in the floodplain that cover up to 80% of the vegetated area. In contrast to the Estuary, Central, and Upper Amazon regions, forests do not dominate the floodplain landscape but are restricted to high-elevation levees where the water column ranges from 0-2 m depth. It is these abundant and highly productive grasslands that make the region today so attractive to cattle ranching. In addition, the predictable, monomodal pulsing of relatively shallow floods (7.5 m on average) permits management of cattle on the floodplain, with the use of adjacent uplands for ranching during the high-flood season. The major threat to forests is the constant passage of cattle and water buffalo through forests seeking grasslands for grazing. Daily trampling by cattle and water buffalo herds damage understory plants and compact soils, compromising woody plant regeneration. The impacts of cattle in floodplain forests are visually striking, as noted by the openness of the forest understory in areas of high livestock traffic (Figure 1-1).

Amazonian white-water floodplains serve important ecological and economic roles for fisheries (McGrath et al. 1993), agriculture (WinklerPrins 1999), timber (Anderson et al. 1999) and non-timber forest products (Fortini et al. 2006). Over 70% of the Amazonian population resides on or near floodplains, and the *várzea* supports higher rural population densities than those of uplands. The social, economic, and political context of land use by riverine people in the *várzea* has been reviewed in two books (Padoch et al. 1999, Padoch and Steward 2011). Some challenges that riverine landholders in the study region of Santarém face are the communal management of common-pool resources such as fish (McGrath et al. 1999a), shifts from artisanal to

commercial fishing (McGrath et al. 1993), migration to uplands following economic downturn of jute (WinklerPrins 2002), and changing land tenure policies (McGrath et al. 2011). Relatively few ecological studies have investigated the impacts of land use transformations on the extent, diversity, species composition, and ecosystem function of Amazonian floodplain forests (Zarin et al. 1998, Zarin et al. 2001, Pereira et al. 2002, Fortini et al. 2010).

### **Cattle Ranching in Floodplains**

A leading threat to the conservation and sustainable management of many tropical and sub-tropical floodplains is the intensification of livestock densities. While floodplains sustain the impacts of many large grazers, the intensification of activities related to livestock ranching has resulted in the degradation and alteration of floodplain habitat in Africa (Hughes 1988), Australia (Gatewood and Cornwell 1976, Robertson and Rowling 2000, Jansen and Robertson 2001), India (Dahdouh-Guebas et al. 2006), and South American tropics (Junk and de Cunha 2005). Management of livestock impacts in riparian floodplain systems is known to have been an issue of concern since at least the 1600s in Europe (Klimo and Hager 2001) and more recently in the U.S. (Kauffman and Krueger 1984, Belsky et al. 1999). In the floodplains of the Central and Lower Amazon River, the most recent major cycle of land-use transformation is the conversion of floodplains to cattle pasture (Mertes et al. 1995). Introduced water buffalo and cattle herds are increasing at annual rates of ~13% and 4%, respectively (Sheikh et al. 2006). Livestock move through forest understories to reach the lush grasslands and meadows of the floodplain. As flood levels rise, cattle may concentrate on higher elevations, which is where floodplain forests occur. Livestock can trample vegetation in the forest understory and compact soil, reducing the density of understory woody plants

(Sheikh 2002). Over time, the continual effects of dense livestock herds in floodplain forests are hypothesized to clear forest understories and result in 'standing dead forests' with no recruitment of woody species as well as the potential invasion of grasses. We know of no previous test of the effects of cattle disturbance on seedling regeneration and successional dynamics in floodplain forests over time.

### **Fishing in Floodplain Forests**

Conservation and management of floodplain forests are essential for sustaining Amazonian fisheries (Goulding et al. 1993). Floodplain forests provide food and shelter for diverse aquatic and floodplain biotic communities. In synchrony with the annual flood pulse, floodplain forests yield an abundance of fruits and seeds, which are consumed by fishes migrating into the floodplain. Over 200 fish species of the Amazon consume fruits and seeds from flooded forests, including such commercially valuable species as *Colossoma macropomum* (Araujo-Lima and Goulding 1998).

In this thesis, I first investigated the seed germination, seedling establishment, and forest dynamics of tree species that serve as important food sources for economically valuable fishes that consume their fruits (Lucas 2008). In the study region of Santarém, smallholders practice three main resource-based livelihood strategies: fishing, farming, and livestock ranching (Almeida 2004). Fishing is the most common strategy, practiced by 95% of families and is the main source of protein for floodplain families. Timber harvesting is no longer a prominent activity in the region of Santarém, as timber has been depleted in the region and wood for construction is purchased from the uplands.

### **Theoretical Contribution to Plant Community Ecology**

The drivers of succession remain a central area of investigation within plant community ecology. Although the dynamics of forest succession have been studied for

over a century, new questions have emerged: What are the synergistic effects of multiple factors on forest recovery from disturbance? Forested wetlands are excellent systems for investigating how local anthropogenic disturbances interact with flooding stress to influence forest succession. These ecosystems have adapted to several environmental stresses, most importantly flood-induced anoxia, and have also experienced extensive manipulation by human land-use practices (Messina and Conner 1998). Flooding stress can interact with land-use activities to create a mosaic of plant communities at various stages of succession, although little is known of how flooding and anthropogenic disturbances interact to affect the earliest stages of succession (*e.g.*, seed dispersal, establishment, seedling growth, and seedling community dynamics).

In light of the global focus on climate change, there is increasing research on the changes in carbon storage and sequestration in forests over time. The few estimates available for floodplain forests suggest that although total above ground biomass may be lower than upland moist tropical forests, carbon sequestration by Amazonian floodplain forests is substantial. While successional forests can portray high biomass accumulation rates that offset carbon emissions (Asner et al. 2010), degradation of forests can lead to reductions in biomass and carbon sequestration (Aide et al. 1995, Hughes et al. 1999, Steininger 2000). A large area of floodplain forest in the Eastern Amazon basin is secondary, recovering from deforestation and degradation from multiple land-use activities (Anderson et al. 1999, Zarin et al. 2001, Wittmann et al. 2006). The rapid growth rates of early-mid successional tree species in secondary floodplain forests could result in high rates of biomass accumulation (Schöngart et al. in press). Alternatively, degradation of secondary floodplain forests by land-use activities

such as logging, extraction of fuelwood, and trampling by livestock (Sheikh et al. 2006) could reduce rates of biomass accumulation via high stem mortality and poor recruitment (Chazdon et al. 2007).

### **Participatory Research in Rural Riverside Communities**

Scientific research can contribute to sustainable grassroots development of natural resources by integrating user participation and capacity building into the research process (Chambers and McBeth 1992, Moller et al. 2004). Participatory research aims to involve local people, communities, and institutions in the research process to shift scientific learning from an extractive process to that of exchange and collective learning (Agrawal and Gibson 1999, Klooster 2002, Arnold 2004). There has been a recent increase in participatory approaches to scientific research, but further evaluation and application of these methods is needed. The participatory approach to ecological research can build adaptive capacity, knowledge, and skills among local people, communities, and researchers to manage and conserve natural resources. Resource users and communities utilize knowledge and experience to create and adapt development criteria to changing social and ecological circumstances (Armitage 2005).

The field research for this work was carried out in collaboration with community members, landholders, students, and governmental and non-governmental institutions. The research involved the participation of riverine community residents in the research process, from hypothesis formation to the analysis and application of results to resource management. At a regional scale, I collaborated with three floodplain communities and the local branch of EMBRAPA (Empresa Brasileira de Pesquisa Agropecuaria) in Santarém to monitor the effects of livestock activity and flood level on seedling community diversity, regeneration strategy, and availability of locally valuable

resources. At the local scale, two communities participated in a series of experiments to test how variation in flood level and cattle activity affect seedling community dynamics, and ultimately, forest succession. The collective learning process during research has the potential to contribute to individual and community capacity to manage and conserve floodplain forest resources. Research results were disseminated to communities and institutions in written and oral forms and evaluated by participants. Beyond basic research, we developed learning activities with local schools to share knowledge about the *várzea* ecosystem and the use of its resources, and to share information on scientific methods of research.

### **Scope of the Dissertation**

This dissertation addresses aspects of seedling ecology and forest succession in secondary floodplain forests of the Amazon River. The overall objective of this work is to understand the dynamics of recovery of tropical forests at multiple scales in the context of extreme seasonal floods and chronic disturbance by introduced livestock. I first review the history of land use and forest conversion in Eastern Amazon floodplains since the pre-Colonial period (Chapter 2). The remaining Chapters are a series of studies that examine the effects of various ecological drivers on seed germination, seedling growth and mortality, tree communities, and ecosystem processes. I tested the effect of water saturation and submergence time on seed germination of ten floodplain forest species (Chapter 3). Once seeds germinate on the floodplain, growth and survival during the first year of establishment is critical. Using common gardens, I tested the synergistic effects of flood stress, shade stress, and mechanical damage on seedling growth and survival during the first year of establishment (Chapter 4). At a broader scale, I used a 4.9 ha network of forest plots to test how flood level and

livestock activity affect seedling and tree community dynamics (Chapter 5). These inventories are a continuation of work initiated by Pervaze Sheikh in 1999. To examine the role of floodplain forests for biomass storage and sequestration, I measured aboveground biomass and biomass change in collaboration with colleagues from the Max-Planck Institute and INPA. We explored trends in biomass sequestration across flood level and forest age (Chapter 6). Together, these chapters address the history of land uses, the driving factors for forest diversity and productivity, and the capacity of forests to recover amidst many stresses in 'working' Amazonian floodplain forests.

A



B

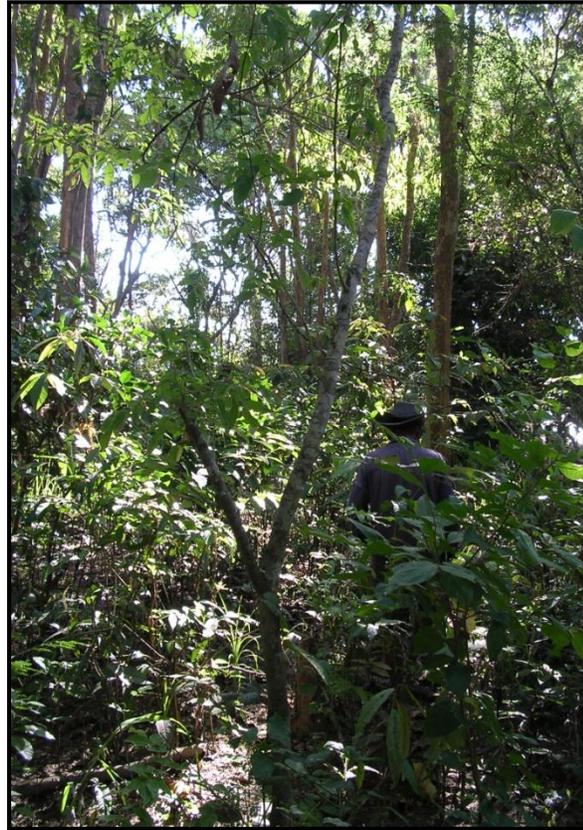


Figure 1-1. Amazonian floodplain forests of the Santarém region that differ in livestock activity. A) Forest with heavy cattle activity and (B) light activity. Photos courtesy of Christine Lucas.

## CHAPTER 2 HISTORICAL LAND-USES IN THE VÁRZEA OF THE LOWER AMAZON RIVER

### Overview

The white-water floodplains along the Amazon River, known as *várzea*, have a long history of multiple land uses. Pre-Colombian history in the *várzea* suggests that these nutrient-rich floodplains provided important agricultural land and fishing grounds for riverine people and adjacent upland chiefdoms. The floodplains and upland bluffs of the Santarém region in Pará state, extending 225 km from the towns of Óbidos to Monte Alegre, is rich with archeological evidence of inhabitation on and adjacent to floodplains, including large shell middens and areas of *terra preta* (Smith 1999). Following European colonization, the floodplain landscape experienced a series of boom and bust cycles in land use, including conversion of forests for agriculture, cacao plantations, rubber extraction, jute plantations, and cattle ranching. Throughout these cycles of land-use, *várzea* forests have served as a valuable resource for fisheries and extraction of timber and non-timber forest products. Today, approximately 70% of the Amazonian population live on or adjacent to Amazonian river-floodplain systems (IBGE 2007 sensu calculations by Padoch and Steward 2011), and the *várzea* supports higher rural population densities than the *terra firme* (Hiraoka 1995). The proximity of urban centers such as Belém, Santarém, Manaus, Tefé, and Iquitos places increasing demands on *várzea* ecosystems for natural resources. In this chapter, I discuss the historical accounts of land-use in the *várzea* of the Santarém region since pre-Colombian times through the twentieth century.

## Pre-Colombian Land-Use on the Floodplain

Archeological evidence near the floodplain at the confluence of the Tapajós and Amazon Rivers suggests inhabitation of multiple indigenous communities and civilizations. While the natural cycles of erosion and sedimentation of the floodplain may have erased most archeological evidence of pre-Colombian indigenous inhabitation on the floodplain, it is speculated that the floodplains had indigenous villages and provided agricultural fields for both floodplain and upland settlements (Denevan 1984, Smith 1999). Among the earliest and best-known evidence for large villages near the floodplain is a shell midden of 7 m depth over several hectares wide on an ancient river terrace 50 km downstream of Santarém. Shells, coal, tools, and pottery shards date between 7000 to 8000 y B.P., and suggest permanent settlement along the Santarém floodplains (Roosevelt et al. 1991).

The developmental sequence at Santarém sheds light on human adaptation to the tropical environment over the millennia, revealing that tropical resources supported the earliest pottery-age cultures yet known in the Americas, as well as diverse other cultures...[Lowland archeology] shows that Amazon floodplains were extensively exploited for thousands of years and may be more appropriate for development efforts than poor hinterlands... (Roosevelt et al. 1991: 1624).

While there has been much scholarly debate regarding the extent and distribution of Pre-Colombian indigenous peoples in Amazonia (Meggers 1971, 1996, Heckenberger et al. 2003), there is agreement that white-water floodplains provided abundant natural resources and nutrient-rich soils for farming. Periodic flooding and occasional exceptionally high floods (e.g., 1819, 1953, 2006, 2009) could have limited dense settlement (Denevan 1984, 1996). Long-term settlement on the floodplain of Carmo Island between Santarém and Óbidos is suggested by a mound with *terra preta*

and pottery shards (Smith 1999: 27-28). The juxtaposition of rich floodplains and secure, dry uplands, described as the bluff model, was likely advantageous for the development of large, long-term settlements and complex societies in the Santarém region by 1000 years BP (Roosevelt 1992, Denevan 1996). The extent of bluff settlements is indicated by the present-day distribution of blackened anthrosols, known as *terra preta do indio*, some of which extend into the high elevation *várzea* (Denevan 1996, Smith 1999). The distribution of *terra preta*, pottery shards, and shell middens suggest that Tapajó satellite villages extended at least 30 km downstream along the upland bluffs of the south shore of the Amazon River (Smith 1999). The largest *terra preta* site in the Brazilian Amazon (350 ha) is found in Juruti, on an upland riverside bluff between Santarém and Parentins (Smith 1999).

### **First Encounter with European Colonists**

The first written account of the large indigenous civilizations in the region Santarém was made by Carvajal in 1541 during Orellana's descent down the Amazon River from Peru (Medina 1934, Palmatary 1965). At a location on the Amazon where the tide was first noticed (between Santarém and Oriximiná), Carvajal described gleaming white villages that stretched for miles on the river bluff. The land was so populated on the south shore of the Amazon below the Tapajós River that the brigantine stayed to the north shore to avoid conflict and attacks. On June 25, Orellana and his men were approached by over 200 canoes of 20-40 men each (Medina 1934, Palmatary 1965). Smith (1999) speculates that in order to support such numbers of warriors, the Tapajó civilization must have been at least 40,000 people. In reference to the floodplain near the Tapajós, after surviving a series of Indian attacks, Carvajal writes of the "many inhabited islands, to which they went to obtain food." Carvajal makes this

observation in June of 1541, when flood levels are high, suggesting that residence on the floodplain was not confined to the dry season.

In the 200 years following Orellana's first expedition, there was little European activity or economic interest in the Amazon upstream of the estuary. There were a few failed attempts by the Spanish and Portuguese to retrace Orellana's voyage. As such, the second written account was not until 1640 by the father Cristoval de Acuña on the Texeira expedition from Peru to Belém (Markham 1963, Furneaux 1969). Although Acuña does not appease the ecologist's curiosity with descriptions of the surrounding vegetation, he does give much detail about indigenous peoples. Acuña states that the Tapajó Indians bartered fish, flour, and ducks, which could have come from floodplains nearby (Markham 1963: 124-125).

### **Resource Extraction and Exportation: 1755-1798**

The second half of the eighteenth century in the state of Pará defined a new period in the history and land-use of the Amazon. The Portuguese took a newfound interest in natural resources from the Lower Amazon, and extraction systems were soon set in place. For the floodplain, this signified the implementation and expansion of cacao plantations, initial efforts at systematic agriculture, and exploitation of indigenous people for labor. The Directorate system was a state-run program established in 1758 to encourage indigenous assimilation, agricultural production, and resource extraction in the Amazon (Anderson 1999). Directorate villages were established in pre-existing *Aldeas* or indigenous villages, with a director and a few white settlers (known as *moradores* or *agregados*). The most important economic activity in Directorate villages in the eighteenth century was forest and riverine collection trips (*negócios do sertão*) in search of spices, oils, and other exotic forest products, known as *drogas do sertão*

(Anderson 1999). Non-timber forest products collected included the spice and medicinal herb *salsaparrilha* used to cure syphilis (*Smilax santarémensis*), wild clover (*cravo grosso*), and Brazil nut (largely the upland species, *Bertholletia excelsa*, but also including the floodplain species *Lecythis pisonis*). Various tree barks were collected for caulking materials (*estopa*); tree resins to make tar for ship construction and repair (*breu*); and tree aromatic oils from floodplain tree species, *andiroba* (*Carapa guianensis*), as well as a cotton-like stuffing material from the seed pod of the kapok tree, *samauma* (*Ceiba pentandra*) (Anderson 1999). Riverine resources included turtle (*Podocnemis expansa*) meat, salted *pirarucu* (*Arapaima gigans*), and manatee (*Trichechus inunguis*) meat and oil. The importance of turtles in Amazonia is summarized as, “What the bison was to the North American Indians, the fifteen or more variety of turtles were to the American Indians” (Anderson 1999: 54). The overexploitation of the giant river turtle (*Podocnemis expansa*) led to its eventual population crash in the 1870s. (Smith 1999). Thirty years after the implementation of the Directorate system, the economic value of Amazonian exports shifted from an emphasis on the harvest of non-timber forest products to crops: coffee, cacao, rice, corn, and cotton (Anderson 1999). Cacao, rice, beans and tobacco were among the crops grown on *várzea* floodplains.

### **Chocolate from the Amazon Floodplain, 1640-1870**

As early as 1640, cacao was recognized as an important commodity from the Eastern Amazon (Palmatary 1965). The value of cacao is reiterated in 1743 as the primary trade commodity of Indians for European fabrics, needles, mirrors, scissors, and combs (Palmatary 1965). The cities of Santarém and Óbidos (120 km upriver from Santarém) became widely known as a cacao center of the Amazon. By 1823, cacao

was considered the “most important commodity” in the region of Santarém and Óbidos (Spix and Martius 1823/1968). The margins of the Amazon and its meandering tributaries (*paranamirims*) in the Óbidos district are described as “extensive lines of cacao with few intervals” (Penna 1869). The first accounts of the Amazon River from American and European naturalists in the 1800s coincide with the zenith and subsequent decline of the cacao industry. As such, botanical observations of the *várzea* around Santarém and Óbidos are typical of the following:

Had the vegetation of the South bank, along which our course lay, been more interesting, I would not have demurred at the delay, for I was unable to get on the shore everyday...but nearly the whole coast, to a considerable breadth, was clad with plantations of cacão...for it is this part of the Amazon that cacão cultivation is most extensively carried on. The cacoals either reach to the very margin of the river or have an intervening narrow fringe of such weeds, shrubby and herbaceous, that grow commonly on inundated river-banks (Spruce 1908/1970: 78).

Wild cacao grew naturally on the floodplains (*Theobroma spruceana*), but largely domesticated varieties (*Theobroma cacao*) were planted on the floodplain levees, sometimes in groves of thousands of trees. Single plantations with 40,000 planted cacao trees, stretching for kilometers along the riverbank, are reported around the peak of cacao (Penna 1869). The region between Santarém and Óbidos appears to have been the number one exporter of cacao in the Amazon, until 1790, when the Furo district farther upstream took the lead (Anderson 1999).

Once the Directorate system was terminated in 1798, cacao plantations were transferred to private landholders, by either legal or illegal means. A typical family on the *várzea* in the vicinity of Óbidos may have managed a cacao plantation of 10,000 to 15,000 trees in 1850, which were harvested for fruits once each year (Bates 1864/1962). Despite the civil strife associated with national independence (e.g.,

*Cabenagem*) and the lack of a coherent policy for land ownership in the Brazilian Amazon, much of the *várzea* land, particularly around the old Directorate villages, was held by legal land title or illegal squatters (*posseiros*) (Anderson 1999). Following cacao, the most important export items from the region were tobacco, wild clover, rice, cotton, manioc flour (*farinha*), and salted *pirarucu* (a replacement for salted cod). The *várzea* was also important for planting corn, cotton, sugar-cane, and tobacco (Smith 1879).

There are many potential reasons behind the slow decline of cacao. From the accounts of naturalists, there were inefficiencies in cacao seed production as well as poor management of the plantations (Wallace 1853/1969, Bates 1864/1962, Spruce 1908/1970). Fruit and seed yield were low in the dark, dank environment of the cacao understory. Cacao seeds, once harvested, were not dried properly and as much as half the crop was thrown out due to fungal infestations of damp seeds (Spruce 1908/1970). By the mid-1800's the sizes of some century-old cacao plantations were reduced to a tenth of their original size due to little effort for managing, pruning, or replanting (Penna 1869). Landholders in the *várzea* today claim that cacao declined due to a combination of extremely high flood years that killed stems and economic demand for alternative forest products such as rubber and jute.

The accounts of vast cacao plantations, bluff villages, extraction of riverine resources, and population crash of the giant river turtle in the Lower Amazon leaves the impression that the *várzea* in the region of Santarém was heavily cultivated, harvested, and populated in the eighteenth and nineteenth centuries. However, there remains question as to how much of the *várzea* forest was converted to cacao plantations and to what extent forests were maintained for forest products such as timber, fruits, and, after 1866, fuelwood for steamships. In 1862, Bates described the *várzea* forest between

Santarém (River Maica) and the Xingu River as “low and swampy” and “an entangled mass of irregular and rank vegetation” (Bates 1864/1962: 147). Having passed Santarém and headed to Óbidos, Bates noted that the bank of the river was dotted with homes, each surrounded by cacao plantations. Above Óbidos the forest along the river banks was described as “wild and solitary” (Bates 1864/1962, Orton 1870) where the existence of man is forgotten and only wild paradise resides (Edwards 1847/2004). Whether or not these regions above Óbidos and below Monte Alegre did have old-growth *várzea* forests, it seems that it is at these stretches of river that the landscape appeases the traveler’s fantasy of primal, virgin forest at the river’s edge.

### **Botanical Observations by Naturalists, 1843-1850**

The presence and use of *várzea* forest species in the nineteenth century indicates that some of the same species are still common, while others have severely declined, potentially due to increased flood levels. Spix and Martius (1823/1968) observed *embauba* (*Cecropia latifolia*), and *munguba* (*Pseudobombax munguba*), the bark of which is stripped to make cords to pull canoes upstream. Some trees were suffocated by cucurbitaceous vines, a sight still common today. The great kapok tree (*Ceiba pentandra*), known locally as the *samauma*, was noted as a common and very distinct emergent tree. The “cotton” from the seed pod was collected to make felt for light summer hats or to stuff pillows and mattresses. *Samauma* is now a very rare sight on the floodplain of the Santarém municipality. Residents of the Tapará region today know of two large trees in the entire municipality, and no seedlings have been observed in floodplains. The abundance of *Ceiba pentandra* was noted repeatedly throughout the nineteenth century, particularly downriver of Santarém where cacao plantations were rarely mentioned and perhaps less extensive (Spix and Martius 1823/1968, Edwards

1847/2004). Another common *várzea* species was pau-mulato (*Calycophyllum spruceanum*). cited as a species of extremely beautiful wood “esteemed of no value” (Edwards 1847/2004). Twenty years later, this view has changed dramatically, as *pau mulato* became known as a prized wood for fuelwood for steamships (Sternberg 1975, Sears 2003). Today, *Calycophyllum spruceanum* has multiple uses among *várzea* residents for fuelwood, construction material, and anti-fungal treatment (Sears 2003).

### **Black Gold in the Amazon: Rubber Boom of 1870-1911**

The rubber boom had an immense impact on the Amazonian economy, culture, and development, particularly in urban centers such as Santarém (Smith 1999). Rubber superseded cacao as Para state’s number one export at 20 million lbs. per year (Smith 1879). The impact of the rubber boom on land-use, livelihoods, and forest structure in the *várzea* may have been minimal, given the relatively small size and low density of rubber tree stands in comparison to the uplands and sites along Amazon tributaries. The *várzea* of the estuary was initially an important producer of rubber, but by 1874 rubber trees in the region suffered losses from over-extraction, and rubber tappers were forced further upstream the Amazon to the Tocantins, Madeira, Purus, and Negro Rivers (Smith 1879).

Despite the abundance of rubber plantations along the Tapajós River near Santarém, and the later development of rubber plantations in nearby Belterra and Fordlandia in the 1920s, rubber trees in the *várzea* of Santarém were not abundant (Penna 1869). Nonetheless, the social and economic changes associated with the rubber boom and bust had long-lasting effects on residents of the region. Cacao plantations, already in decline by 1870, were abandoned by laborers to tap rubber elsewhere. The “cacao towns” of nearby Monte Alegre and Alenquer diminished in size

and economic activity, as cacao declined in the wake of rubber. Rubber also attracted colonists, particularly from the Northeast following the great drought of 1877-1879. When the rubber industry in the Amazon crashed in 1911, many colonists resettled in cities and on the *várzea* floodplains (Smith 1999). Many *várzea* residents today, including those in Santarém, can trace their roots back to Northeastern settlers that moved to the floodplains in the early 1900s (Smith 1999).

### **Fibers from the Floodplain: Jute boom of 1931-1990**

Jute was a very important cash crop for riverine residents (*ribeirenhos*) in the *várzea* of Santarém. Jute (*Corchorus capsularis*) was introduced into the *várzea* floodplains of the central and lower Amazon River by the Japanese in 1931. Jute, a native herb of India, was cultivated for its fiber, used for making sacks for coffee and sugar (Smith 1999). The success of jute was attributed to its value as a cash crop for local residents, as well as an economic solution to the poverty that followed the rubber crash in 1911 (Medeiros 1968). Jute plantations in the *várzea* of Santarém were planted on old cacao plantations or in newly cleared and burned forests. The plant was harvested post-flowering when waters were rising (Medeiros 1968). By 1971 jute reached its peak production in Amazonia – approximately 60,000 ha. of floodplain soils were in jute fields, most of which lied between Monte Alegre and Manacapuru (Smith 1999). Soon after, in the early 1980s, jute fibers were replaced by synthetic fibers, and residents witnessed yet another economic crash. Some middle-aged *várzea* residents recall harvesting jute with their parents at a young age and clearing old cacao plantations to plant jute. Today, jute can still occasionally be observed in small plantations in the Santarém municipality (Figure 2-1). One can also view the jute factory in Santarém, which was closed in the 1980s.

## Rise in Cattle Ranching: 1970 - present

Although this chapter focuses on the land-use and ecology of *várzea* forests in the Santarém region, the *várzea* is also composed of vast native grasslands. These grasslands support the growing cattle industry, which is a current economic boom in the *várzea* of the region. While the economic and ecological impacts of cattle ranching on the floodplain and riverine residents are of major concern today, cattle ranching has had a long history on the floodplains. Cattle ranches in the *várzea* were first established in the 1500s on Marajó Island at the mouth of the Amazon River (Smith 2002). In general, cattle ranches were separate from Directorate villages, and were owned by Portuguese ranchers with African slave work hands (Anderson 1999). By at least 1846, cattle ranches were established on the floodplains near Santarém (Edwards 1847/2004). “The campos in the vicinity [of Santarém] support large herds of fat cattle, in every way superior to those of Marajó; and were steamboats plying upon the river, Santarém beef would be in great demand at Pará” (: 106Edwards 1847/2004).

Given the abundance of grasslands and the quality of beef, one wonders why cattle ranching did not become a dominant land-use practice sooner, particularly after the arrival of the steamboat in 1866 to facilitate transport. In 1869, 40 landowners had 10,600 head of cattle in the municipality of Santarém (Penna 1869). The majority of these cattle were upstream of Santarém at Lago Sapucuá (at the confluence of the Amazon and Trombetas Rivers), Lago Mariapixi, and Lago Grande do Curuai (Penna 1869), where today there remain large cattle ranches (M. Crossa, personal communication, June 1, 2007). The extent of cattle ranching in the nineteenth and early twentieth century was limited by the same environment that supported the industry’s success. For while annual floods nurtured abundant pasture grasses, they could also

have devastating impacts on cattle herds. Exceptionally high or rapidly rising floods killed many cattle, increasing the economic risk associated with investment in cattle herds (Anderson 1999). Cattle also died from disease and snake bites, both exacerbated by the onset of the flood season. For example, the great flood of 1859 reduced cattle herds of 5-6,000 head to 100-300 head (Penna 1869). Ranchers also lacked access to boats to transport cattle to the uplands during the flood season.

The conversion of floodplains to pasture and the intensification of cattle ranching constitute the most recent major cycle of land-use transformation in the *várzea* of the Santarém region (McGrath et al. 1999b). Water buffalo and cattle herds in the lower Amazon floodplains are increasing at annual rates of 12% and 4%, respectively (Sheikh 2002). Simultaneously, forest cover has decreased to approximately 10% of the area of vegetated floodplain, with the majority of the forested area being secondary growth following deforestation for jute, timber, and agriculture (McGrath 2005, Sheikh 2002). In the floodplains of Santarém, Pará, deforestation and intensification of livestock husbandry have created conflicts among community stakeholders regarding management, land rights, and regulatory authority (Sheikh 2002). Conflict and trends in forest conversion are expected to increase with growing development pressures from the urban center of Santarém and the paving of BR-163. The capacity of institutions to inform decision-makers in appropriate management strategies for the floodplain is hindered by the paucity of data on the ecology, land-use change, and stakeholder values of the floodplains resources.

Initial research on the impacts of cattle and water buffalo on floodplain forests suggests that expanding unmanaged water buffalo and cattle herds are a potential threat to floodplain forest regeneration (Sheikh 2002). Research by the Brazilian

government's agricultural research agency (EMBRAPA) suggests these ecological impacts may be reduced through the application of management strategies, e.g. the exclusion of livestock by fencing, management of herd size and density, and removal of livestock during the flood season. However, few small-scale residents have the capital for the necessary infrastructure. Recent community-based initiative for livestock and forest management is demonstrated by local reforestation programs and the construction of fences to exclude livestock from forests that serve as fishing habitat. With fishing providing 31% of family incomes in floodplain communities of the Lower Amazon, the sustainable management of fishing habitat is a specific goal of community residents and partner institutions (Almeida 2004).

### **Summary**

The abundant natural resources of the *várzea* ecosystem have supported Amazonians for millennia. Despite a number of dynamic changes in land-use since European arrival, the ecosystem remains an essential resource as well as a biodiversity reserve for flora and fauna of the Amazon. The *várzea* around Santarém has supported multiple cycles of agricultural production, from maize and manioc planted by indigenous peoples, the cacao boom of 1755-1870, rubber plantations of the late 1800s, to the jute boom of 1930-1980. Meanwhile, the floodplain has consistently provided fishing habitat, non-timber forest products, timber and fuelwood, as well as fertile pasture for small-scale cattle ranching. The integrity of the *várzea* today is challenged by the intensification of cattle and water buffalo husbandry. The resilience of the system to land-use change gives hope that minimal efforts for improved management could create an opportunity for forests and grasslands to maintain their naturally high productivity and diversity. While much of the international attention for conservation and sustainable

management focuses on the vast forests of the uplands, it is important to recognize the economic, cultural, and ecological value of the Amazon floodplains. Their history of land-use indicates that the *várzea* is of immeasurable value for the future of Amazonia.

A



B



Figure 2-1. Jute cultivation on the *várzea* of Ilha do São Miguel. A) Drying jute fibers. B) Retting jute plants in the water to separate fibers. Photos courtesy of Christine Lucas.

CHAPTER 3  
EFFECTS OF SHORT-TERM AND PROLONGED SATURATION ON SEED  
GERMINATION OF AMAZONIAN FLOODPLAIN FOREST SPECIES

**Overview**

Seeds in seasonally flooded forests have adapted to submergence, such that some species may require flooding to break seed dormancy. In this study, we tested seed germination response to time in water among Amazonian floodplain species. To test short-term effects, seeds from ten flood-tolerant woody species were air-dried or placed in water (*i.e.*, saturated) for 45 h before germination. While non-pioneer species increased germination success after saturation, most pioneer species had higher germination success after air-dry treatments. Long-term saturation (removing seeds from water at two-week intervals over 12 weeks) revealed opposite responses among two flood-tolerant trees with different dispersal strategies. Whereas wind-dispersed *Pseudobombax munguba* seed germination rates decreased with increasing submergence time, water- and fish-dispersed *Crataeva benthamii* seed germination rates increased with submergence time, peaking at 6 wks and maintaining > 80% germination for up to 12 wks. Overall, no species required prolonged saturation to germinate. However, five of ten species required short-term saturation to initiate germination, and *Crataeva benthamii* provides an example of increased germination success with prolonged submergence. Strategies for avoiding prolonged submergence among study species included seed buoyancy, delayed fruit maturation, and dispersal mechanism. These results suggest there are diverse strategies among Amazonian trees for colonizing floodplains.

## Background

The alternating wet and dry periods of seasonally inundated wetlands are major driving factors for seedling recruitment (Grime 1979, Lopez 2001). Environmental cues for seed dispersal and germination such as moisture and oxygen availability are mediated by the timing of flood and low-water seasons (Leck 1989, Stella et al. 2006). In many riparian wetlands, germination often occurs soon after flood drawdown on recently exposed soils (van der Valk and Davis 1978, Middleton 2000, Stella et al. 2006). Prior to germination, seeds can be subjected to variable periods of saturation and hypoxia, which may threaten seed viability (Baskin and Baskin 1998). Seed tolerance of flooding can be advantageous as hydrochory is an important means of dispersal in flooded ecosystems (Middleton 2000, Lopez 2001). Seeds of wetland plants have variable responses to flooding, including enhanced germination (Martin et al. 1991, Jutila 2001, Cornaglia et al. 2009), reduced germination (Pierce and King 2007, Geissler and Gzik 2008), and delayed epicotyl emergence (Scarano et al. 2003). Some species may require anoxia associated with flooding to break seed dormancy (Jutila 2001). However, such adaptations have been poorly studied in tropical wetlands, despite evidence that some woody species may require exposure to anoxia for germination (Kubitzki and Ziburski 1994).

Seasonally flooded forests of the Amazon Basin have an extreme flood regime to which tropical tree species have adapted strategies for seed germination and establishment. Floodplain forests on the Amazon River are exposed to prolonged inundation of up to 7 months and average river-level fluctuations of up to 10 m (Goulding et al. 2003). Fruit maturation for the majority of arboreal species occurs during the flood season (Kubitzki and Ziburski 1994, Waldoff and Maia 2001). Seeds

are subsequently dispersed by vectors including water, fish, wind, and other vertebrates (Goulding 1980, Moegenberg 2002, Lucas 2008). While seeds pass through the digestive tracts of fish in a few days (Silva et al. 2003), they may spend up to several months underwater in hypoxic conditions or floating at the water's surface (Kubitzki and Ziburski 1994, Lopez 2001). In the case of such extreme flooding conditions, some species may not only tolerate prolonged submergence but also require a period of hypoxia to break seed dormancy. Dormancy prior to hypoxic exposure may be advantageous for timing seed germination with flood recession and the onset of low-water growing season. However, such a requirement would limit plant colonization of high-elevation forests or micro-topographic sites flooded supra-annually. Despite the importance of seed germination as a bottleneck for establishment on the floodplain, little is known about the germination behavior of the >900 species of Amazonian floodplain forests (Wittmann et al. 2006). Furthermore, few data are available to test the hypothesis that tropical species display dormancy that is broken by prolonged periods of submergence.

Seeds that do not require exposure to anoxia may still require imbibition (*i.e.*, water absorption) for germination. Many tropical forests species lack dormancy and germinate quickly after imbibition presumably to avoid seed predation and fungal attack (Garwood 1989). Imbibition is critical for germination and early seedling survival for most species (Bradford 1995), and as such is a common treatment to prime recalcitrant seeds (Baskin and Baskin 1998). Imbibition is generally rapid for seeds with permeable seed coats, requiring 10-14 h to saturate tissues without resulting in anoxia-related seed death (Baskin and Baskin 1998, Meyer et al. 2007). Similar to upland species, Amazonian floodplain forest species, particularly non-pioneers, are predicted to be

recalcitrant (*i.e.*, unable to survive desiccation Garwood 1989, Sautu et al. 2006), and as such display enhanced germination after only short-term imbibition.

The purpose of this study is to test the effects of short-term saturation and prolonged submergence on seed germination of floodplain tree species and explore evidence for saturation breaking seed dormancy. I use the term 'saturation' to include both instances in which seeds are completely submerged or floating on the water surface, depending upon seed buoyancy and time in water. Following saturation treatments, seeds were placed on moist, sterile sandy substrates in temperature-controlled germination chambers and monitored for time of radical emergence and full cotyledon expansion. I selected 10 woody species common to secondary floodplain forests on the Lower Amazon River to address the following questions: 1) What are the effects of short-term saturation (45 h) vs. long-term submergence (2-12 weeks) on seed germination rates and success?, 2) Is there evidence for prolonged submergence to break seed dormancy among flood-tolerant species?

## **Methods**

### **Study Region**

This study was conducted in floodplain forests within the municipality of Santarém, Pará, at the confluence of the Amazon and the Tapajós Rivers in Brazil (02°25'S, 54°42'W). In this region, extensive whitewater floodplains of up to 40 km wide, known as *várzea*, are composed of grasslands, lakes, stands of giant aroids (*Montrichardia arborescens*), and forested levees (Deneven 1984). The *várzea* is characterized by an annual, monomodal flood pulse, averaging 7.5 m in amplitude from 1975 to 2008 and peaking in mid-May to mid-June (Capitania dos Portos - Santarém 2008). Mean annual

rainfall is 2100 mm y<sup>-1</sup> (Fitzjarrald et al. 2008) with 80% falling during the rainy season (January–June; WinklerPrins 1999).

### **Study Species**

I selected ten woody species common to mid-low elevation floodplain forests of the Lower Amazon River (Sheikh 2002). *Vitex cymosa*, *Crataeva benthamii*, *Cordia tetrandra*, and *Cecropia latiloba* are considered early-mid secondary species (Worbes and Junk 1999) with foliar cotyledons and low shade-tolerance. *Vitex cymosa* disperses buoyant diaspores during flood drawdown, with four embryos encased in a single buoyant cork-like endocarp (Kubitzki and Ziburski 1994). *Cordia tetrandra* fruits throughout the flood season and disperses seeds with hard bony endocarps and a viscid mesocarp. *Pseudobombax munguba* is a widely-distributed species of late secondary forests that disperses seeds during flood drawdown by kapok fibers that suspend seeds in the air and on the water's surface (Worbes and Junk 1999). *Garcinia brasiliensis* and *Maytenus* sp. are shade-tolerant mid-late successional species with hypogeal storage cotyledons. *Tabernaemontana* sp. and *Casearia aculeata* are shade-tolerant forest understory species with dehiscent fleshy fruits.

### **Collection and Experimental Design**

Mature fruits of 10 species (hereafter referred to by genus, 3-1) were collected from 3 individuals per species in forest stands of the Ituqui (02°29'S, 54°24'W) and Tapará regions (02°21'S, 54°32'W) in June-July, 2006. Maturity was recognized by exocarp coloration or dehiscence before falling into the river. Fruits were transported in plastic bags to the Seed Laboratory at the Universidade Federal Rural da Amazônia (UFRA) in Santarém-PA. Within 1-3 days after collection, seeds were extracted from fruits by washing with untreated (non-chlorinated) well water in 0.5 m mesh size wire

strainers and dried in the shade for 1 h. A subsample of seeds was weighed and measured (length, width) with a digital caliper. Mature seeds without obvious damage were randomly assigned to one of two treatments, 45 h air-dried (dry treatment) and 45 h placed in water (wet treatment) in 11 x 11 x 3 cm plastic trays in an air-conditioned room (19-21°C). Well water was added to half the trays to 2.5 cm depth, to submerge non-buoyant species, and changed after 24 h to prevent stagnation. Number of seeds per treatment per species varied between 13 and 100 seeds with two replicates (seed trays) per species (except for 1 replicate for *Maytenus* and *Cordia*), as determined by seed availability.

Following treatments, smaller seeds, separated by species, were placed with sterilized tweezers in 11 x 11 x 3 cm plastic germination trays with a sterilized fine sand substrate. Larger seeded species, *Garcinia* and *Crataeva*, were placed in 15 x 30 x 4 cm germination trays. Sand substrate had been previously washed and sterilized in a drying oven at 150°C for 6 h. Prior to seeding, the substrate was saturated with distilled water (Baskin and Baskin 1998). Trays with seeds were placed in a germination chamber at 30°C under florescent lighting. Seeds and sand substrate were watered every 1-2 days to avoid desiccation. Germination, defined as radicle emergence, was monitored daily during the first week, then every 2-4 days during a 145-day period (June-December 2006). Germination success was the total percent seed germination of combined replicates. Germination rate was the number of seeds germinated per unit time, or days to 50% germination success (3-1). Seeds attacked by fungi were washed with a 1% solution of HCl in distilled water for 30 min, and substrate was changed when necessary. Germinants were transferred to a greenhouse after full expansion of cotyledons.

To test the effects of prolonged intervals of submergence on seed viability, *Cecropia*, *Pseudobombax*, *Crataeva*, and *Vitex* seeds (diaspores) were placed in separate buckets with untreated well-water that was changed daily. At two-week intervals, 50 seeds of each species were removed and placed in groups of 25 into 11 x 11 x 3 cm plastic germination boxes with a sterilized fine sand substrate in the germination chamber, as described above. Seeds were removed every two weeks until germination success reached 0% or termination of the study at 12 weeks. Seed germination was monitored every 2-4 days as described above.

*Pseudobombax*, *Crataeva*, and *Cecropia* seeds were also seeded in an open greenhouse at UFRA to measure potential differences in germination rate and timing in ambient conditions as opposed to indoor germination chambers. For each species, N=50 seeds were seeded on *terra preta* mixed with sandy soil in wooden boxes (65 x 40 x 12 cm). Seeds were monitored by the same protocol as in the lab, except germination is defined as cotyledon expansion, as radicle emergence was not visible.

### **Statistical Analyses**

Species-based comparisons of percent germination were conducted by 2-sample test for equality of proportions (Crawley 2007). To test the significant difference between germination curves in response to soaking and dry treatments, time-failure analysis was used where un-germinated seeds are considered right-censored data (Traveset et al. 2008). Kaplan-Meier survival probability functions were calculated using the `survfit()` function in the survival package for R 9.2.0 (Therneau 1999, R Development Team 2006). To compare response curves for seed treatments within each species, log-rank test statistics (Mantel and Haenszel 1959) and Gehan-Wilcoxon

test statistics (Peto and Peto 1972) were calculated using the `survdif` () function in R 9.2.0 (Pyke and Thompson 1986, Therneau 1999).

## Results

Five of ten species increased in germination success by 14-100% after 45-hour saturation versus air-drying (Figure 3-1). Among those five, none of the air-dried *Crataeva*, *Tabernaemontana*, and *Maytenus* seeds germinated, but saturated seeds achieved 69%, 62%, and 100%, germination success, respectively (Table 3-1). Three of the ten species (*Pseudobombax*, *Cordia*, and *Vitex*) had higher germination success (3-48% increase) following the air-dry treatment. Among *Pseudobombax* seeds, the difference between germination success in the two treatments was only 3%, but time to 50% germination was reduced by 10 days. Finally, *Cecropia* and *Laetia* had poor germination success overall (<20%) and small differences ( $\leq 3\%$ ) between treatments (Table 3-1). Log-rank test statistics showed significant differences in wet vs. dry treatments among all species except *Laetia* (Figure 3-1). Germination rates varied broadly across species, achieving 50% germination in 12-58 d among saturated seeds and 2-84 d among air-dry seeds (Table 3-1).

In the prolonged submergence experiment, more *Crataeva* seeds germinated with each additional two-week period up to 6 weeks, and germination success after up to 12 weeks saturation remained > 80% (Figure 3-2). *Crataeva* germination rates increased rapidly from 54 to 5 to 2 days with increasing submergence time of 2, 14, and 28 days, respectively. *Pseudobombax* seeds displayed similar germination rates and high germination success at > 90% after 0 and 14 days in water. In contrast, *Pseudobombax* seeds were unviable (0% germination) after 28 days in water. *Vitex* seeds decreased in germination rate and success (51% decrease) after soaking for 2 weeks. *Cecropia* had

low germination success (< 20%) across saturation times, and no apparent trends with increasing duration in water. Log-rank test statistics showed significant differences among germination curves within all species (Figure 3-2).

In greenhouse conditions with natural sunlight, *Crataeva* seeds achieved 82-100% germination success after 45 h in water. Saturation enhanced germination success by 24-32% in comparison to air-drying, and, unlike in the germination chamber, air-dry seeds germinated. Air-dried *Pseudobombax* seeds increased germination by 12-28% relative to saturated seeds. Saturated *Cecropia* seeds had higher germination success than in germination chambers (46% in 14 d), and air-dried seeds had low germination success (< 20%).

### **Discussion**

I found that short-term imbibition enhanced germination of five of ten species I evaluated. This response pattern is similar to that of many tropical forest recalcitrant species (Sautu et al. 2006). Long-term submergence was not required for germination, but rather enhanced germination of *Crataeva* and decreased germination of *Pseudobombax* and *Vitex*. Only one of four flood-tolerant species maintained high germination success over prolonged submergence, a potential strategy for maintaining seed viability over 1-4 months of submergence by Amazon River floodwaters. *Pseudobombax* and *Vitex*, highly tolerant of flooding as adults, displayed decreased germination success following prolonged submergence. Those species likely avoid prolonged submergence in hypoxic floodwaters via delayed seed dispersal during flood drawdown and diaspore morphology to promote buoyancy (Wittmann et al. 2007).

## **Effect of Short-Term Saturation on Seed Germination**

Short-term soaking treatments showed that imbibition was sufficient to initiate seed germination among floodplain forest species. Submergence of seeds in oxygenated water is a common treatment for recalcitrant seeds of tropical upland forests (Baskin and Baskin 1998). As dryness is an important limiting factor for moist tropical tree seed germination and early seedling survival (Slot and Poorter 2007), germination is often delayed until seeds imbibe sufficient water above a minimum seed moisture content (Vozzo 2002, Sautu et al. 2006). Imbibition is generally rapid for seeds with permeable seed coats, requiring 10-14 h to saturate tissues without resulting in anoxia-related seed death (Baskin and Baskin 1998, Meyer et al. 2007). Seed soaking over short periods in oxygenated water, as conducted here, likely increases seed water content, while not inducing dormancy due to hypoxia.

Pioneer and shade-tolerant species may have responded differentially to saturation due to differences in germination requirements. Germination cues for tropical pioneers include irradiance and temperature, cues for the presence of gaps in the forest canopy. Surface soils in gaps have low water availability (Marthens et al. 2008), for which some pioneers have adapted high tolerance of low moisture content (Daws et al. 2007). In Amazonian floodplains, exposed soils high in sediment (>70%) and clay composition (10-33%; unpubl. data), may have, low water availability at the surface, making germination on drier soils a potential advantage colonization by early successional species.

Seed germination among species with < 30% germination may have been reduced or delayed following saturation due to hypoxia while underwater, insufficient irradiance, or lack of other germination cues such as temperature change (Pearson et al. 2002).

*Cecropia latiloba* may have had exceptionally low germination rates due to low irradiance levels in germination chambers (Vazquez-Yanes and Orozco-Segovia 1990, Pearson et al. 2002). In a sunlit greenhouse, *Cecropia* had higher germination success. *Laetia corymbulosa* displayed exceptionally low germination rates (4-7%), and may also require light for germination (Guariguata 2000). In another study, *L. corymbulosa* germination increased from an average of 6% to 39% after 35 days in water, suggesting that this species may require prolonged flooding for germination (Wittmann et al. 2007, but see Kubitzki and Ziburski 1994). Our results indicated a variation in species-specific responses similar to upland tropical forests and suggested that many floodplain species have retained the ability to germinate without exposure to prolonged submergence (Scarano et al. 1997, Lopez 2001).

### **Effects of Long-Term Submergence on Seed Germination**

Specific seed responses to prolonged submergence provided an example of different germination strategies of two common floodplain trees, *Crataeva* and *Pseudobombax*. *Crataeva* showed increasing germination rates and success with increasing submergence time, reaching peak percent germination (98%) after 6 weeks. Its seed coat softened underwater, and in some cases split open to reveal the cotyledons, suggesting that soaking treatments may break physical barriers to germination. Enhanced germination success of *Crataeva* seeds after prolonged soaking may be attributed to morphological traits (e.g., impermeability) for enduring long-term submergence. In the field, *Crataeva* trees have non-buoyant fruits and seeds that fall into floodwaters where they are consumed by frugivores including fishes (Goulding 1980, Lucas 2008). As such, seeds are underwater for up to 4 months. In contrast, *Pseudobombax* seeds performed best in air-dry treatments. *Pseudobombax* seeds are

wind-dispersed seeds that also land on the water, suspended above the water's surface by kapok fibers. Due to rapid flood drawdown (2-6 cm per day; Capitania dos Portos - Santarém 2008) during the dispersal period, seed submergence time may be minimal before germinating on exposed floodplain soils. Only among *Pseudobombax* was long-term saturation found to inhibit germination. Although hydrochorous and ichthyochorous, *Vitex* diaspores displayed higher germination success after drying. *Vitex* fruits mature during flood drawdown and diaspores are buoyant, which may limit submergence time.

Whether species like *Crataeva benthamii* experience dormancy that is broken by submergence depends upon how dormancy is defined (Baskin and Baskin 1998). Observations from this study suggest that *Crataeva benthamii* may have an impermeable seed coat that is slowly made permeable by prolonged submergence. Such traits may be considered a form of morphological dormancy (Baskin and Baskin 1998). Kubitski and Ziburski (1994) demonstrate that seeds of some species of Amazonian floodplains exposed to an oxygen-poor nitrogen atmosphere break physiological seed dormancy. Regardless of the mechanism by which flooding suppresses germination, species germinated quickly when released from anaerobic conditions. In tropical floodplains, rapid germination maximizes seedling growth during the dry season (Wittmann et al. 2007). Concordantly, study species here all germinated in < 3 months.

An alternative hypothesis for observed differences between seed germination in short-term wet and air-dry treatments may be that air-dry seeds dehydrated. While the air-drying treatment was considered a control for saturation, the loss of moisture to cool air may have adversely affected the germination of recalcitrant seeds. While the

reduced germination rates observed in *Garcinia* and *Casearia* could reflect desiccation, it is questionable whether seed moisture content was reduced to critical levels of 30-70% (Baskin and Baskin 1998). While *Garcinia* can display decreased viability after partial dehydration (Rodriguez et al. 2000), other studies of *Garcinia* in ambient conditions support our findings of lower germination without prolonged submergence (Kubitzki and Ziburski 1994). The same study reports 92% germination for *Crataeva* seeds when removed from fruits, suggesting that the 0% germination of air-dried seeds reported here may be a result of dehydration or immaturity.

## **Summary**

I found differential responses among species to saturation and submergence treatments. Species responses to short-term saturation grouped by successional guild, whereby pioneers had enhanced germination rates and/or success in dry treatments, but shade-tolerant species had enhanced germination after 45 hours of saturation. Prolonged submergence responses, however, differed among co-occurring species of similar successional stages. Seed tolerance of prolonged submersion likely corresponded with the timing of fruit maturation and dispersal mode. The observed variation in seed response to imbibition and submergence may explain niche differentiation and diversity in floodplain forests.

These findings have implications for both *várzea* forest and fisheries restoration efforts. Floodplain forests are a principal food source for fishes throughout the Amazon Basin (Araujo-Lima and Goulding 1997). I contribute to a growing pool of data on germination rates for *várzea* forest species (Parolin 2001b, Wittmann et al. 2007). I also tested easily applied germination treatments of variable time in water that can be crucial for enhancing the germination success of some species. In particular, I report

germination rates for many seeds consumed by frugivorous fishes in the Amazon (e.g., *Crataeva*, *Pseudobombax*, *Cordia*, *Cecropia*; Goulding 1980, Claro-Jr et al. 2004, Lucas 2008). Forest restoration by planting seedlings is one proposed way to increase local populations of *Colossoma macropomum* and *Piaractus brachypomus*, two commercially valuable fish for the region (McGrath et al. 2005). Further studies on seed germination of the > 200 fruiting tree species consumed by Amazon fishes (Goulding et al. 1993) would be useful for forest and fisheries restoration projects.

Table 3-1. Seed characteristics of the ten study species in order of wet-tolerant (higher germination after saturation) and dry-tolerant (high germination after air-drying) species.

Species	Family	CM	Mass (g)	H x w (mm)	G <sub>wet</sub>	G <sub>dry</sub>	Logrank test	T50 <sub>wet</sub>	T50 <sub>dry</sub>
Wet-tolerant species									
<i>Garcinia brasiliensis</i> *	Clusiaceae	CH	2.93	27.8 x 14.6	1.00 (42)	0.86 (42)	$\chi^2=29.1$ , p<0.0001	58	84
<i>Maytenus</i> sp.	Celastraceae	CH	0.374	13.4 x 9.75	1.00 (15)	0 (13)	$\chi^2=293$ , p<0.0001	53	-
<i>Crataeva bentharii</i> **	Brassicaceae†	PE	0.290	9.16 x 4.67	0.69 (100)	0 (100)	$\chi^2=965$ , p<0.0001	47	-
<i>Tabernaemontana</i> sp.	Apocynaceae	PE	0.047	9.65 x 3.82	0.62 (55)	0 (55)	$\chi^2=406$ , p<0.0001	16	-
<i>Casearia aculeata</i>	Salicaceae††	PE	0.011	3.80 x 2.83	0.23 (77)	0.04 (76)	$\chi^2=66.6$ , p<0.0001	-	-
Dry-tolerant species									
<i>Pseudobombax munguba</i>	Bombacoideae, Malvaceae	PE	0.045	5.32 x 4.01	0.97 (100)	1.00 (100)	$\chi^2=160$ , p<0.0001	12	2
<i>Vitex cymosa</i>	Lamiaceae‡	PE	0.354	10.3 x 6.68	0.52 (42)	0.90 (42)	$\chi^2=11.1$ , p<0.0001	19	7
<i>Cordia tetrandra</i>	Boraginaceae	PE	0.139	-	0 (21)	0.24 (21)	$\chi^2=53.4$ , p<0.0001	-	-
<i>Cecropia latiloba</i>	Urticaceae	PE	0.002	2.53 x 1.42	0.18 (100)	0.15 (100)	$\chi^2=9.7$ , p=0.0018	-	-
<i>Laetia corymbulosa</i>	Salicaceae††	PE	0.069	3.07 x 2.60	0.04 (100)	0.07 (100)	$\chi^2=0$ , p=0.901	-	-

Cotyledon morphology (CM) is indicated as phanerocotylar epigeal (PE) or cryptocotylar hypogeal (CH). Seed size is shown as wet weight (Mass) and height x width. Germination proportion (G) and time (days) to 50% germination (T50) are provided for wet and dry treatments, with sample sizes in parentheses. Log rank test statistics indicate differences in germination curves in time-failure analysis. Families are shown according to the Angiosperm Phylogeny Group (Stevens 2001 onwards). Common names in order listed in table: *bacuri*, *ashua*, *catauari*, *culhão de porco*, *limorana*, *munguba*, *tarumã*, *urua*, *embauba*, and *meracoroa*.

\**Garcinia brasiliensis* = *Rheedia brasiliensis* (Tropicos.org 2009)

\*\**Crataeva bentharii* = *Crateva tapia* (Cornejo and Iltis 2008)

†formerly Capparidaceae or Capparaceae

††formerly Flacourtiaceae

‡formerly Verbenaceae

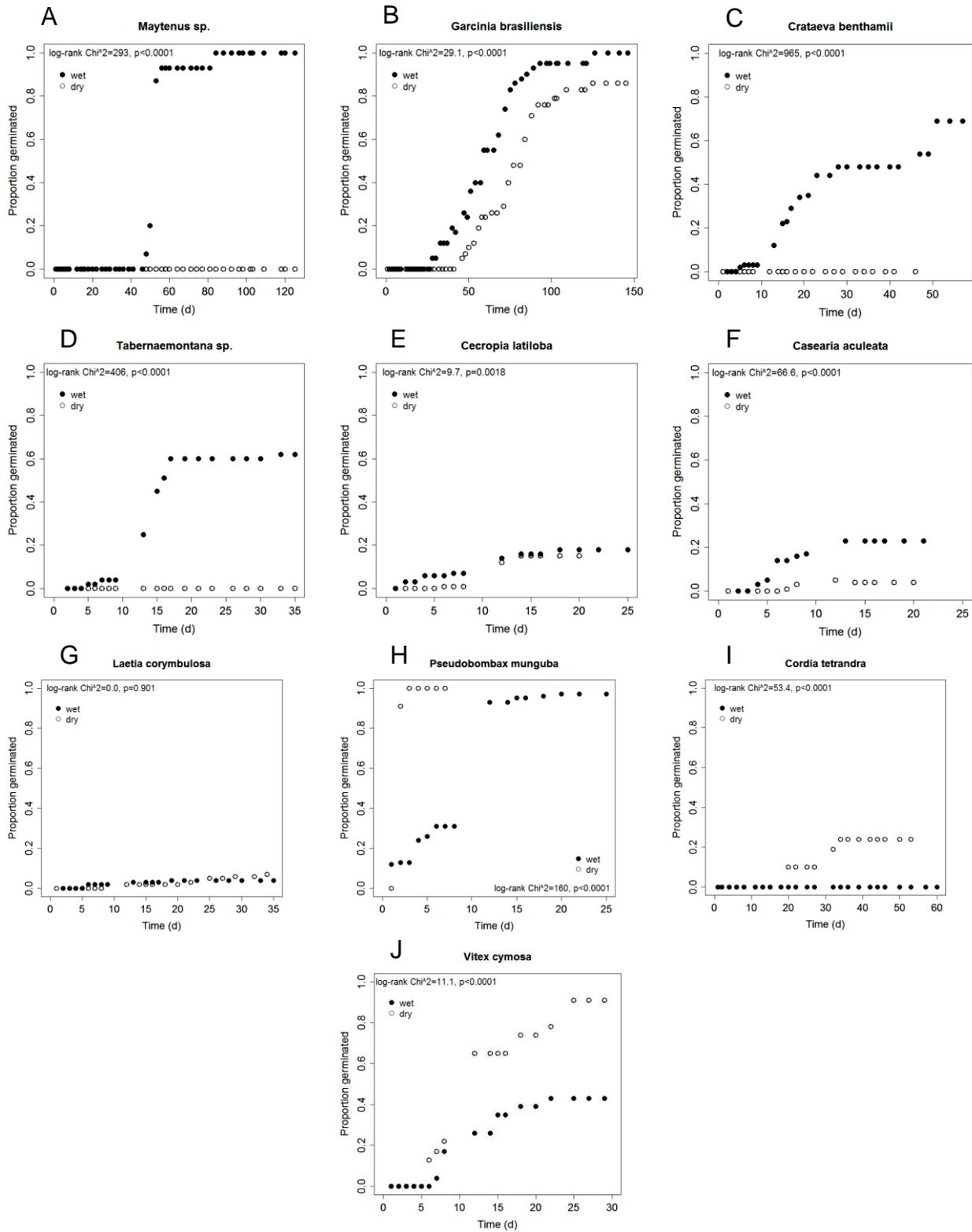


Figure 3-1. Germination curves for ten study species with log-rank test statistics for differences in Kaplan-Meier survival curves. Species names indicated above (A-J).

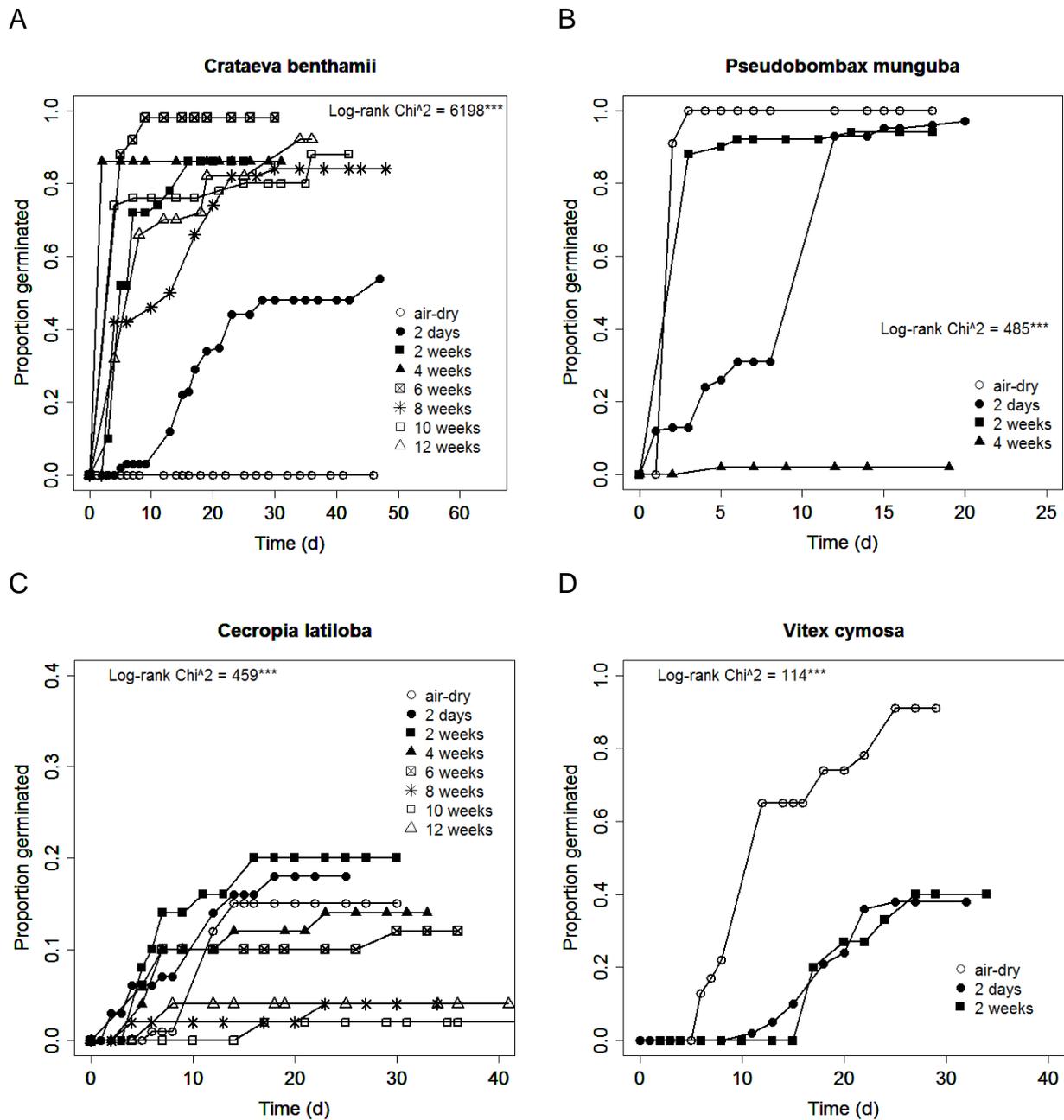


Figure 3-2. Germination curves and log-rank test statistics for significant (\*\*\*) differences in Kaplan-Meier survival curves for four study species (A. *Pseudobombax munguba*, B. *Crataeva benthamii*, C. *Cecropia latiloba*, D. *Vitex cymosa*) subjected to prolonged waterlogging. X-axis scale changes for each species, depending upon timing of termination of the experiment.

## CHAPTER 4 EFFECTS OF MULTIPLE STRESSORS ON SEEDLING SURVIVAL AND GROWTH IN A TROPICAL FLOODPLAIN FOREST

### **Overview**

Environmental stressors act synergistically to affect plant communities. Species-specific responses to stressors mediate species composition and diversity across gradients of stress. We investigate whether species show trade-offs in stress tolerance or whether a few species emerge as tolerant of multiple stressors. I tested the main and interactive effects of flood duration and mechanical damage on seedling survival and growth of ten woody species of seasonally flooded Amazonian forests. Seedlings were planted in common gardens along gradients of flooding and light availability. Half of the seedlings were clipped at 5 cm aboveground, removing ~50% total plant biomass. I found that damage severely limited growth and survival during a critical growth window in the low-water season. After one year, clipping reduced seedling survival by an average of 50% and reduced relative growth rates such that most species failed to recover lost biomass. Flood duration of 3-6 months of submergence had no effect on seedling survival for all but two low-flood-tolerant species. Damage effects on seedling growth and survival were independent of flood duration. Increased light availability enhanced seedling growth and survival and ameliorated the negative effects of damage, particularly among pioneer species. Tropical flood-tolerant species have a broad range of tolerance to mechanical damage, a key limiting factor for seedling persistence in forests. Damage tolerance and flood tolerance among species was highly correlated, suggesting that these combined stresses favor the persistence of a few species. These results highlight the importance of examining multiple factors to understand seedling regeneration.

## Background

Plants cope with a suite of environmental stresses that act synergistically to affect population dynamics. While the individual effects of stress on plants are well-known (Kozlowski and Pallardy 2002), the interactive effects of multiple factors are an increasingly critical aspect of understanding plant communities (Chapin et al. 1987, Tockner et al. 2010) and predicting their responses to anthropogenic disturbance and climate change (Aber et al. 2001, Rhind 2009). Combined stresses can cause severe declines in plant growth (James et al. 2005, Ali et al. 2011) or survival (Niinemets 2010). Alternatively, species adapted to one kind of stress can be tolerant of additional stresses (Myers and Kitajima 2007). Species differences in response to multiple stressors ultimately affect species composition and successional change in forests (Butler et al. 2007). The selective pressure of environmental stresses on trees can be greatest on seedlings, a critical bottleneck for species persistence in tropical forests (Grubb 1977, Poorter 2007).

Flooding stress is a major driver of population dynamics in riparian and coastal ecosystems. Research based on temperate species previously suggested that tree seedlings only tolerated short-term submergence due to the build-up of phytotoxins during anaerobic respiration (Kozlowski 1984). However, Amazonian tree seedlings in seasonally flooded forests display remarkable tolerance to complete submergence and darkness for < 270 days (Parolin 2002, Parolin 2009). No temperate or boreal tree species are apparently able to withstand complete submergence for such prolonged periods as found in Amazonia (Junk et al. 1989, Mitsch and Gosselink 2000). There is little understanding of how seedlings tolerate such prolonged flooding (Ferreira et al.

2009) as well as how flooding interacts with other stresses prevalent in floodplain forests to affect seedlings (but see Wittmann and Junk 2003, Parolin et al. 2010).

Damage to plants from herbivory, litterfall, and disturbances such as logging is pervasive in many ecosystems (Bond and Midgley 2001). Mechanical damage removes biomass and disrupts apical meristem dominance in tree seedlings, thus placing a stress on plants for additional resources for recovery. Seedlings are thought to be particularly vulnerable to damage as a result of their size, shallow root system, and limited reserves for tissue repair and defense (Weisberg et al. 2005, Holdo et al. 2009). Species vary in sprouting ability to sprout as a result of seed size, cotyledon morphology (Green and Juniper 2004), and storage reserves (Canham et al. 1999). Large-seeded species have enhanced reserves for sprouting after damage, thus increasing their survival in comparison to small-seeded species (Harms and Dalling 1997). The sprouting ability of species in tropical floodplain forests is poorly known.

The interactive effects of prolonged flooding and damage could have severe effects on seedlings. Seedlings in floodplain forests are affected by myriad damage agents, including trampling and grazing by herbivores when floods recede (Robertson and Rowling 2000). Flooding stress limits growth by reducing carbon assimilation and potentially losing carbon to rotted roots or prematurely senesced leaves (Kozlowski and Pallardy 1997). As such, flooded seedlings may have reduced reserves available for tissue repair and defense after damage (Waring 1987). Although damage and flooding could decrease seedling survival, regeneration via sprouting is a survival strategy for many flood-tolerant species (Frangi and Lugo 1991, Deiller et al. 2003, Ernst and Brooks 2003). Given the resource demands associated with flood tolerance and

sprouting, a trade-off between flood and damage tolerance and may explain species differences in survival.

Light availability acts synergistically with flooding to affect species survival in floodplain ecosystems. A flood-/shade-tolerance trade-off model explains species distribution in temperate floodplain forests, whereby high-flood-tolerant species tend to be light-demanding and low-flood-tolerant species are shade-tolerant (Hall and Harcombe 1998, Battaglia and Sharitz 2006). Increased light availability increases photosynthetic activity in the growth season, thus increasing storage reserves and plant height for submergence tolerance in the flood season (Hall and Harcombe 1998, Parolin 2002). This model was based on observations that few shade-tolerant species persist in dark understories of temperate flooded forests (Walker et al. 1986). Few studies in the tropics examine how light and flood level interact to affect woody plant survival (but see Wittmann and Junk 2003).

I examined the main and interactive effects of flood duration, mechanical damage, and light availability on woody seedlings in a seasonally flooded forest of the Lower Amazon River. Stem clipping simulated one type of mechanical damage that occurs in forest understories. Using a series of common gardens along a flood gradient, I addressed three questions: (1) What are the effects of flood duration, light availability, and stem damage on seedling growth and survival?; (2) How does variation in flood duration interact with damage and light availability to affect seedling growth and survival?; (3) Are there trade-offs in flooding and damage tolerance and flooding and shade tolerance that explain species differences in survival?

## Methods

### Study Site

This study was conducted in floodplain forests near Santarém, Pará, Brazil (02°25'S, 54°42'W). The Santarém region lies within the Transverse Dry Corridor of the Amazon Basin, with rainfall of 1800-2000 mm y<sup>-1</sup> and 5 consecutive dry months with rainfall below 100 mm (July-November; Sombroek 2001). Flood waters of the Amazon River in the region peak on average in mid-May, rising 7-8 m and extending up to 40 km from the main channel. Peak flooding lags behind the mid-rainy season by 1-3 months (Figure 4-1). Floodplains in the region are a mosaic of natural grasslands, forested levees, lakes, and dense stands of a giant aroid (*Montrichardia arborescens*), all shaped by the annual flood regime. Many floodplain forests in the region are only ~20-80 years old, having regenerated on abandoned plantations of jute (*Corchorus capsularis*), cacao plantations (*Theobroma cacao*), and stands of rubber trees (*Hevea brasiliensis*) (WinklerPrins 1999, Sheikh 2002). Cattle and water buffalo ranching are currently prominent threats to floodplain forests in the region, as animals move through forests to reach grasslands for pasture, trampling soils and seedlings (Sheikh 2002). For this study I selected forests with medium to low cattle impact as indicated by cattle head counts and hoof print density (Sheikh 2002) to avoid highly compacted soils. Forest stands were 100-150 m wide and located on private property on 3 levees 1-5 km apart.

### Experimental Design

I used a regression design experiment (Cottingham et al. 2005) to measure changes in seedling growth and survival as a function of flood level and mechanical damage in three floodplain forests. Using a split-plot design, 21 fenced plots of 5 x 5 m

(N = 7 per forest) were established in random locations across a flood gradient, and two treatments (damaged and undamaged) to were applied seedlings within plots. Plots were off trails and cattle were excluded from plots with barbed wire fences > 0.5 m from the nearest planted seedling. When plots were flooded by the river, I measured water column depth in plots at peak flood levels (15 May 2008) with a weighted line dropped into the water from a canoe. Relative flood level was calculated as the difference between maximum river level (8.36 m a.s.l. in 2008) and water column level (0.7 to 2.5 m in 2008). To calculate flood duration, I used daily river levels from Capitania dos Portos in Santarém to count the number of days for the river to rise from relative flood level of each plot to 8.36 m (peak) and then fall back to the same level. Flood duration is the days seedling belowground tissues are waterlogged in saturated soil because the number of days of complete submergence varies with seedling height (see Results).

Seedlings were germinated from seeds collected from nearby floodplain forests in the flood season (May-July 2007) and grown in shaded, raised nursery beds in a mixture of composted cattle manure, palm fibers and floodplain soil. Ten species (after first mention referred to by genus) were selected that vary in flood tolerance, cotyledon morphology, and seed size (Table 4-1). After expansion of the first true leaves, seedlings were transplanted to individual bags in a shaded forest understory and watered daily for 2-8 wk. After floodwaters receded, seedlings (N=2268) were transplanted into plots at randomly assigned locations 50 cm apart. Newly planted seedlings had 2-9 true leaves ( $\pm 1$  within species), mostly due to species differences in the timing of germination.

Three weeks after transplanting (October 2007), all seedlings were measured and a subset (N=210; one per species per plot) was harvested to measure initial biomass. Unharvested seedlings were randomly assigned to a treatment, damaged or undamaged. Stems of seedlings assigned to “damaged” treatment were clipped with scissors (Green and Juniper 2004) and true leaves below 5 cm on the stem were removed. Clipping removed maximum aboveground biomass without removing the dormant buds at cotyledon nodes that provide seedlings with the physiological capability to sprout (Harms and Dalling 1997, del Tredici 2001). Foliar cotyledons (when present) were not removed as this could deplete carbohydrate reserves and reduce phanerocotylar seedling survival (Kitajima 2003). There were five seedlings per species per treatment per plot, except for *Guarea guidonia*, for which there were four seedlings per plot. Seedlings in both treatment groups were subjected to natural damage during the study. Damage to stems was classified as “broken stem” or “dried apex,” in which the apical meristem appeared dry and a new dominant shoot sprouted.

### **Measurement of Environmental Covariates**

Light availability was estimated with hemispherical canopy photos taken at 50 cm aboveground at the center of each plot in the late dry season (November 2007) after most deciduous species had already flushed new leaves. Photos were taken just before sunrise and oriented to magnetic north with a Nikon Coolpix 990 and FC-E8 Fisheye lens, with an F-stop of 5.8 and automatic speed (Frazer et al. 2001). Photos were analyzed with Gap Light Analyzer Version 2.0 to calculate % transient total light [ $100 * (\text{transient diffuse} + \text{direct light}) / (\text{direct} + \text{diffuse radiation incident})$ ] as a measurement of light availability to seedlings, accounting for both direct light from overhead gap openings and diffuse light reflected off leaves (Frazer et al. 1999). Soil

cores were collected at four points 1.5 m from the plot center in the low water season (January 2008). At each point, litter depth was measured with a ruler and averaged across the plot. The 7 x 10 cm soil cores were extracted with a PVC tube and rubber mallet and divided into two sections, 0-5 cm and 5-10 cm depth, placed in plastic bags, and weighed in the lab. A 25 g subsample from each core was dried at 105°C for 48 h, and used to calculate volumetric soil water content, SWC ( $1 - (\text{Mass}_{\text{dry}} / \text{Mass}_{\text{wet}})$ ), and soil bulk density ( $1 - (\text{SWC} * \text{Mass}_{\text{wet core}}) / \text{Vol}_{\text{core}}$ ). Soil pH was measured with an Oyster portable pH kit and standard polymer pH electrode (Model #6015WC, Extech, Waltham, MA) from a 20 g subsample of wet soil mixed with 40 mL of deionized water. To measure soil texture, sand particles were extracted with a sieve (#230: 0.063 mm), silt was decanted, and the clay fraction was calculated by subtracting the sand and silt fractions from total dry weight of the sample in the LBA-Santarém soil laboratory (Kettler et al. 2001, adapted by Beldini). Soil samples collected in September 2008 were sent to the Embrapa-Belém soil laboratory in Brazil for soil nitrogen (organic N,  $\text{NH}_3$ , &  $\text{NH}_4$ ) concentration, using the Kjeldahl method, and extractable soil phosphorous, using the Mehlich method (Embrapa 1997).

### **Measurement of Survival and Growth**

I measured seedling survival, height, and diameter at 5-week intervals for seven censuses when seedlings were above water (October 2007-February 2008 and August-September 2008) to span a single monomodal flood pulse (Figure 4-1). Because plots emerged from flood waters at different times, the February and August censuses of 2008 were incomplete, excluding 7 and 9 plots, respectively, that were still underwater. All seedlings were harvested after one year to measure final above- and belowground biomass after drying to a constant weight. Relative growth rate (RGR) was calculated

as  $[\ln(\text{biomass}_{\text{final}}) - \ln(\text{biomass}_{\text{initial}})]/\text{time}$  for the change in total dry plant biomass from initial (October 2007) to final harvest (September 2008), where time = 11.25 months. Initial biomass for damaged seedlings was considered as biomass after damage. Initial biomass of unharvested seedlings was estimated by the linear regression equation for initial plant biomass as a function of stem volume of all species combined ( $h \cdot \pi \cdot (\text{mid-stem diameter}/2)^2$ ;  $r = 0.84$ ).

### **Tolerance and Resource Allocation Trade-offs**

Trade-offs between flood tolerance and shade-tolerance as well as flood tolerance and damage tolerance were examined by comparing species survival according to the following definitions of tolerance. Flood tolerance was defined as the proportion of undamaged seedlings surviving the flood season. Damage tolerance was defined as the difference between seedling survival in damaged and undamaged treatments per plot during the low-water season. For example, if the difference between survival of damaged and undamaged seedlings of a given species was 5%, it would be considered high damage-tolerant, while if the difference was 80% it would be considered low damage-tolerant. A damage / flood tolerance trade-off among species was explored by plotting the damage tolerance and flood tolerance of all species. Shade tolerance was defined as the survival of seedlings in low-light levels (9-12% canopy openness) in the low water season. A shade / flood tolerance trade-off among species was explored by plotting shade tolerance and flood tolerance levels for all species. Trade-offs between growth and survival were also explored by comparing RGR and percent survival of damaged and undamaged seedlings for each species (Kitajima 1994, Sack and Grubb 2001).

## Statistical Analyses

The effects of damage, flooding, light, damage × flooding and damage × light on the proportion of survival within each plot were tested with logistic weighted generalized linear mixed models (GLMMs) with a binomial error structure and Laplace approximations for model fitting (Crawley 2007). Models were weighted by sample size using a two-vector response variable for survival – number of successes (N live) and failures (N dead; Crawley 2007). This approach avoids errors associated with transformation and violation of model assumptions, such as normality and constant variance (Bolker et al. 2009). Forest and plot were included as random effects. As anova tables were not available for GLMMs with binomial errors in R, I used the anova function with a Chi-squared test statistic to test the significance of removing each parameter from the full model (Crawley 2007). The relationship between seed size and seedling height of the previous census and seedling survival was tested with binomial models.

To explore the effect of flooding and mechanical damage on survival over time, the unequal time intervals between censuses due to flooding violated assumptions for standard survival analysis (Collett 2003). As such, survival is analyzed in three key survival windows: one-year (October 2007 – September 2008), low water season (October 2007-January 2008), and flood season (January-August 2008). To test for differences between low water and flood season survival, I used a GLMM repeated measures model with season, flooding, damage, and light as fixed effects. To test for survival differences between censuses, a similar GLMM was constructed with census month instead of season as a fixed effect. Damage treatment was included as a random effect nested within plot in both models. Models for survival of pooled and

individual species were created in R 2.9.0 (R Team 2006) using the lme4 package (Bates and Maechler 2009).

The effects of damage, flooding, light, damage × flooding, and damage × light on relative growth rates (RGR) were analyzed with linear mixed models, with plot and forest as random effects, using the nlme package (Pinheiro et al. 2008). The same models were created for other growth response variables – root:shoot ratios, post-flood shoot biomass, and seedling height – for comparison. To determine if seed size correlated with average stem volume ( $h \cdot \pi \cdot (\text{mid-stem diameter}/2)^2$ ) of sprouts within species, I used Pearson's product-moment correlation coefficients (Crawley 2007). To compare average initial and final root biomass within species to determine if root biomass of damaged seedlings changed over a year, I used two-way pair-wise t-tests. All analyses were conducted using R 2.9.0 (R Team 2006).

## Results

### Effect of Flooding and Damage on Annual Seedling Survival

Seedling survival after one year for pooled species was decreased by damage, but no effects of flood duration or a flood × damage interaction were found (Table 4-2). Damage decreased average seedling survival after one year by 29% ( $z = 4.3$ ,  $p < 0.0001$ , Figure 4-2), but differences between undamaged and damaged seedling survival varied widely among species (12-75%; Table 4-1). Damage decreased flood season survival by almost half (43%), whereas undamaged seedlings lost only 34% of individuals ( $t_9 = 3.7$ ,  $p = 0.0047$ ). Survival differed by species (Table 4-2), supporting species-specific models (Table 4-3). Although species cotyledon morphology helped explain one year survival ( $\chi^2 = 259$ ,  $p < 0.0001$ ), the effect disappeared when removing the three low-flood-tolerant species, all with hypogeal cotyledons (*Hevea*, *Guarea* and

*Ormosia*). Species with large seeds did not display enhanced survival after damage ( $r = -0.33$ ,  $t = 0.98$ ,  $p = 0.35$ ). Damage consistently decreased survival within species after one year, with the exception of *Coccoloba* ( $\chi^2 = 7.2$ ,  $p = 0.066$ ) and *Hevea* for which all individuals died during flooding. Seedlings in the 'undamaged' treatment group experienced natural damage to stems. During the low water season, 3% (N=31 of 1117) of undamaged seedlings had dry apices and 1% had broken stems. In the flood season, an additional 14 of 579 (2%) seedlings displayed dried apices and 31 (5%) broken stems.

Flood duration (113-208 days) had no apparent effect on pooled species survival over one year (Table 4-2). Given an average height of 25 and 12 cm for undamaged and damaged seedlings after one year, the average estimated duration of entire seedling submergence was 100-200 d and 107-200 d, respectively. During flooding, 5 species senesced leaves (*Vitex*, *Guarea*, *Cordia*, *Hevea*, *Pseudobombax*; Figure 4-3) and 5 were evergreen. I found no interactive effects of flooding and damage on seedling survival among or within species (Table 4-2). Within species, flooding had no effect on survival, except for *Guarea* and *Ormosia*, which showed decreasing survival with increasing flood duration, reaching 0% survival at approximately 160 days (Figure 4-4, Table 4-2). Species differed in response to flooding among damaged seedlings ( $\chi^2 = 402$ ,  $p < 0.0001$ ) but not among undamaged seedlings ( $\chi^2 = 5.4$ ,  $p = 0.49$ ).

### **Seasonal Differences in Survival**

Survival differed by season ( $z = 16.6$ ,  $p < 0.0001$ ), whereby average low-water season survival (November to January;  $0.90\% \pm 0.37$  SD) was higher than flood season survival (February-August;  $0.77\% \pm 0.23$  SD; Figure 4-5). While undamaged seedlings suffered decreases in survival only during the flood season (Figure 4-4), damaged

seedlings suffered decreases in survival in both the dry period (November - December) and flood season (August, Table 4-3). The drop in damaged seedling survival in December occurred at the end of the peak dry period in the region, following three consecutive months of rainfall < 100 mm (August-November 2007; Figure 4-5). Despite the potential for low water availability in dry upper soil horizons to decrease damaged seedling survival, there was no correlation between survival and soil water content in January 2008 ( $\chi^2 = 1.3$ ,  $p = 0.26$ ; range: 21-37% in soils of 3% sand, 79% silt, and 18% clay, on average). Flood duration had a marginally significant effect on flood season survival ( $\chi^2 = 5.8$ ,  $p = 0.055$ ). There was a flood  $\times$  damage interactive effect on flood season survival ( $\chi^2 = 5.6$ ,  $p = 0.018$ ; Figure 4-2). Within species, *Cordia*, *Mouriri*, and *Trichilia* showed an interactive effect in which damage enhanced the deleterious effects of prolonged inundation on flood season survival (Table 4-3).

### **Effect of Light on Survival**

Light, measured as percent canopy openness, was consistently the most important environmental factor for predicting seedling survival. The positive effects of light availability on one-year survival were greater for damaged than undamaged seedlings (Table 4-2, Figure 4-2). Light enhanced the survival of pioneer species with epigeal cotyledons (e.g., *Cordia* and *Pseudobombax*), but not for most shade-tolerant species (Figure 4-6). In addition to canopy openness, models were improved by incorporating litter depth on a log scale ( $\chi^2 = 11.2$ ,  $p = 0.0008$ ,  $\Delta AIC=9.2$ ) and the interaction between log litter depth and damage ( $\chi^2 = 4.6$ ,  $p = 0.031$ ,  $\Delta AIC=2.6$ ). Litter depth was particularly important for explaining low survival among damaged seedlings, which were more vulnerable to burial (estimate = -0.54,  $z = 2.6$ ,  $p = 0.0098$ ).

## Effects of Damage and Flooding on Relative Growth Rates

Among species, both damage and increasing flood duration reduced RGR (Figure 4-7). There was no apparent interaction between damage and flood duration for pooled species ( $F = 0.06$ ,  $p = 0.80$ ) and within most species (Table 4-4). Species had a strong effect on RGR ( $F = 6.0$ ,  $p < 0.0001$ ). Within all surviving species except *Garcinia*, damaged seedlings had low RGR, indicating that most species failed to recuperate lost biomass in one year. Increasing flood duration decreased RGR among five species (Table 4-4), and fast-growing species such as *Cordia* and *Vitex* had steeper declines in RGR across the flood gradient than slow-growing species (*Garcinia* and *Trichillia*). Pioneer species (*Pseudobombax*, *Cordia*) experienced growth spurts immediately after flood drawdown.

## Effects of Damage and Flooding on Biomass Allocation

Clipping removed an average of 50% ( $\pm 73\%$  SD) of total plant biomass, ranging from 19% ( $\pm 7\%$ ) in *Garcinia* to 65% ( $\pm 31\%$  SD) in *Vitex* (Table 4-5). Seedlings responded to damage by sprouting a median of 1 (range 0-4) aboveground shoots, generally from the cotyledon node or leaf node closest to the point of damage. The biomass of newly sprouted shoots 5 weeks after damage did not correlate with seed size ( $r = -0.19$ ,  $t_8 = -0.54$ ,  $p = 0.60$ ) nor after 1 yr ( $r = -0.45$ ,  $t_6 = 1.2$ ,  $p = 0.26$ ), indicating that seed size does not explain new shoot biomass. The biomass of new shoots, however, did correlate with initial plant size ( $r = 0.98$ ,  $t_{347} = 102$ ,  $p < 0.0001$ ). Damaged seedlings had higher root:shoot ratios one year after damage than undamaged seedlings (Table 4-6), but these effects were significant within only four species (Table 4-4). As this difference was likely a result of the damage treatment and not differential allocation to roots, I compared estimated initial and final root biomass for all species.

Only for *Coccoloba*, *Garcinia*, and *Trichilia* were roots significantly bigger after one year ( $t = 2.5$ ,  $p = 0.015$ ;  $t = 6.9$ ,  $p < 0.0001$ ;  $t = -3.6$ ,  $p = 0.0007$ , respectively).

Root:shoot ratios were the only biomass measurement to display a strong damage  $\times$  flood duration interaction ( $F = 9.6$ ,  $p = 0.006$ ). Root:shoot ratios among damaged seedlings were greater than those of undamaged seedlings across the gradient of increasing flood duration (Figure 4-8). A positive correlation between root:shoot ratios and flood duration was observed among five species, but the interactive effect was observed within one species (Table 4-7). Shoot extension in the two months after flood recedence was also affected by an interaction between flooding and damage ( $F = 7.2$ ,  $p = 0.016$ ), whereby undamaged seedlings were able to allocate more biomass to aboveground shoots at higher elevations than damaged seedlings.

### **Effect of Light on Growth and Biomass Allocation**

Light availability increased RGR ( $F = 11.3$ ,  $p = 0.0039$  for pooled species; Table 4-4 for within species). However, light did not affect root:shoot ratios, except for two species (*Vitex* and *Coccoloba*, Table 4-7) for which shoot biomass was relatively higher with high light availability. Neither RGR nor root:shoot ratios were affected by an interaction between light and damage (Table 4-6). Incorporating all independent environmental variables into a linear mixed model, manual backward stepwise selection revealed that RGR is a function of damage ( $F = 190$ ,  $p < 0.0001$ ); canopy openness ( $F = 69$ ,  $p < 0.0001$ ); flood duration ( $F = 20.9$ ,  $p = 0.0018$ ); litter depth ( $F = 10.3$ ,  $p = 0.012$ ); and nitrogen  $\times$  litter depth ( $F = 28.0$ ,  $p = 0.0007$ ).

### **Species Trade-offs for Flood, Damage, and Shade Tolerance**

There was a positive correlation between flood tolerance and damage tolerance among species ( $r = 0.84$ , Figure 4-9). Highly flood and damage tolerant species

Coccoloba and Garcinia, both had relatively slow growth rates and high root:shoot ratios. Garcinia was highly damage tolerant and had the lowest percent biomass removed by clipping. A positive correlation between shade tolerance and flood tolerance was also found ( $r = 0.64$ , Figure 4-10). Species with high survival in low light conditions also displayed high survival after flooding. Coccoloba and Trichilia, two large woody shrubs, were highest in shade and flood tolerance.

A negative relationship between survival and growth among undamaged seedlings was observed, such that species with rapid RGR had lower survival rates (Figure 4-11). This trend, however, was largely driven by two extremes: the rapid RGR / low survival of Ormosia and Guarea and the slow RGR / high survival of Coccoloba. In contrast, damaged seedlings showed the opposite trend, with survival increasing with RGR (Figure 4-11). For example, although Coccoloba was the most tolerant of damage in terms of survival, it ranked 5th in RGR of resprout biomass. Vitex, a damage-tolerant and light-demanding species, also had high root:shoot ratios and slow RGR as well as early leaf senescence (Figure 4-3). The average RGRs of undamaged and damaged seedlings within species were not correlated ( $F=0.15$ ,  $p=0.70$ ,  $R^2= 0.11$ ), indicating different rates of growth vs. re-growth following damage.

## **Discussion**

The purpose of this study was to explore how flood-tolerant seedlings respond to mechanical damage along gradients of flooding and light availability. I found that damaged seedlings have lower survival than undamaged seedlings in the flood season, but the response of damaged seedlings to flooding is not dependent upon flood duration. The independence of the effects of flood duration and damage after one year for survival and growth implies that damage does not affect seedling tolerance to long

periods of anoxia and darkness (Parolin 2009). Complete submergence for 3-6 months did not affect seedling survival, except for two species with low flood tolerance. In contrast to flooding, damage substantially reduced seedling survival and growth, such that most species were unable to recover lost biomass within one year of damage. However, more open canopies alleviated the negative effects of damage on growth and survival, particularly among fast-growing species. Species varied widely in their response to damage, but I did not find a trade-off between damage and flood tolerance nor between shade tolerance and flood tolerance. Rather, a few species emerged as highly tolerant of both prolonged flooding and shade. These results are among the few available to understand how such extremely flood-tolerant tree seedlings respond to damage incurred during the critical growth season.

### **Independence of Effects of Flooding and Damage on Growth and Survival**

In contrast to the growing evidence for the importance of interactive effects of stress and disturbance in plant population dynamics, I found little evidence to support the hypothesis that mechanical damage interacts with flood duration to affect seedling growth and survival. Damaged seedlings were more susceptible to death during the flood season, although their susceptibility did not increase at extremely prolonged flood periods (180-207 d). The time scale over which I measured interactive effects in this study is important. During the flood season, damage interacted with flood duration to affect seedling survival, but this effect was damped across a year, such that there was no effect over one year. Seedling persistence under the sequential perturbations of damage and flooding may be attributed to the 4- to 5-month gap between damage and flooding events. A single damage event during the early growth season allows some recovery of photosynthetic tissue, shoots, and reserves that may later facilitate flood

tolerance and diminish submergence time. Floodplain forest seedlings are likely subject to multiple damage events from herbivory, browsing, litterfall, and trampling. The effect of repeated damage events throughout the growing season could select for highly damage-tolerant species and potentially reduce seedling community diversity.

Repeated damage to woody plants by ungulate browsing in an Alaskan riparian forest was found to interact with erosion and accretion of flooded areas to alter successional trajectories (Butler et al. 2007).

Damaged seedlings may have maintained constant survival rates with extremely prolonged flooding due to the relative increase in root:shoot ratios with increased flood duration (del Tredici 2001). The increase in root:shoot ratio among damaged seedlings is likely a consequence of removal of aboveground biomass for most species, rather than active investment in root biomass as a response to clipping. Among the species ranking top four in survival, three displayed an increase in allocation to roots among damaged seedlings over one year. While root biomass is not directly correlated with storage reserves (Canham et al. 1999), the relative increase in root biomass may indicate allocation to storage reserves. Future studies should investigate carbohydrate reserve availability in flood-tolerant seedlings and allocation to sprouts vs. anaerobic respiration and adventitious root production during flooding.

### **Strong Effects of Damage on Growth and Survival**

Damage is pervasive in tropical forest understories (Clark and Clark 1989, Alvarez-Clare and Kitajima 2009). Although the role of damage in seedling communities is less known for tropical floodplain forests, this study shows that damage differentially affects species growth and survival (Fine et al. 2004). Given reductions in biomass, height, and the vulnerability of small stems to burial by litter and sediment

deposition, damaged seedlings were predicted to have a severe disadvantage in survival compared to undamaged seedlings. Although damage substantially reduced survival, responses varied widely among species (12-75% survival). Species differences in survival of damaged seedlings did not support the hypothesis that large-seeded species with belowground storage cotyledons would have higher survival (Harms and Dalling 1997, Green and Juniper 2004, Baraloto and Forget 2007). Given that damage was applied at 4-9 weeks after germination, seedling dependence on cotyledon reserves for new shoots may be low (Kitajima 1996, Myers and Kitajima 2007). Storage reserves in root and stem tissues after damage could explain species differences in survival (Myers and Kitajima 2007), as species with higher root biomass and slower relative growth rates tended to have higher survival after damage in this study. Oddly, some species with epigeal cotyledons also displayed high root:shoot ratios and low RGR, contrary to the typical allocation patterns among upland tropical seedlings (Paz 2003). Such responses among 'fast-growing' species may be due to relatively low light levels in the forest understory and unobserved additional damage or disease defense in damaged seedlings. Overall, species variation in survival suggests that mechanical damage agents, when present, are an important selective force on species composition and distribution in floodplain forests.

The growth and survival advantage for seedlings in high light conditions has led to the hypothesis that increased light availability permits increased establishment by flood-tolerant species (Battaglia et al. 2000, Parolin 2002). Light enhances resource availability necessary for flood tolerance (Hall and Harcombe 1998) and damage recovery (Kabeya and Sakai 2005). In this study, survival and growth after damage

were enhanced by light availability, particularly for light-demanding species. Moreover, high light availability decreased the difference in survival and growth between damaged and undamaged seedlings of light-demanding species. Among mid-late successional species with storage cotyledons, the effects of light and damage were independent (Baraloto and Forget 2007). High light availability makes damaged seedlings less susceptible to death likely via increased carbon reserves for damage recovery (Kabeya and Sakai 2005). However, a canopy openness of 9-19% was still insufficient for seedlings to recover a positive carbon balance in one year after stem loss.

There was substantial decrease in survival of damaged seedlings during the peak dry season. Drought is a potentially important factor for floodplain seedling survival (Parolin 2001a, Lopez and Kursar 2007, Parolin et al. 2009), but I were unable to provide direct evidence for limited water availability to seedlings. Following three consecutive months of extremely low and infrequent rainfall (Figure 4-1), damaged seedlings could experience drought stress that reduced survival during the peak dry season. Although variation in soil water content did not explain dry season survival, the low rainfall and low water availability of silt-loam soils with 10-33% clay fraction (Brady and Weil 2000, Guyot et al. 2007) could limit water available to shallow roots. Nonetheless, the dry season decline in survival is confounded by the effect of time, as seedlings are most vulnerable to mortality at early stages in development (0-2 months) (Alvarez-Clare and Kitajima 2009).

### **Flood Duration Effect on Seedling Survival**

Based on species zonation along a flood gradient, variable flooding stress should differentially affect seedling survival among species (Worbes et al. 1992). While species differed in overall survival, I found no effect of increased flood duration on

seedling survival, except for low-flood-tolerant species *Guarea* and *Ormosia*, and the submergence-intolerant *Hevea*. For *Guarea* and *Ormosia*, there was a distinct threshold for survival at ~140-160 d flooding. Flood-tolerant seedlings of the Amazonian floodplain species *Himatanthus sucuuba* survived prolonged flooding by maintaining high alcohol dehydrogenase (ADH) activity in root tissue, which prevented the build-up of toxic acetaldehyde during anaerobic respiration (Ferreira et al. 2009). The lack of an effect of flood duration on seedling survival in most species may simply indicate their high flood tolerance and broad species ranges across the flood gradient. Given the changes in climate and topography on a geological time scale (Hoorne 2006), many species in the floodplain may have adapted to very broad ranges in flood duration.

### **Species Resource Allocation Trade-offs**

Species trade-offs in resource allocation are thought to be a key mechanism for maintaining species diversity in tropical forests (Wright 2002). Species should display different strategies for survival and growth in response to many stresses, for which seedlings have limited reserves to permit tolerance (Grime 1977). If flooding and damage place competitive demands on plant resources, species should display a trade-off between damage and flooding tolerance. In this study, ten species showed no trade-offs to support this hypothesis. Rather, a few species emerge as highly tolerant of both flooding and damage. Those species share traits of high root:shoot ratios and low RGR, in concordance with other studies showing that high allocation to belowground reserves is advantageous for both damage and flood tolerance (Kozłowski 1984, del Tredici 2001, Myers and Kitajima 2007). If belowground reserves foster damage and

stress tolerance, then such an attribute may represent a single strategy to cope with a combination of stress and disturbance (Craine 2005).

Species differences in survival suggest tolerance to multiple stressors among few species. There was little evidence for a flood-/shade-tolerance trade-off, whereby species with high flood tolerance have low shade tolerance, while low-flood tolerant species have high shade tolerance. Such a trade-off has explained why shade tolerant species occur at higher elevations (Battaglia and Sharitz 2006) and why fewer species occur in some shady, low elevation floodplains (Menges and Waller 1983). Our results suggest that light availability and flood level are 'coarse filters' for species survival (Battaglia et al. 2004), and that survival varies widely according to multiple abiotic conditions as well as random events such as litterfall or herbivory. Species also did not sort in survival in the shade according to their physiological shade tolerance (Hall and Harcombe 1998). For example, *Coccoloba*, a species with epigeal cotyledons, had extremely high shade tolerance, while *Hevea*, with storage cotyledons, had low shade tolerance. Such responses suggest that species sort in survival primarily by flood tolerance, and that high flood tolerance may permit persistence in the shade. In Amazonian floodplain forests, very few species have fast growth rates sufficient to avoid submergence by floods of 1-4 meters depth in forests (Parolin et al. 2002). A tolerance vs. escape model proposes that species at lower elevations must have strategies to tolerate submergence at the seedling phase, while species at higher elevations may escape submergence by long stem growth in the first growth season (Parolin 2002). Our results support such a model, whereby species at low elevations are tolerant of flooding and shade.

A growth-survival trade-off explained species differences in survival among undamaged seedlings. Species should fall along a continuum of fast-growing pioneer species with low survival to slow-growing, long-lived species with high survival (Kitajima 1994, Wright 2002). However, in this study, species were not positioned along the growth-survival continuum in order of shade-tolerance. Given that survival during flooding is not a function of cotyledon morphology or RGR (Parolin 2002, Battaglia et al. 2004), I might expect species position on the survival-growth continuum to be a function of some measurable value of flood tolerance (e.g., ADH production). In contrast to undamaged seedlings, damaged seedlings with higher RGR also displayed higher survival. In the case of damaged seedlings, high RGR could increase storage reserves available for survival and recovery after damage (Myers and Kitajima 2007).

## **Summary**

The goal of this study was to explore the main and interactive effects of flooding and mechanical damage on seedling population dynamics and to compare species-specific responses. Given the potential frequency of damage events in forest understories, damage-tolerant species are likely to persist, ultimately influencing successional trajectories and adult species composition (Grubb 1977, Bond and Midgley 2001, Laurance and Curran 2008). The interactive effect of flooding and damage was significant only in the flood season. The observed seedling responses to damage are thus influenced by the time of measurement, and likely by the timing of damage and stress events. These results suggest substantial resilience among stress-tolerant seedlings in disturbed and stressed environments. The vast majority of seedlings in tropical forests suffer damage before reaching juvenile stages/sizes (Kammesheidt 1998, Scariot 2000). Given the variable intensity of flooding and drought

(Schongart and Junk 2007, Marengo et al. 2008), overlapped by disturbance from wind, fire, logging, herbivores, and introduced ungulates in many tropical floodplain ecosystems (Anderson et al. 1999, Finlayson 2005, Junk and de Cunha 2005), sprouting may be a key strategy for seedling survival (Kozlowski 1992).

Table 4-1. Physiological traits of ten floodplain forest study species.

Species	Family	Cot	Seed (mg)	Survival (%)		RGR		Root:shoot	
				Undam.	Damaged	Undam.	Damaged	Undam.	Damaged
<i>Coccoloba ovata</i>	Polygonaceae	PEF	39	94 ± 13	82 ± 21	0.044	-0.015	0.84 ± 0.05	0.96 ± 0.07
<i>Pseudobombax munguba</i>	Malvaceae (Bombacoideae)	PEF	45	74 ± 28	29 ± 37	0.102	0.027	0.51 ± 0.11	0.64 ± 0.10
<i>Vitex cymosa</i>	Lamiaceae	PEF	350	87 ± 17	61 ± 36	0.048	-0.017	0.71 ± 0.16	1.07 ± 0.15
<i>Cordia tetrandra</i>	Boraginaceae	PEF	140	81 ± 29	29 ± 29	0.084	-0.018	0.80 ± 0.02	1.14 ± 0.05
<i>Ormosia paraensis</i>	Fabaceae	PES	600	14 ± 29	0 ± 0	0.164	-	0.37 ± 0.06	-
<i>Mouriri acutiflora</i>	Melastomataceae	CHS	230	79 ± 22	4 ± 10	0.055	-0.063	0.47 ± 0.06	1.05 ± 0.10
<i>Guarea</i> sp.	Meliaceae	CHS	580	11 ± 23	2 ± 7	0.084	-0.068	0.82 ± 0.05	0.97 ± 0.37
<i>Trichilia singularis</i>	Meliaceae	CHS	390	85 ± 14	56 ± 32	0.075	-0.006	0.62 ± 0.06	1.16 ± 0.11
<i>Garcinia brasiliensis</i>	Clusiaceae	CHS	2930	86 ± 20	59 ± 29	0.078	0.031	0.55 ± 0.06	1.19 ± 0.13
<i>Hevea brasiliensis</i>	Euphorbiaceae	CES	3930	0 ± 0	1 ± 4	-	-	-	-

Seed size is presented in fresh weight (mg). First year survival (mean & SD) is the percent of undamaged seedlings and of damaged seedlings averaged across 21 plots with standard deviations. Abbreviations for Cotyledon morphology (Cot): Phanerocotylar epigeal foliar (PEF), Cryptocotylar hypogeal storage (CHS), Cryptocotylar epigeal storage (CES). Mean relative growth rates over one year [RGR ( $\text{g} \cdot \text{g}^{-1} \cdot \text{cm}^{-1}$ )] and average root:shoot ratios (mean & SD) harvested at the end of the experiment are shown.

Table 4-2. Survival response to flood level, damage, and light in three time periods: one-year, low-water season, and flood season. Results shown for pooled species and individual species.

Species	Damage		Flood duration		Light		Flood x damage		Light x damage	
	X <sup>2</sup>	p	X <sup>2</sup>	p	X <sup>2</sup>	p	X <sup>2</sup>	p	X <sup>2</sup>	p
One year	186	<0.0001	3.37	0.19	15.05	0.0005	2.8	0.094	5.58	0.018
Low-water season	386	<0.0001	1.00	0.60	10.53	0.0052	0.054	0.82	0.097	0.76
Flood season	172	<0.0001	5.81	0.055	10.74	0.0047	5.56	0.018	2.27	0.13
<i>Coccoloba</i> <sub>e</sub>	7.19	0.066	0.05	9.98	3.64	0.16	0.042	0.84	0.14	0.71
<i>Pseudobombax</i> <sub>e</sub>	64.1	<0.0001	0.77	0.68	9.03	0.011	0.26	0.61	1.06	0.30
<i>Vitex</i> <sub>e</sub>	29.0	<0.0001	4.94	0.085	22.4	<0.0001	0.86	0.35	8.40	0.0037
<i>Cordia</i> <sub>e</sub>	78.5	<0.0001	2.10	0.35	6.51	0.039	2.08	0.15	0.81	0.37
<i>Ormosia</i> <sub>e</sub>	30.9	<0.0001	8.76	0.013	4.36	0.11	<0.001	1.00	<0.001	1.00
<i>Mouriri</i> <sub>h</sub>	142.6	<0.0001	4.45	0.11	1.24	0.54	0.87	0.35	1.11	0.29
<i>Guarea</i> <sub>h</sub>	8.25	0.041	6.82	0.033	1.00	0.61	0.26	0.61	0.003	0.96
<i>Trichilia</i> <sub>h</sub>	31.5	<0.0001	1.91	0.38	8.61	0.013	0.91	0.34	1.97	0.16
<i>Garcinia</i> <sub>h</sub>	21.6	<0.001	5.61	0.060	1.24	0.54	0.75	0.39	0.24	0.62

Chi-squared test statistics with p-values for pair-wise model comparisons between the full model with and without each parameter removed are shown. Cotyledon morphology is displayed as a subscript (e = epigeal, h = hypogeal) for each genus. *Hevea* is excluded from individual species due to 0% survival after one year.

Table 4-3. Summary of generalized mixed model results for the effects of damage, flooding, light, and their interactions on seedling survival in the low-water and flood season.

Species	Damage		Flooding		Light		Flood x damage		Light x damage	
	X <sup>2</sup>	p	X <sup>2</sup>	p	X <sup>2</sup>	p	X <sup>2</sup>	p	X <sup>2</sup>	p
LOW-WATER SEASON										
<i>Coccoloba</i> <sub>e</sub>	4.73	0.19	2.65	0.27	8.82	0.012	0.89	0.34	3.95	0.047
<i>Pseudobom</i> <sub>e</sub>	56.0	<0.0001	3.77	0.15	5.99	0.050	1.57	0.21	0.028	0.87
<i>Vitex</i> <sub>e</sub>	13.4	0.0039	5.79	0.055	15.2	0.010	2.31	0.12	4.77	0.029
<i>Cordia</i> <sub>e</sub>	43.8	<0.0001	5.37	0.068	8.15	0.017	1.37	0.24	1.54	0.21
<i>Ormosia</i> <sub>e</sub>	181	<0.0001	4.78	0.09	1.97	0.37	0.70	0.40	0.078	0.78
<i>Mouriri</i> <sub>h</sub>	127	<0.0001	2.47	0.29	2.50	0.29	2.47	0.12	2.17	0.14
<i>Guarea</i> <sub>h</sub>	50.0	<0.0001	0.34	0.84	2.32	0.31	0.32	0.57	0.0054	0.94
<i>Trichilia</i> <sub>h</sub>	14.5	0.0023	5.11	0.078	0.61	0.74	0.94	0.33	0.0079	0.93
<i>Garcinia</i> <sub>h</sub>	1.99	0.58	2.95	0.23	0.52	0.77	0.12	0.73	0.044	0.83
<i>Hevea</i> <sub>h</sub>	61.9	<0.0001	2.13	0.34	1.06	0.59	0.55	0.46	0.032	0.86
FLOOD SEASON										
<i>Coccoloba</i> <sub>e</sub>	16.3	<0.0001	3.85	0.15	0.29	0.86	2.46	0.12	0.06	0.80
<i>Pseudobom</i> <sub>e</sub>	41.9	<0.0001	0.86	0.84	7.29	0.063	0.77	0.68	0.35	0.84
<i>Vitex</i> <sub>e</sub>	32.7	<0.0001	4.51	0.21	22.5	<0.0001	0.44	0.80	4.42	0.11
<i>Cordia</i> <sub>e</sub>	69.4	<0.0001	11.7	0.008	11.4	0.010	10.85	0.004	9.98	0.006
<i>Ormosia</i> <sub>e</sub>	24.3	<0.0001	6.94	0.074	2.76	0.25	0.050	0.98	0.050	0.98
<i>Mouriri</i> <sub>h</sub>	68.9	<0.0001	11.7	0.009	2.22	0.53	7.75	0.021	1.88	0.39
<i>Guarea</i> <sub>h</sub>	6.62	0.16	6.85	0.077	3.05	0.38	1.17	0.56	2.38	0.30
<i>Trichilia</i> <sub>h</sub>	34.1	<0.0001	6.58	0.087	14.7	0.002	6.51	0.039	5.31	0.070
<i>Garcinia</i> <sub>h</sub>	20.8	0.0003	8.34	0.039	1.57	0.67	1.04	0.60	1.05	0.59

Chi-squared test statistics with p-values are shown for pair-wise model comparisons between the full model with and without each parameter removed. Cotyledon morphology is displayed as a subscript (e = epigeal, h = hypogeal) for each genus. *Hevea* is excluded from B due to 0% survival after one year.

Table 4-4. Summary of generalized linear model results (F-tests & p-values) for the effects of flooding, damage, and canopy openness (light) on seedling relative growth rate (RGR).

Species	Damage		Flood duration		Light		Flood x damage		Light x damage	
	F	p	F	p	F	p	F	p	F	p
ALL	177.5	<0.0001	10.9	0.004	11.3	0.004	0.065	0.80	1.48	0.24
<i>Coccoloba</i> <sub>e</sub>	71.5	<0.0001	3.9	0.065	8.06	0.012	0.010	0.92	0.88	0.36
<i>Pseudobom.</i> <sub>e</sub>	93.9	<0.0001	4.4	0.053	9.1	0.008	4.69	0.058	1.56	0.24
<i>Vitex</i> <sub>e</sub>	44.9	<0.0001	7.5	0.015	8.6	0.010	0.001	0.99	1.47	0.24
<i>Cordia</i> <sub>e</sub>	66.7	<0.0001	7.2	0.017	6.0	0.03	4.18	0.066	0.002	0.97
<i>Ormosia</i> <sub>e</sub>	-		0.051	0.55	0.19	0.70	-	-	-	-
<i>Mouriri</i> <sub>h</sub>	28.6	0.033	18.8	0.001	13.6	0.002	-	-	-	-
<i>Guarea</i> <sub>h</sub>	183.2	0.047	1.56	0.34	1.25	0.38	-	-	-	-
<i>Trichilia</i> <sub>h</sub>	164.5	<0.0001	6.4	0.023	7.8	0.013	7.05	0.017	0.55	0.47
<i>Garcinia</i> <sub>h</sub>	56.8	<0.0001	10.8	0.004	6.5	0.022	0.09	0.76	0.009	0.93

Species listed by genera with cotyledon morphology in subscript (e = epigeal, h = hypogeal).

Table 4-5. Species traits and survival according to damage tolerance, flood tolerance, and shade tolerance of damaged and undamaged seedlings.

Species	Habit	Guild	Elevation	% Biomass lost ( $\pm$ SD)	Flood tolerance	Damage tolerance	Shade tolerance
<i>Coccoloba</i>	Shrub	Mid-late	Low	41 $\pm$ 19	97%	92%	67%
<i>Vitex</i>	Tree	Early	Low	65 $\pm$ 31	95%	85%	49%
<i>Trichilia</i>	Shrub	Mid	Low	44 $\pm$ 16	89%	85%	53%
<i>Garcinia</i>	Tree	Mid	Low	19 $\pm$ 7	88%	91%	67%
<i>Cordia</i>	Tree	Early	Low	55 $\pm$ 31	86%	63%	33%
<i>Psuedobombax</i>	Tree	Mid	Low-High	52 $\pm$ 32	83%	63%	24%
<i>Mouriri</i>	Tree	Mid	Low	53 $\pm$ 14	81%	47%	37%
<i>Guarea</i>	Tree	Mid-late	High	52 $\pm$ 23	15%	71%	0%
<i>Ormosia</i>	Tree	Mid	High	52 $\pm$ 18	15%	54%	0%
<i>Hevea</i>	Tree	Introduced	High	62 $\pm$ 13	0%	21%	0%

Damage tolerance = average difference between monthly survival of undamaged and damaged seedlings; flood tolerance = proportion of undamaged seedlings surviving the flood season (February-September); and shade tolerance = survival in low light (9-12% canopy openness).

Table 4-6. Summary of generalized linear model results (F-tests & p-values in parentheses) for the effects of damage, flood duration, light availability on three growth parameters of seedlings over one year: relative growth rate (RGR), root:shoot ratios, and shoot growth after the flood season, averaged across all species.

Species	Damage		Flood duration		Light		Flood x damage		Light x damage	
	F	p	F	p	F	p	F	p	F	p
RGR	177.5	<0.0001	10.9	0.0045	11.3	0.0039	0.07	0.80	1.48	0.24
Root:shoot	296.4	<0.0001	16.7	0.0009	0.74	0.40	9.6	0.006	0.67	0.43
Post-flood growth	26.5	<0.0001	8.1	0.012	4.08	0.062	7.2	0.016	5.92	0.028

Table 4-7. Summary of results from linear mixed models (Chi-squared tests and p-values in parentheses) on the effects of damage, flood duration, and light availability on root:shoot ratios of seedling species, listed by genera with cotyledon morphology in subscript (e = epigeal, h = hypogeal).

Species	Damage		Flood duration		Light		Flood x damage		Light x damage	
	X <sup>2</sup>	p	X <sup>2</sup>	p	X <sup>2</sup>	p	X <sup>2</sup>	p	X <sup>2</sup>	p
ALL	296	<0.0001	16.7	0.0009	0.74	0.40	9.62	0.006	0.67	0.43
<i>Coccoloba</i> <sub>e</sub>	0.20	0.66	71.5	<0.0001	8.06	0.012	0.01	0.92	0.88	0.36
<i>Pseudobom.</i> <sub>e</sub>	9.6	0.015	1.76	0.21	0.011	0.92	5.64	0.045	1.07	0.33
<i>Vitex</i> <sub>e</sub>	6.17	0.026	13.3	0.0024	9.11	0.008	4.59	0.058	0.59	0.45
<i>Cordia</i> <sub>e</sub>	3.33	0.095	1.31	0.27	0.58	0.46	3.03	0.11	1.42	0.26
<i>Ormosia</i> <sub>e</sub>	-	-	0.12	0.76	2.49	0.26	-	-	-	-
<i>Mouriri</i> <sub>h</sub>	13.6	0.066	7.62	0.014	1.87	0.19	-	-	-	-
<i>Guarea</i> <sub>h</sub>	0.43	0.63	0.47	0.57	4.55	0.17	-	-	-	-
<i>Trichilia</i> <sub>h</sub>	23.4	0.0002	14.6	0.0015	0.84	0.37	3.11	0.097	2.02	0.17
<i>Garcinia</i> <sub>h</sub>	1.12	0.28	2.74	0.015	2.14	0.049	0.32	0.75	0.093	0.93

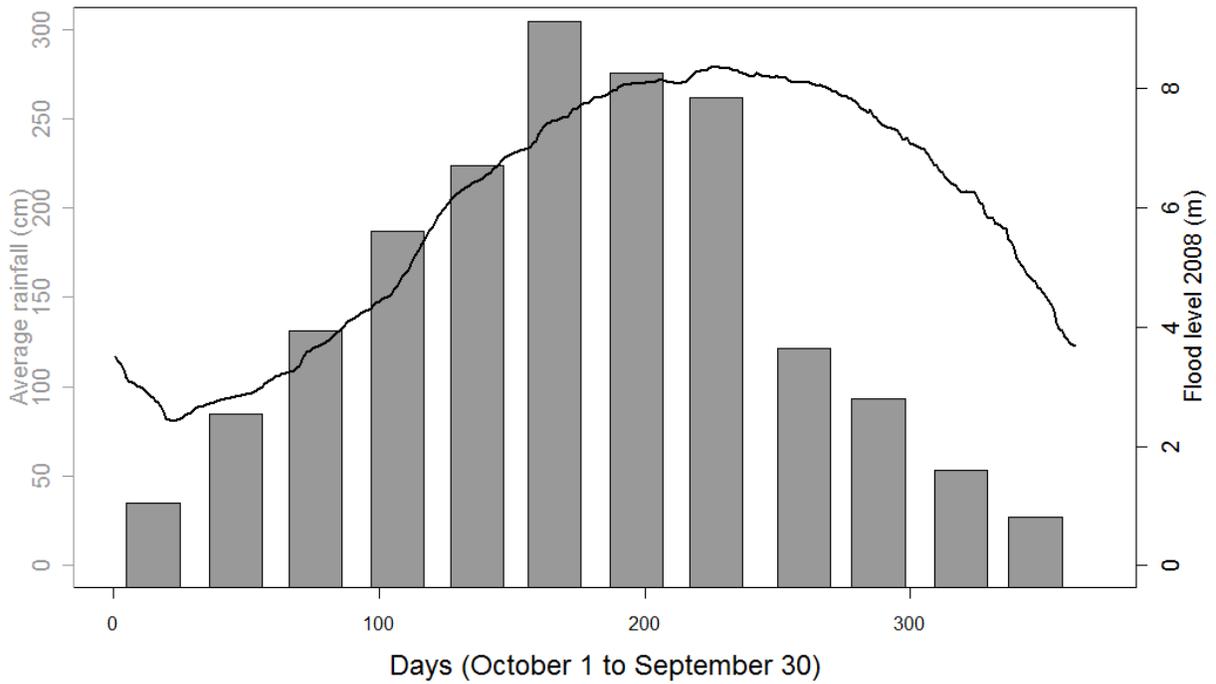
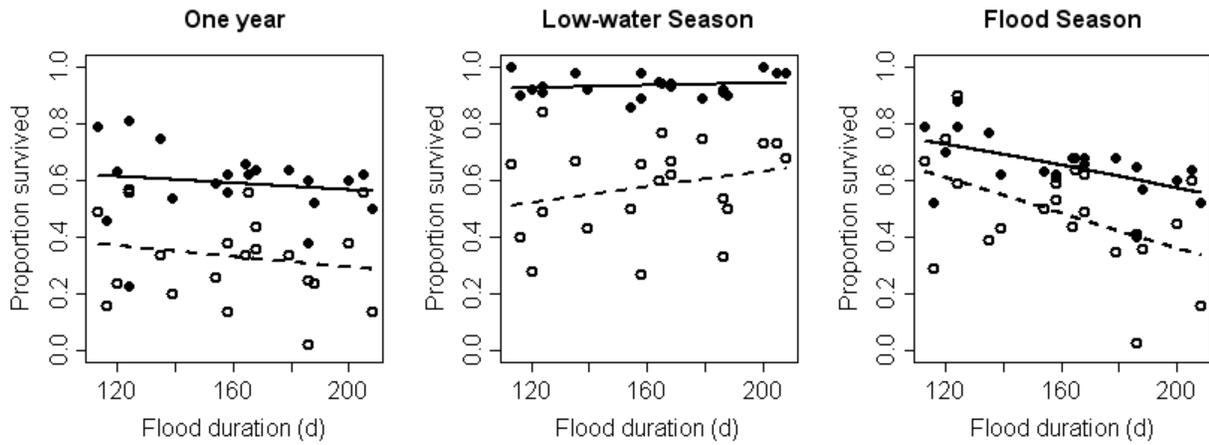


Figure 4-1. Rainfall and flood pulse in the study region. Mean monthly rainfall from 1982-2008 on the left y-axis was provided by the Large-Scale Biosphere-Atmosphere (LBA) Station in Santarém-PA. Change in river level from day 0 (01 October 2007) to day 365 (30 September 2008) is indicated on the right y-axis (Capitania dos Portos - Santarém 2008).

A



B

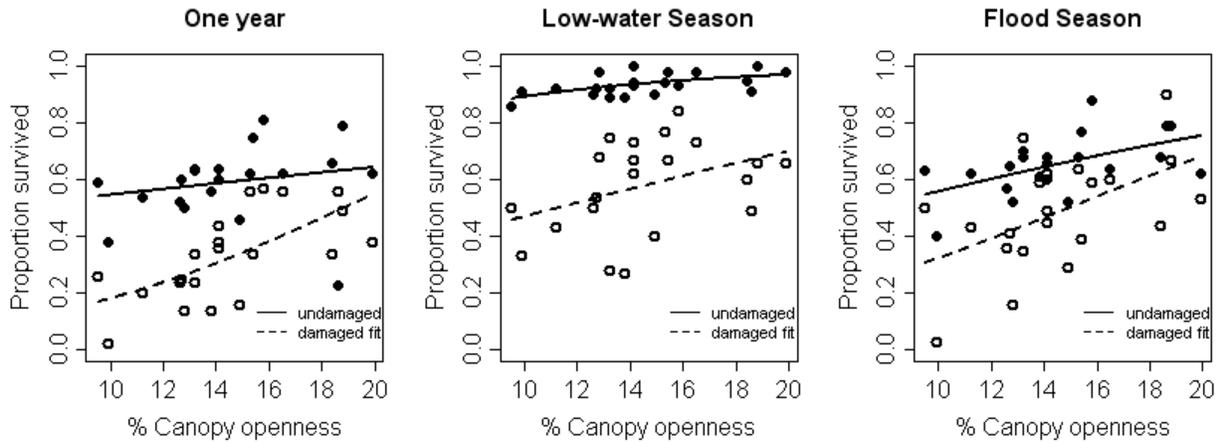


Figure 4-2. Seedling survival across a gradient of flood levels (A) and light availability (B) for undamaged (solid dots) and damaged (white dots) seedlings, averaged across species. Lines are weighted regression model fit to the data for undamaged (solid line) and damaged (dashed line) seedlings.

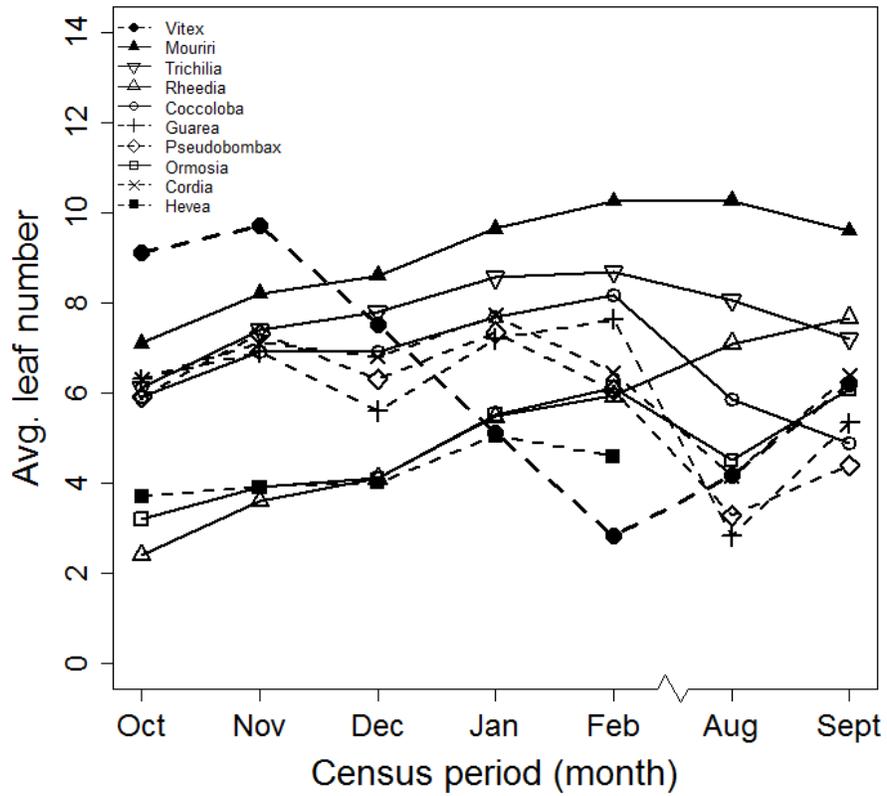


Figure 4-3. Average leaf number of undamaged seedlings for all species over time. Deciduous species are indicated with dashed lines, evergreen species with solid lines. Note the early decline in leaf number for *Vitex cymosa*.

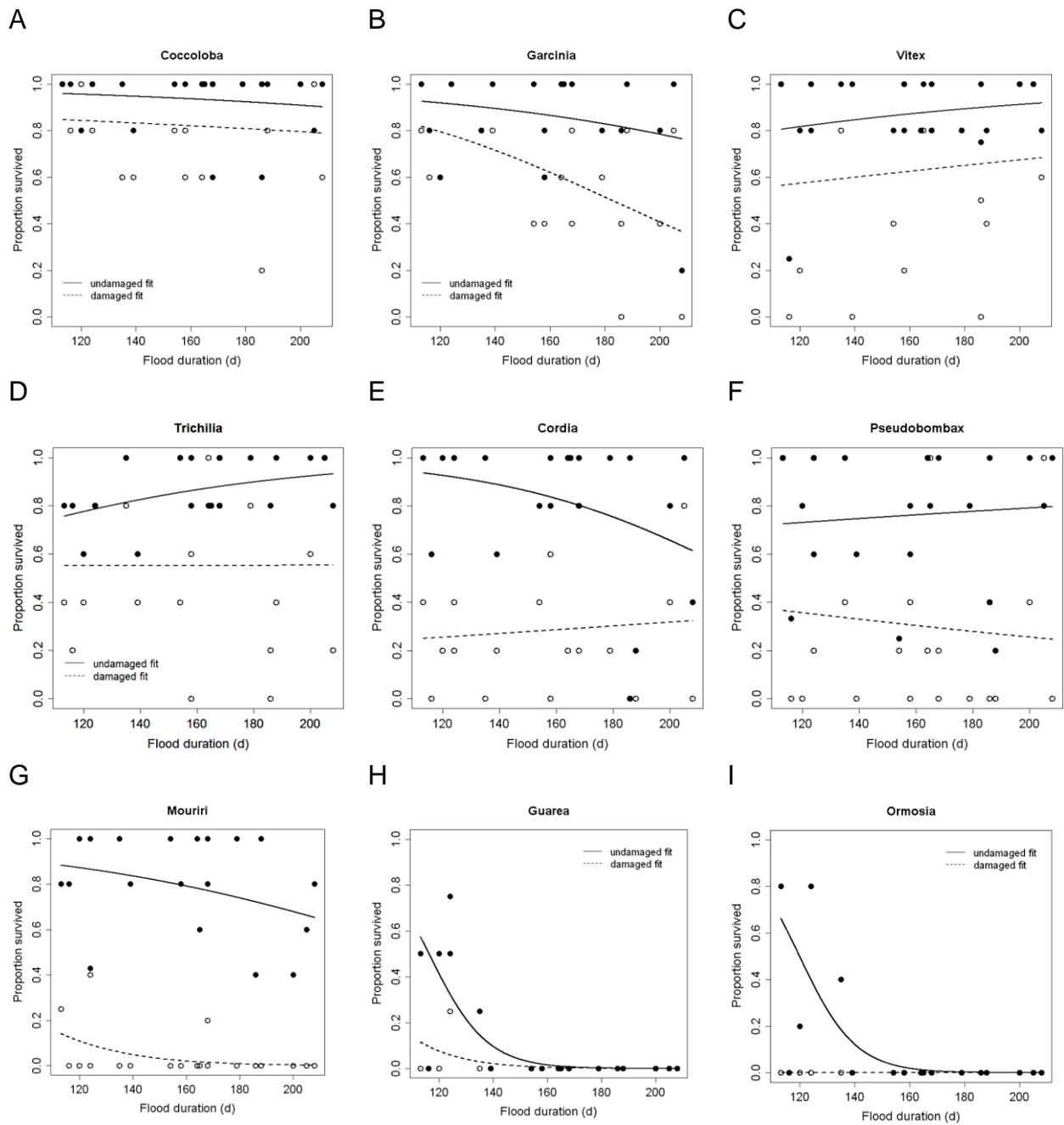


Figure 4-4. Seedling survival across flood duration and damage treatments for all species (A-I), excluding *Hevea*. Points indicate the proportion of individuals surviving after one year of undamaged (black dots) and damaged (white dots) seedlings in each plot. Lines indicate the predicted survival curves calculated by weighted regression models for undamaged and damaged seedlings.

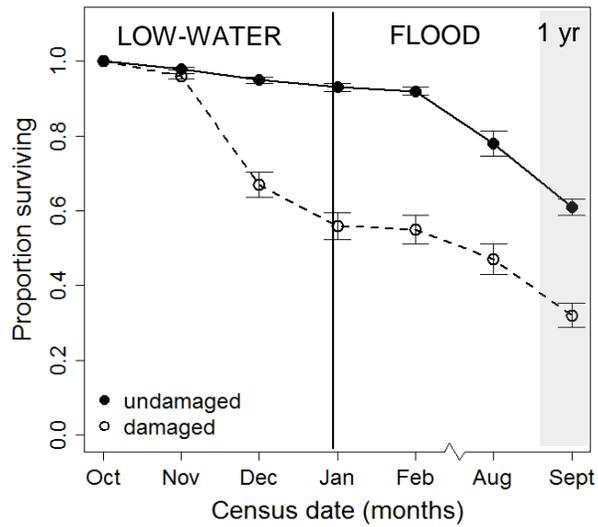


Figure 4-5. Seedling survival (means & SE) of grouped species over the seven censuses. The time gap during flooding (February-August) is indicated by a zig-zag on the x-axis. Survival is broken into three periods: low-water season (October to January), flood season (February-September), and one year (September).

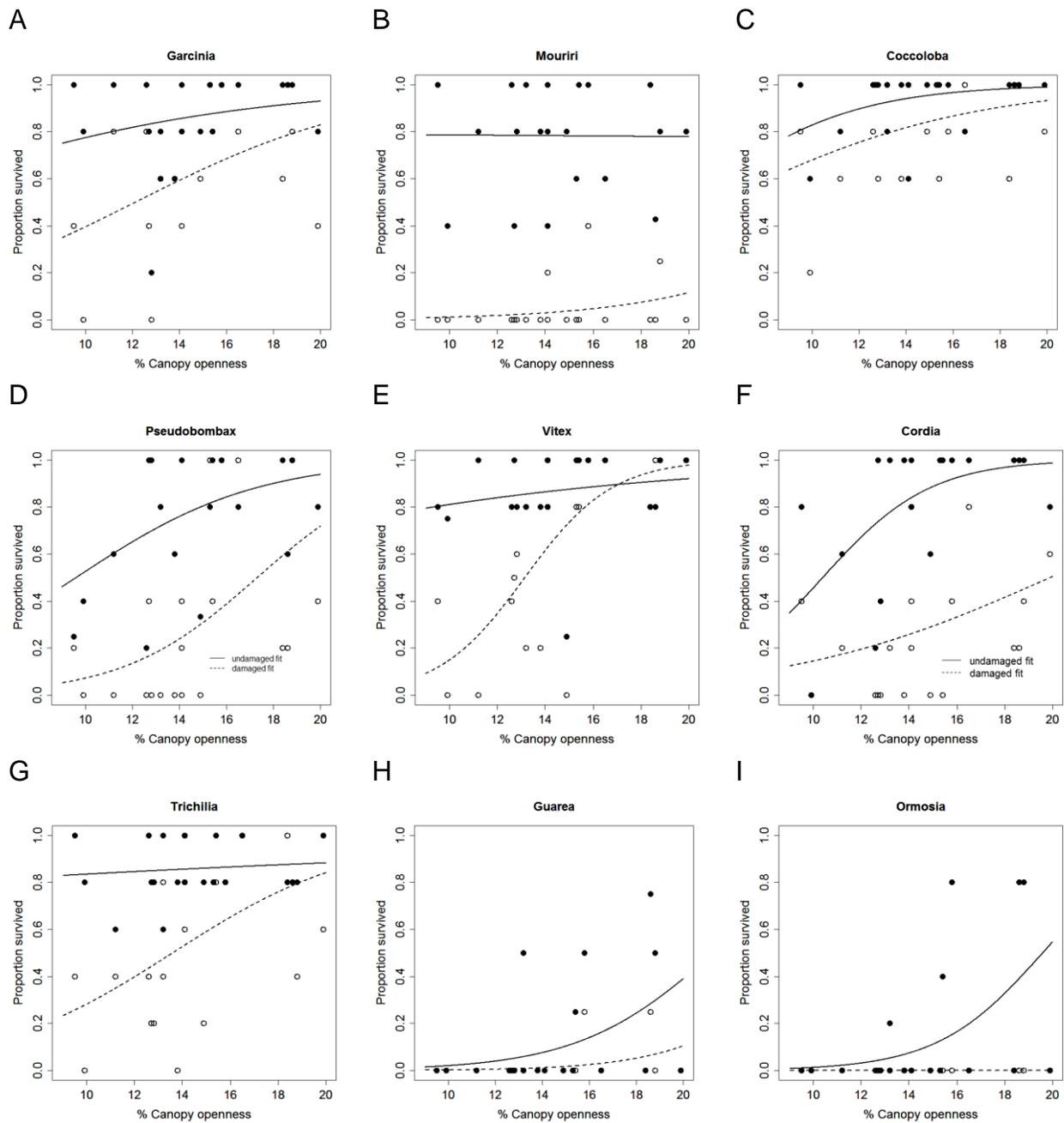


Figure 4-6. Seedling survival across a gradient of light availability for all species (A-J), excluding *Hevea*. Points indicate the proportion of surviving individuals after one year of undamaged (black dots) and damaged (white dots) seedlings in plots. Lines indicate the predicted survival curves calculated by weighted regression models for undamaged and damaged seedlings.

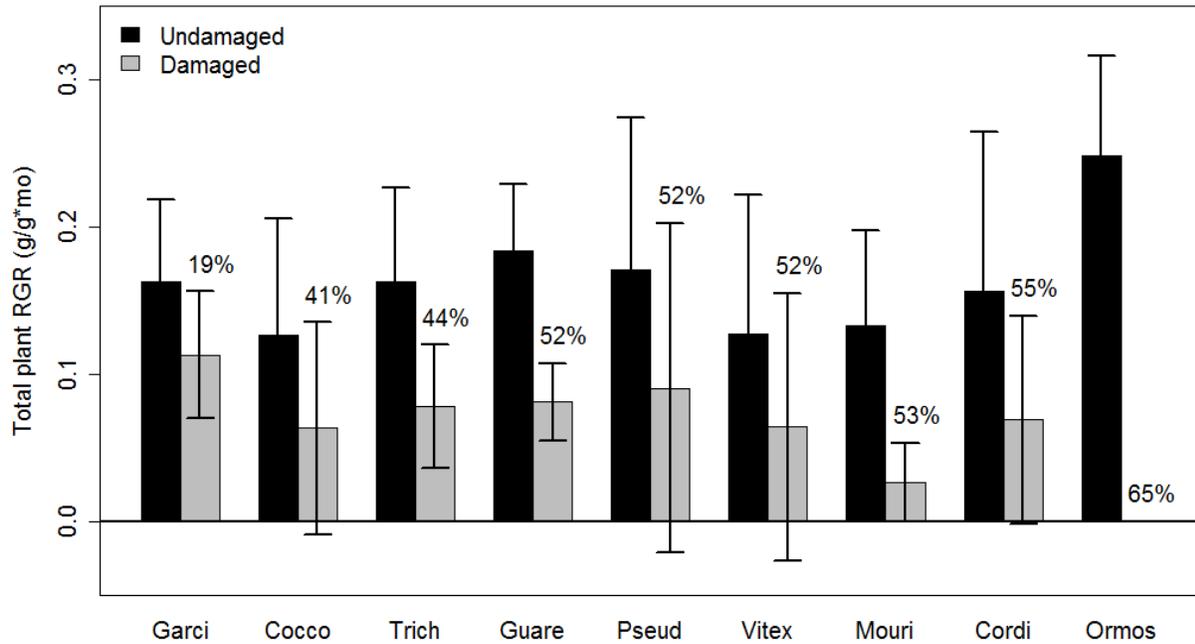


Figure 4-7. Relative growth rates (RGR; means & SD) of damaged and undamaged seedlings. Species on the x-axis are ordered by increasing average percent biomass removed after clipping stems at 5 cm aboveground (values shown above bars).

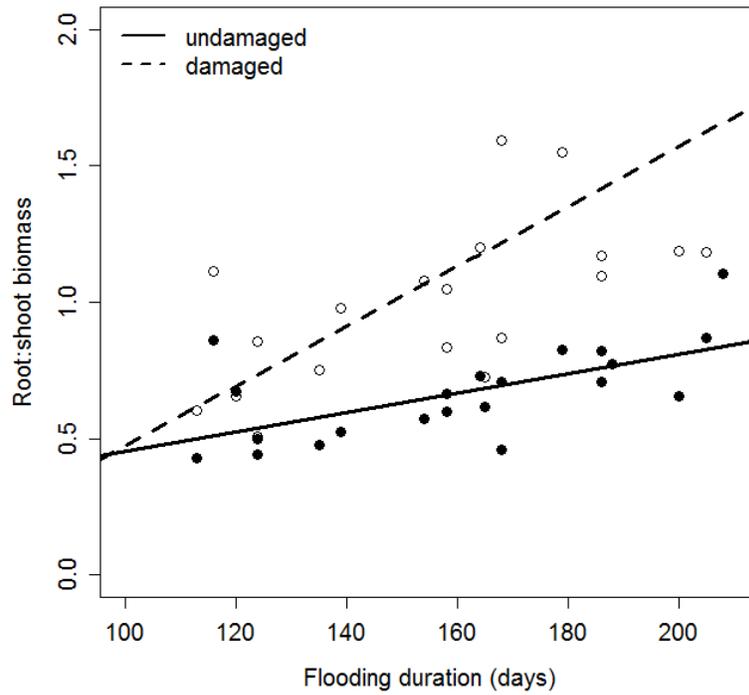


Figure 4-8. Root:shoot biomass ratios as a function of flood duration and for undamaged (black dots) and damaged (white dots) seedlings, illustrating the interaction between damage and flood duration. Linear mixed models tested the fixed effects of flooding, damage and light on root:shoot ratios (Table 4-3).

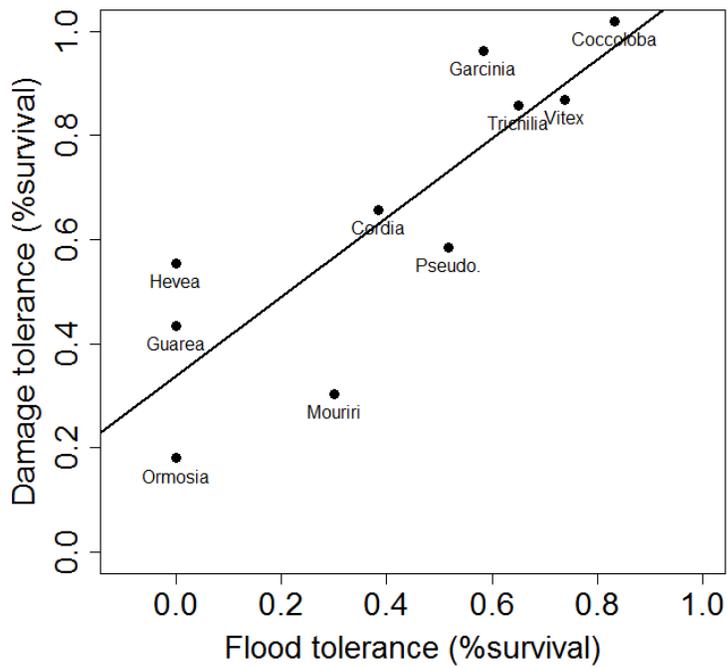


Figure 4-9. Positive correlation between damage tolerance and flood tolerance for ten seedling species, indicated by genus.

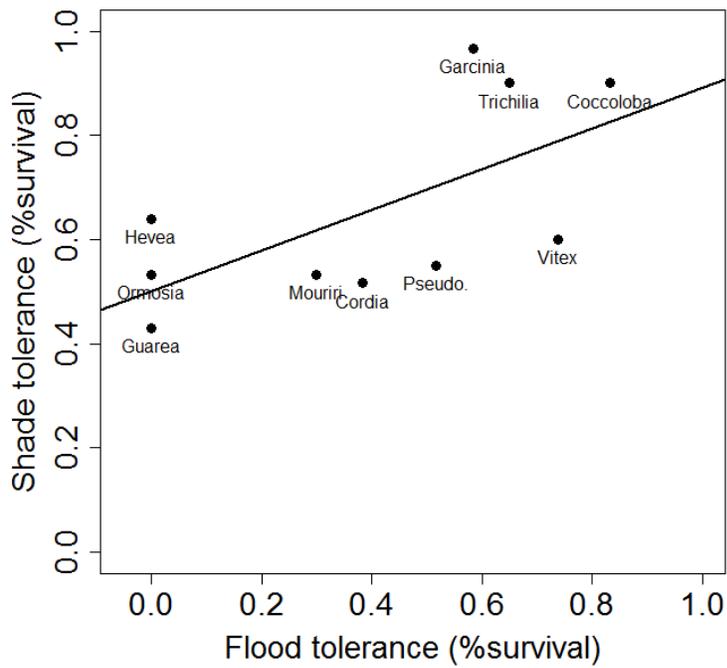


Figure 4-10. Positive correlation between shade-tolerance and flood-tolerance of ten study species indicated by genus, excluding *Hevea*.

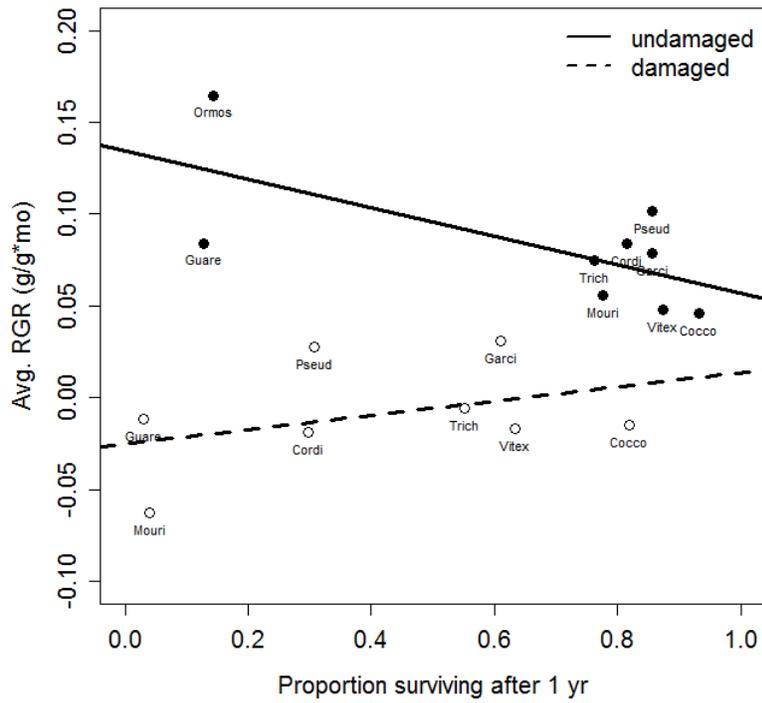


Figure 4-11. Trade-offs between relative growth rate (RGR) and survival over one year for undamaged seedlings (solid line, black dots) and damaged (dashed line, white dots) of the ten study species, indicated by genus abbreviation.

CHAPTER 5  
TREE COMMUNITY DYNAMICS ACROSS FLOOD AND DISTURBANCE GRADIENTS  
IN AMAZONIAN FLOODPLAIN FORESTS

**Overview**

The rates and patterns of forest recovery are mediated by the interplay of disturbance intensity and environmental stress gradients. Amazonian floodplain forests (*várzea*) - a critical ecosystem for aquatic diversity and productivity – face multiple disturbances, but few long-term data are available for determining rates of change during secondary succession. In floodplain forests recovering from agricultural abandonment, I tested the synergistic effects of flood level and introduced livestock activity on change in seedling and tree density and diversity over a nine-year period. Interactions between livestock and flood level affected seedling density, but the effects of livestock and flood level on seedling species density were independent. Seedling species density was best described by interactive effects between flood level and light, supporting a flood-tolerance / shade-tolerance trade-off model. High livestock activity in forest understories limited seedling density, and alleviation of this pressure resulted in a net influx of seedlings. Flood level was the major driver of temporal change in stand structure and species richness. I found no effect of livestock activity on tree recruitment or mortality, nor did I find interactions between livestock and flood level. Overall, livestock disturbance, light availability, and flood level affect the seedling community synergistically. In contrast, forest stand structure and rates of change in stems and species were largely guided by the main effects of flood level. The recuperation of seedling density following disturbance alleviation may contribute to the persistence of these forests despite intensive land-use history.

## Background

Floodplain forests are dynamic ecosystems exposed to multiple disturbances (Ward and Wiens 2001). Nonetheless, they remain among the world's most depleted forests (Tockner and Stanford 2002), with losses in area of up to 80% in temperate regions and rapid rates of loss in the tropics (Alho et al. 1988, Kingsford 2000). Amazonian white-water floodplain forests (*várzea*) are highly productive forests that comprise approximately 200,000 km<sup>2</sup> (Junk 1997) and contain >1000 woody species (Wittmann et al. 2004). Tree diversity in the *várzea* is remarkable given periods of inundation of up to 7 months and flood heights of up to 14 m (Goulding et al. 2003). Natural floodplain forests are composed of stands at different stages of recovery from periodic erosion and deposition of sediments associated with flooding and river meandering (Salo et al. 1986, Terborgh and Andresen 1998, Godoy et al. 1999). In addition to natural disturbance, floodplain forests have long histories of human land-use that also affect successional dynamics. There is a paucity of data about forest stand dynamics of Amazonian floodplain forests (Steege et al. 2003), particularly in the context of anthropogenic disturbance (Zarin et al. 1998, Anderson et al. 1999).

The effects of multiple interacting factors on forest succession are a major gap in plant community ecology (Chazdon 2003). Forest succession – the rate and trajectory of change in stand structure and species composition – is directed by an interplay of multiple factors, including disturbance regimes (White and Pickett 1985) and environmental stress gradients (Grime 1979). Numerous studies from tropical forests have demonstrated how disturbances such as logging, hurricanes, and livestock use affect forest stand structure and species composition (see reviews by Finegan 1996, Gauriguata and Ostertag 2001). Fewer studies have addressed the effects of

disturbance on rates of change (e.g., stem and species turnover) in successional forests (Chazdon et al. 2007). Environmental stresses such as flooding and shade also affect successional dynamics, limiting species richness with increasing stress (Grime 1979). In undisturbed floodplain seedling communities, a shade-tolerance / flood-tolerance model may explain species richness and composition (Hall and Harcombe 1998).

Disturbance and environmental stress act synergistically to affect forest structure (e.g., basal area, stem density, and species richness) including seedling communities. For example, hurricanes damaged regeneration less severely in higher parts of the floodplain (Frangi and Lugo 1998). Across a gradient of flooding, trends in basal area vary (Conner et al. 2002), tending to peak at moderate flood levels in Amazonian floodplains (Ferreira 1997, Wittmann et al. 2004). Disturbance events in floodplains such as logging, windstorms, and livestock use could have different effects at different levels within the flood plain. Longer flooding periods in lower elevation forests could limit the time forests are exposed to trampling by livestock, but could also limit the recovery period in the dry season.

Livestock impacts are pervasive in tropical floodplains world-wide (Robertson and Rowling 2000, Junk and de Cunha 2005). The accessibility of water, shade, and forage make understory vegetation in floodplain forests particularly vulnerable to browsing and trampling. While the effects of livestock in forests are most severe for seedlings, the long-term effects of livestock activity in riparian forests include poor tree recruitment (Robertson and Rowling 2000), exotic invasions (Jansen and Robertson 2001), and conversion to pasture (Pettit et al. 1995). In addition, livestock activity over time can increase tree mortality via damage to superficial roots, soil compaction, and browsing

(Ramirez-Marcial 2003, Mayer et al. 2005). In the Eastern Amazon, cattle and water buffalo move through seasonally flooded forests during the low-water season, trampling seedlings and compacting soils (Sheikh 2002). Removal of livestock from floodplains occurs during the rising of annual floods, which then submerge or waterlog seedlings for up to 6 months per year (Parolin 2002). The combined effect of intense livestock activity and extremely prolonged flooding in *várzea* could decrease seedling density and diversity. Sustained limitation of seedling regeneration could lead to low rates of tree recruitment. Alternatively, prolonged flooding could loosen compacted soils, compensating for the effects of trampling in the low-water season, potentially alleviating the detrimental effects of livestock on seedlings.

My goal was to test the main and interactive effects of flood level and livestock activity – a chronic disturbance in the forest understory – on seedling and adult stand structure and species richness, as well as rates of change over nine years in Amazonian floodplain forests. Among the inventories available for floodplain forests in the Amazon, few provide long-term data for monitoring rates of change (for review see Wittmann et al. 2006). Using a network of 0.1 ha plots across a flood gradient and varying in livestock activity, I address the following questions: 1) How do flooding and livestock activity affect seedling density and diversity? 2) What are the effects of livestock activity and flooding on stand structure and species richness? 3) How do livestock affect seedling and tree species composition?

## **Methods**

### **Study Site**

This study was conducted in floodplain forests of the Amazon River near Santarém, Pará, Brazil (02°25'S, 54°42'W). The Santarém region lies within the

Transverse Dry Corridor of the Amazon Basin, with rainfall of 1800-2000 mm  $y^{-1}$  and 5 consecutive dry months with rainfall below 100 mm (July-November; Sombroek 2001). Seasonal floods in the region peak between May and June, rising to an average of 7.5 m a.s.l. (1975-2008, Capitania dos Portos Santarém 2008) and extending up to 40 km from the main channel. Floodplains in the region are a mosaic of natural grasslands, forested levees, lakes, and giant aroid stands of *Montrichardia arborescens*. Forests occupy ~15% of the area (M. Crossa, personal communication, June 1, 2007) and are restricted to higher elevation levees. Forest species composition varies with hydrological geomorphological factors such as water chemistry and flow and soil structure (Godoy et al. 1999). Land-use history of floodplain forests include conversion to cacao plantations (*Theobroma cacao*) and small rubber tree stands (*Hevea brasiliensis*), followed by deforestation for jute (*Corchorus capsularis*) plantations in the 1940-80s (Winklerprins 2006). Forests have regrown on abandoned jute plantations and currently face increasing impacts of livestock grazing in the floodplain (Sheikh et al. 2006).

### **Experimental Design**

A network of 43 0.1 ha (20 x 50 m) plots was established in 1999 at random locations within forested stands of three floodplain levees (Figure 5-1). Forest stands ranged from 15-50 years since abandonment of jute plantations and were located on private property of local landholders. Plots were classified as light (1), medium (2), or heavy impact (3) of livestock in 1999 and 2008 based on average hoof print density in five 9 m<sup>2</sup> seedling plots (0-10 = light, 11-20 = medium, 21-80 pugmarks = heavy) and herd activity as observed in behavioral studies (Sheikh 2002). Hoof print density was deemed a surrogate variable for herd densities in forests as they remained in soils

throughout the low-water season (Sheikh 2002). Average livestock activity over nine years was calculated from the 1999 and 2008 data. For graphical purposes, average cattle activity in Figures was grouped into three levels (light = light & med-light; medium = medium; heavy = heavy & med-heavy). I calculated flood level as the average water depth in forests during the flood season from 1999 to 2008. Water depth was measured at 10 m intervals in forest plots with a weighted line during peak flooding in June 2006 (river level was 8.6 m a.s.l.). To calculate average flood level over 9 years, I subtracted the difference between levels in 2006 and the average for 1999-2008. Flood depth is thus a relative measure of the difference in maximum water column within plots. Forest plots were located on four different levees within the floodplain, two along the main Amazon channel and two along different branches of the Amazon River (Figure 5-1). To control for differences in stand structure and species composition due to unmeasured variables such as water chemistry and soil structure, levee was considered a random effect in statistical models.

To address the effect of flood level, light, and livestock activity on seedling communities, five 3 x 3 m subplots were established in random locations in each 0.1 ha plot (Figure 5-1). Plots were monitored in 1999 for seedling density only, and in 2008 for seedling density and species composition. Seedlings included all woody plants 10-130 cm tall and, in 2008, were measured for stem height and identified to species or morphotype. Change in seedling density was the difference between average densities per plot in 2008 and 1999. Each plot was assigned one of nine livestock change trajectories (*i.e.*, light to light, light to medium, etc.) for each combination of the three livestock impact levels in 1999 and 2008. Livestock change trajectory was used to test

the effect of disturbance alleviation – e.g., heavy to light and medium to light impact - on the change in seedling densities. I used livestock impact levels in 2008 to test the effects of livestock on seedlings in 2008, assuming that the most recent livestock activity would have the largest influence seedlings in the forest understory. I refer to ‘species density’ as the number of species per plot to distinguish from estimated species richness calculated from rarefied data (Chazdon 2007). Canopy openness was measured at the center of each subplot in four cardinal directions with a spherical densiometer held at 1.3 m height (Lemmon 1956). Percent grass cover was estimated visually (Kennedy and Addison 1987).

To test the effect of flood level and average livestock activity on adult stand structure and rates of change, all trees  $\geq 10$  cm DBH (diameter at 1.3 m height) were censused during the low-water season (November-January) of 1999/2000, 2003/04, and 2008/09 ( $N > 3,000$  trees). I measured tree DBH, visually estimated height, and identified trees to species or morphospecies. I distinguished new trees in 2004 and 2008 as ‘recruits’. Voucher specimens from a subsample of trees were made in 2007-2008 and deposited at the INPA (Instituto Nacional de Pesquisa Amazônica) herbarium in Manaus, Brazil (collector C.M. Nunes Nascimento, no.1-60). Stem density and basal area were calculated for all three censuses. Importance values were calculated for each species as the sum of relative frequency, relative density, and relative dominance of individuals (Brown and Curtis 1952). Rates of change – recruitment, mortality, species loss and gain, change in stem density, change in basal area, and change in species richness – were calculated for 1999-2003 and 2003-2008. I tested the effects

of average livestock impact levels in 1999-2008 on adult stand structure and species composition.

## **Statistical Analyses**

### **How do flood level and livestock activity interact to affect seedling density and species density?**

Analyses of seedling density were conducted at the sub-plot scale, using pugmark density as a predictor variable, and at the plot scale using livestock activity as the predictor variable and average density as the response variable. The effects of hoof print density, relative flood level (water column 0-1.9 m), and percent canopy openness in 2008 on seedling density in subplots were assessed with a linear mixed model (LMM). Seedling density and percent canopy openness were log transformed to achieve normality of model residuals, according to a Shapiro-Wilk test.

The effects of livestock activity (2008), flood level, and average percent canopy openness on seedling species density were assessed with LMMs at the plot scale. Due to low species counts (mean =  $3.7 \pm 2.3$ ) and violation of model assumptions, the effect of flooding and livestock activity was tested on the sum of all species observed in the five 9 m<sup>2</sup> subplots. Homoscedasticity was tested for all response variables across livestock impact levels with the Bartlett test (Crawley 2007). All models predicting seedling parameters were fit by restricted maximum likelihood (REML), which accounts for unbalanced designs (Bolker et al. 2009). Levee and plot (nested within levees) were treated as random effects. Tukey's HSD tests were used to compare mean values for density and species density across livestock activity, as well as the difference in seedling density across livestock change trajectories.

### **What are the effects of livestock activity and flood level on stand structure and species richness?**

To test the effects of average livestock activity, flood level, and their interactions on adult stand structure, I used repeated measures LMMs fit by restricted maximum likelihood and an autoregressive correlation structure (Crawley 2007). Models tested the effects of livestock impact, flood level, and their interactions on stand structure: stem density (stems ha<sup>-1</sup>), basal area (m<sup>2</sup> ha<sup>-1</sup>), and species density (species count per plot). Levee, plot, and year were treated as random effects. The effects of flood level and livestock activity on species density were assessed with a linear mixed model where (flood level<sup>2</sup>) was included as a quadratic term (Crawley 2007).

To test the effects of flooding on estimated species richness, plots were grouped into three flood level categories (0-0.60; 0.60-1.30; 1.30-2.0 m). Species richness values for adult trees and seedlings were calculated using the Chao 1 abundance-based species richness estimator (Chao 1984) in EstimateS Win 8.20 (Colwell 2009). To compare the effects of average livestock activity and flood level category on species richness of adult stems and seedlings, sample-based species rarefaction curves across livestock activity and flood level category were computed by EstimateS using the Coleman method (Coleman 1981).

### **What are the effects of livestock activity and flood level on rates of change?**

To test the effects of livestock activity, flood level, and their interaction on rates of change in forest stands, I used LMMs fit by restricted maximum likelihood with levee as a random effect. Stem and species turnover rates, change in basal area, and change in stem density were calculated as four parameters for rates of change between 1999 and 2008. Recruitment and mortality rates (*i.e.*, stem turnover rates) were calculated as the

relative proportion of trees gained or lost from the total number of live trees in 1999. Species turnover rates were the percents of species lost or gained over nine years (Chazdon 2007). Rates of recruitment, mortality, and percent species loss and gain were logit transformed to achieve normality of model residuals, according to Shapiro-Wilk tests. Differences in rates of change among livestock levels were tested post-hoc with Tukey's HSD tests. All analyses were conducted in R 2.9.0 (Team 2009) using the *nlme* package (Pinheiro et al. 2008).

### **How does livestock activity affect species composition?**

To compare species composition of seedlings and trees among flood levels and livestock impact levels, the Chao abundance-based Sørensen index of similarity (Chao et al. 2005) was calculated in EstimateS 8.0 (Magurran 2004) for each possible pairwise combination of the 43 plots. In two separate tests for flood level (grouped into 3 categories) and livestock impact level, I used two-sample t-tests with unequal variances to compare Chao similarity indices between plots in the same livestock activity category vs. those in different categories.

## **Results**

### **Effects of Flood Level and Livestock Activity on Seedlings**

As expected, seedling density decreased with increasing flood level and livestock hoof print density. Furthermore, flooding and livestock activity interacted such that seedling density was low across all flood levels in plots with heavy livestock activity, while seedling density was negatively related to flooding with low livestock activity (Table 5-1, Figure 5-2). Mean seedling density in low-impact plots was more than three-fold of that in heavy-impact plots ( $2.9 \pm 1.9$  SD for low impact,  $1.3 \pm 1.0$  SD for medium impact, and  $0.7 \pm 0.6$  SD seedlings  $m^{-2}$  for heavy impact). Plots changing from

heavy or medium to low impact showed net increases of seedlings ( $0.81 \pm 1.2$  SD and  $1.4 \pm 1.4$  SD seedlings per  $m^2$ , respectively), indicating recruitment of seedlings into the understory when livestock activity is reduced (Figure 5-3). Canopy openness was positively correlated with seedling density. Seedlings were limited to  $1.2 \pm 1.4$  SD plants  $m^{-2}$  in low light environments (2-7% canopy openness) across the flood gradient (Table 5-1).

Species density was affected by the interaction of light and flood level that concur with the flood-tolerance / shade-tolerance trade-off model. At high light levels, species density was constant along the flood gradient at 10-17 species per 0.1 ha plot. At moderate to low light levels, species density declined across the flood gradient (Figure 5-4A). Species density also declined with increasing flood level ( $F = 3.88$ ,  $p = 0.056$ ), as did estimated species richness (Figure 5-5). No effect of livestock activity was found on species density (Table 5-2), but rarefaction curves across livestock levels seedlings suggested higher species richness in low impact plots (Figure 5-8). Light availability increased species density and ameliorated negative effects of high flood levels and heavy livestock disturbance (Table 5-1; Figure 5-4).

### **Effects of Flood Level and Livestock Activity on Trees**

Flood level affected tree species density, but livestock activity did not interact with flooding to alter stand structure. Heavy-impact plots had relatively low basal area ( $28.1 \pm 8.0$   $m^2$   $ha^{-1}$ ) and were species poor, reaching approximately half of the species richness as found in medium and low impact plots (Figure 5-5). Contrary to trends in other floodplain forests, basal area increased with flooding (Figure 5-5). No differences in stem density between livestock impact levels or flood levels were found (Table 5-2). The relationship between species density and flooding was explained by a quadratic

relationship. Overall, species density peaked at 15-20 species per 0.1 ha at moderate flood levels between 0.6 and 1.2 m (100-120 d flooding; Figure 5-5).

### **Effects of Flood Level and Livestock Activity on Stand Dynamics**

Stem and species recruitment into tree size classes were limited by prolonged flooding (Figure 5-6, Table 5-3). In contrast, livestock activity did not affect stem mortality or limit recruitment of new species (Table 5-3). Rather, livestock activity was associated with low stem mortality, which was lower in heavy impact plots than light and medium impact plots (Tukey HSD  $p = 0.001$  and  $p = 0.0002$ , respectively). No differences in recruitment among livestock impact levels was found ( $F = 0.63$ ,  $p = 0.54$ ), and there was no interaction between flooding and livestock activity, indicating that rates of change in adult stands are largely driven by flood level. Average basal area increment over nine years was  $0.96 \pm 6.9 \text{ m}^2 \text{ ha}^{-1} \text{ y}^{-1}$ . Livestock activity did not decrease gains in basal area over time in forest stands (Table 5-2).

As expected, young forests showed the highest net increases in basal area, stem density, and species density. From 1999-2008, young forest stands (15-25 y) had a net increase in stem density ( $12.3 \pm 26.8$ ) and basal area ( $4.6 \pm 1.9 \text{ SD}$ ), averaging  $0.51 \text{ m}^2 \text{ ha}^{-1} \text{ y}^{-1}$ . In contrast, older stands showed net zero gains in basal area ( $0.23 \pm 6.6 \text{ m}^2 \text{ ha}^{-1} \text{ y}^{-1}$ ) and large reduction in tree density ( $-16.9 \pm 12.4$ ). In terms of species turnover, young and old forest stands had high increases in species density over time ( $16.15 \pm 11.2\%$  and  $14.5 \pm 21.7 \%$ , respectively), but species gain was low in moderate age stands of 30-35 ( $4.9 \pm 8.5 \%$ ). Interestingly, species loss was fairly constant across all ages at 10-13.5% ( $\pm 12.8$ - $13.7 \text{ SD}$ ) of total species density in plots. Forest age had no effect on mortality or recruitment rates ( $F = 3.10$ ,  $p = 0.058$  and  $F = 0.33$ ,  $p = 0.72$ , respectively).

## Effects of Flood Level and Livestock Activity on Species Composition

A total of 32 families, 63 genera, and 88 woody species occurred in forest stands (Appendix A). Species richness of trees was lowest in heavy impact plots (Figure 5-5). In accordance with the hypothesis that species richness should increase with decreasing flood stress, estimated species richness of trees was highest at low flood levels (Chao 1 =  $65 \pm 9.2$ ) in comparison to stands at moderate and high flood levels (Chao 1 =  $60.0 \pm 3.5$  and  $38.3 \pm 5.4$ , respectively). Tree and seedling communities were species rich (Chao 1 =  $75.7 \pm 4.5$  &  $74.6 \pm 4.8$  SD, respectively) in comparison to adult recruits (Chao 1 =  $54.6 \pm 3.4$  SD).

Plots with the same flood level were more similar in species composition than plots with different flood levels among trees, recruits, and seedlings ( $t_{549} = 7.75$   $p < 0.0001$ ;  $t_{443} = 4.48$   $p < 0.0001$ ;  $t_{517} = 5.40$ ,  $p < 0.0001$ , respectively). High elevation plots in the floodplain (maximum flood level = 0.02-0.60 m = 2-40 d flooding) were dominated by *Laetia corymbulosa*, *Andira inermis*, and *Triplaris surinamensis* trees and *Talisia cerasina* and *Tabernaemontana siphilitica* in the understory. Moderately flooded plots (0.60-1.3 m = 40-70 d flooding) were dominated by *Cordia tetrandra*, *Pseudobombax munguba*, and *Ficus* spp. trees with *T. siphilitica* and *Garcinia brasiliensis* in the understory. Low elevation plots (1.3-1.9 m = 70-100 d underwater) were dominated by *Cynometra bauhiniifolia*, *C. tetrandra*, and *P. munguba*, with *T. cerasina* and *Ocotea castanaefolia* in the understory. Tree species composition changed minimally over the nine-year period; however, two low-flood-tolerant tree species valued for timber, *Guarea guidonia* and *Hura crepitans*, were lost between 1999 to 2008.

Plots with the same livestock activity were more similar in species composition of tree and seedlings than plots of different activity ( $t_{530} = 4.7$ ,  $p < 0.0001$ ;  $t_{530} = -4.8$ ,  $p <$

0.0001, respectively). There was no difference in species similarity for livestock levels among recruits ( $t_{590} = -1.7$ ,  $p = 0.09$ ). Light and medium activity plots were dominated by trees of light-demanding species, while heavy activity plots were dominated by *Cynometra bauhiniifolia*, a slow-growing mid-successional species with low species turnover (Figure 5-10). The understory communities of both light and medium activity plots were dominated by the common shrub, *Tabernaemontana siphilitica* and small trees, *Talisia cerasina* and *Trichilia singularis*. In heavy impact plots, recruits were dominated by *C. bauhiniifolia* ( $42\% \pm 7\%$  SE) and ranked 6<sup>th</sup> in abundance among seedlings ( $4.7\% \pm 2.2\%$  SE). The understory was largely comprised of shrubs, including thorn-bearing species, *Xylosoma benthamii* and *Randia armata* (Figure 5-10).

## Discussion

Much of the research on Amazonian floodplain forest succession has focused on changes in stand structure and diversity in relation to the flood gradient (Salo et al. 1986, Wittmann et al. 2004). However, floodplain forests are increasingly dominated by secondary forests degraded by logging (Anderson et al. 1999, Zarin et al. 2001), agriculture (Zarin et al. 1998), and livestock ranching (Sheikh et al. 2006). By incorporating land-use history as an explanatory variable that acts synergistically with flooding to affect forest succession, I gain a broader understanding of floodplain forest trajectories of change through time. In Amazonian floodplain forests recovering after abandonment of agriculture, the effects of increasing livestock activity reduces seedling density by one-third. In stands receiving heavy livestock activity, species richness and basal area were low, but I did not observe an increase in stem mortality and decrease in recruitment with increasing livestock activity. Seedling species count was affected by the interaction of flood level and canopy openness, supporting the hypothesis that many

species require increased light availability for survival at high flood levels (Battaglia and Sharitz 2006). Adult species density peaked in moderately flooded plots, and the complete loss of adult stems of two valuable low-flood-tolerant timber species was observed (*Guarea guidonia* and *Hura crepitans*). Recruitment of stems and species into the tree size class was limited by increasing flood levels, demonstrating that the flood regime is important not only for patterns in species richness and composition, but also for rates of change in forest stands through time.

### **Seedling Response to Livestock Activity, Flood Level and Light**

Flooding and herbivore activity interact in floodplain ecosystems to affect seedling density (Oesterheld and McNaughton 1991, Butler et al. 2007). Chronic disturbance by livestock in floodplain forests acted synergistically with flooding to severely limit understory plant density in sites with prolonged flooding (>160 d) and intense livestock activity. The negative effects of livestock activity on species counts were apparent when flooding stress was low (50-160 d inundation). Such patterns suggest that either the stress of flooding is so severe that it masks the effects of livestock, or that prolonged floods alleviate heavy impacts of livestock.

A consequence of the intensification of livestock in forests is the creation of open forests with sparse vegetation in the understory. In this study, heavy livestock activity decreased seedling density to less than one third of that in light activity forests. Reduced seedling density is likely caused by the continual mortality of seedlings by trampling, soil compaction, and browsing by livestock (Kauffman and Krueger 1984). Compacted soils reduce the survival of some floodplain forest species (Sheikh 2002), which can ultimately affect trajectories of succession of floodplain forests. As canopy trees die, the lack of seedlings and young trees in the understory could favor invasion of

grasses in open gaps. However, the expected increase in grass cover in heavy impact plots was not observed, indicating that while understories are sparsely populated, there is little replacement by grasses. Canopy openness < 35% in this study may provide insufficient irradiance for grass survival and competition with pioneer woody species (Scholes and Archer 1997, but see Veldman et al. 2009).

Species density of seedlings in forest understories was strongly influenced by an interactive effect of light availability and flood level. Contrary to our hypothesis that increased light would favor grass invasion, increasing light availability in the understory increases woody seedling density and species density. At high light levels (10-35% average canopy openness), understories maintain a higher number of species despite prolonged flooding. In turn, at low light levels (< 5% canopy openness) species density diminishes with increased flooding. Such trends concur with the flood tolerance / shade tolerance trade-off hypothesis for seedling diversity in floodplain forests, whereby species with high flood tolerance require higher light availability for growth and survival (Battaglia and Sharitz 2006).

**Mechanisms for recovery.** The regenerative capacity of floodplain forests may contribute to their rapid recovery following multiple cycles of deforestation (Smith 1999). In this study, alleviation of heavy livestock activity resulted in recovery of seedling densities to those in stands with low activity. The re-establishment of understory vegetation could be a result of multiple factors related to annual flooding that facilitate recovery in floodplains. Firstly, the persistence of resprouts following disturbance could promote rapid recovery of woody vegetation. Secondly, seed dispersal by floodwaters (Moegenberg 2002), fish (Goulding 1980, Kubitzki and Ziburski 1994, Lucas 2008), and

birds during the flood season overcome spatial/distance-based barriers to seed arrival (Holl 1999). Finally, the rich sediments deposited by floodwaters may replenish nutrients as well as loosen compacted soils, facilitating seed germination and seedling growth. These factors may alleviate the effects of livestock disturbance on the seedling community and promote recovery of diverse understory vegetation.

### **Secondary Succession of Forests**

The flood regime in Amazonia is among the most important factors for understanding stand structure as well as rates of change in forests. Flood level predicted rates of recruitment of new trees and species. Patterns in basal area and species density were also observed across the flood gradient, although, contrary to other studies, basal area increased with flooding and species density peaked at moderate flood levels. In other studies of neotropical floodplain forests, basal area peaked at moderate (Ferreira 2000) or low flood levels (Nebel et al. 2001b). At high elevations, the increased frequency of late-successional species with high-density wood can cause basal area to remain constant or decline (Wittmann et al. 2004). Species richness should have decreased with increasing flood level, as increasing exposure to anoxic conditions should limit the community to fewer highly flood-tolerant species.

### **Stand structure and species composition**

Basal area in Eastern Amazon floodplain forests reached as high as  $81 \text{ m}^2 \text{ ha}^{-1}$ , peaking in moderately flooded forests comprised of *Pseudobombax munguba*, a fast-growing late pioneer species in forests 30-35 years since abandonment. Average basal area of forests was  $34.2 \pm 16.1 \text{ SD m}^2 \text{ ha}^{-1}$ , higher than many other floodplain forests of the Amazon region. For example, in mature species-rich floodplain forests of the Western Amazon, basal area ranged from  $16.3$  to  $28.8 \text{ m}^2 \text{ ha}^{-1}$ , peaking in total basal

area and net change in basal area at in deeply flooded stands (Nebel et al. 2001a). Late successional Amazon estuarine floodplain forests averaged  $29.5 \text{ m}^2 \text{ ha}^{-1}$  (Cattanio et al. 2002). Patterns in basal area in this study were most similar to those of late secondary Central Amazonia, where basal area of secondary forests reach  $48\text{-}60 \text{ m}^2 \text{ ha}^{-1}$  in 50-year old stands dominated by *P. munguba* at moderate flood levels (Worbes et al. 1992), then decline to  $31\text{-}38 \text{ m}^2 \text{ ha}^{-1}$  in late successional and mature stands (Wittmann et al. 2004). Tidally flooded forest stands dominated by *Prioria copaifera* in Darien, Panama also have high basal area ranging  $31.1 - 71.1 \text{ m}^2 \text{ ha}^{-1}$  for stems  $>10$  cm DBH (Grauel 2004). Basal area thus appears to vary within floodplains by a combination of factors including species composition, flood level, and forest age. Overall, floodplain forests have higher basal area than upland forests, likely due to faster growth on alluvial substrates (Chinea 2002). The floodplain forests of the Santarém region in the Dry Corridor of the Amazon Basin had exceptionally high basal area in comparison to other tropical forests despite their history of deforestation and degradation. The high basal area of stands in this study could be related to the long growing season of the region (Sombroek 2001).

Although basal area of forests was high, accumulation rates of basal area were relatively low. Change in basal area varied widely, averaging  $0.51 \text{ m}^2 \text{ ha}^{-1} \text{ yr}^{-1}$  in forests of 15-25 years old and  $0.025 \text{ m}^2 \text{ ha}^{-1} \text{ yr}^{-1}$  in forests of 40-50 years old. Such accumulation rates are extremely low in comparison to floodplain forests of other regions (Nebel et al. 2001b) and upland forests (Chazdon et al. 2007). High rates of stem loss (10-30%) contributed to low net gains in basal area. Stem mortality is a

function of forest age, as well as unmeasured factors such as exposure to windstorms, bank erosion, and removal of firewood by residents.

As expected, estimated species richness of adult stems was limited by flooding. Some studies suggest that species richness declines across the flood gradient, as fewer species are able to tolerate increasing exposure to anoxic conditions (Terborgh and Andresen 1998, Parolin et al. 2004b). However, other studies of Amazonian forests have found that low elevation forests are also species rich (Ferreira 2000, Nebel et al. 2001b). Species richness in *várzea* forests declines from west to east, with a total of 480 species in the Western Amazon (170 species ha<sup>-1</sup>; Wittmann et al. 2002), 371 species in Central Amazonia, and 133 species in the Lower Amazon Estuary. This study fills an important gap in species richness of the Dry Corridor in the Lower Amazon region. Although reviews show a gradual decline in species richness on a West-East gradient, this study shows that species richness in the Santarém region is exceptionally low (74-76 woody species with stems  $\geq$  10 cm DBH). The drop in observed species richness could be related to many factors including: 1) intense land-use history in the region and multiple cycles of deforestation for cacao plantations, rubber tree planting, and jute cultivation, 2) the relatively young age of forests, and 3) the relatively dry climate and geological history of the region, which accounts for lower species richness in adjacent upland forests (Terborgh and Andresen 1998).

Forest age did not correlate with stand structure or rates of change in forests. I expected to find increasing basal area and decreasing stem density with increasing age (Chazdon et al. 2007, Flynn et al. 2010), but no such trends were observed. Within the nine-year study period, young forests (15-25 y) had a net increase in basal area and

stem density much higher than that of older forests (30-50 y). Older forests had no net gain in basal area over nine years, potentially due to the high mortality of pioneer species (e.g., *Cordia tetrandra* and *Triplaris surinamensis*) in the canopy and the recruitment of mid-late successional species. Forest age may not have affected forest structure due to the narrow range in stand age and the interaction of age with flood level to affect basal area and stem density. In deeply flooded forests, mortality > recruitment, but in plots with low flooding, recruitment > mortality, reaching 300 stems ha<sup>-1</sup> y<sup>-1</sup> in young forests. Overall, trends in stand structure across forest age depended on flood level.

### **Floodplain forest stand dynamics**

Stem and species recruitment gradually decreased with increased flood level. Although many studies have shown that increasing flood level decreases recruitment, few studies measure tree recruitment across a fine gradient of flood levels. Although tree recruitment rates were similar across livestock activity, densities of recruited trees were lower in heavy impact stands. The species recruited into heavy impact plots were thorny shrubs (*Randia armata* and *Xylosoma benthamii*) that may prevent damage from livestock movement in the understory. Poor recruitment of shade-tolerant tree species suggested that successional trajectories of stands with sustained heavy livestock activity could remain species-poor over time. One group of heavy activity plots had exceptionally high mortality (~400 stems ha<sup>-1</sup>), likely attributed to the exposure of stands to winds and strong currents along the main channel of the Amazon River.

An important finding is the exponential decline in rates of stem and species recruitment across the flood gradient. The gradual decline in species recruitment with increasing flood level suggests that with relatively small differences in flood level and

duration, exponentially fewer species are able to survive. Similar results were found for the sapling community in *várzea* forests of the Central Amazon (Wittmann and Junk 2003). The average recruitment of new species in a plot over nine years ranged from 8-16% in stands, while species lost ranged from 7-13%. Such rates of species recruitment are greater than those of 25-year-old upland forests post livestock abandonment (2-5%), but still lower than for lightly disturbed upland forests with no history of livestock impacts (35-55% over 7 years, Chazdon 2007).

### **Successional trajectories of floodplain forests**

Changes in species composition showed transition of forests from early to late successional stages. Early successional light-demanding species (*Cordia*, *Cecropia*, and *Pseudobombax*) were replaced by late secondary species and understory shrubs. of the canopy species *Triplaris surinamensis* and understory shrub *Tabernaemontana siphilitica* were indicators of past degradation or deforestation (F. Wittmann, personal communication, April 20, 2010). The dominant species in plots sustaining high livestock disturbance, *Cynometra bauhinifolia*, is a slow-growing mid-successional species with low mortality rates in comparison to early-successional species (e.g., *Pseudobombax munguba*, *Triplaris surinamensis*, and *Cordia tetrandra*). The establishment of *Cynometra*-dominated stands where heavy livestock impact also occurred may be related to previous land-use history and forest management practices prior to livestock introduction. No data was collected on fuelwood harvesting in forest stands nor land-use history of burning, which could also affect species trajectories (Mesquita et al. 2001).

## Implications for Conservation in the Context of Climate Change

Extreme flooding events associated with climate change likely have important implications for species composition. In forest stands I observed the loss of mid-successional high-*várzea* species, *Guarea guidonia* and *Hura crepitans*, that occur in high-elevation levees that flood supra-annually or annually for short periods (< 50 d, Wittmann et al. 2004). These species are highly valued for timber in Amazonia (Marinho et al. in press). The loss of such high-elevation species is likely due to the recent increase in maximum flood levels from an average of 5.7 m from 1925-1975 to an average peak of 7.5 m from 1975-2008 with exceptional floods of 8.6 m in 2006 and 8.36 m in 2008 (Capitania dos Portos - Santarém 2008). Extreme flooding events such as those of 2006, 2008, and 2009 cause mortality of low-flood tolerant species that occupy high elevations and contribute substantially to the overall diversity of floodplain forests (Salo et al. 1986, Worbes et al. 1992). As such, the species available for future replacement of canopy trees in floodplain forests are limited not only by intense livestock disturbance but also extreme flooding events. Future studies will need to investigate the effects of extreme flooding events on floodplain forest species composition and diversity.

Table 5-1. Summary of linear mixed model results (F-tests and p-values in parentheses) for the effects of flooding, livestock, activity, and light availability on the seedling community.

	Flood	Livestock	Avg. Light	Flood × livestock	Light × flood	Light × livestock	3-way
Seedling density	18.76*** (0.0001)	11.4*** (0.0011)	16.7*** (0.0001)	4.31* (0.039)	9.25** (0.0027)	0.004 (0.95)	2.01 (0.16)
Average seedling density	9.95** (0.0034)	7.67** (0.0018)	2.92 <sup>†</sup> (0.097)	0.94 (0.40)	6.46* (0.016)	0.42 (0.66)	0.92 (0.41)
Average proportion damaged	10.51** (0.0027)	0.37 (0.69)	0.19 (0.67)	0.17 (0.84)	0.0004 (0.98)	2.59 <sup>†</sup> (0.09)	0.21 (0.81)
Total species density	3.88 <sup>†</sup> (0.056)	1.08 (0.30)	8.42** (0.006)	0.0034 (0.95)	5.51* (0.024)	1.84 (0.18)	0.0007 (0.98)

At the subplot scale, the effects of livestock hoof print density, flood level, and canopy openness (light) on seedling density in 3 x 3 m subplots. At the plot scale, the effects of livestock activity, flood level, and average canopy openness on average seedling density, average proportion of seedlings with damage, and species density (number of species in subplots) in 0.1 ha plots.

<sup>†</sup> 0.10 < p; \*p ≤ 0.05; \*\*p ≤ 0.01; \*\*\* p ≤ 0.001

Table 5-2. Summary of linear mixed model results (F-tests and p-values) for the effects of flood level, livestock activity (1999-2008), and their interaction on tree stem density, basal area, and species density.

Rate of change	Flood level			Livestock activity		Flood x livestock		Flood <sup>2</sup>			Flood <sup>2</sup> x livestock	
	Est.	F	p	F	p	F	p	Est.	F	p	F	p
Stem density	740	0.38	0.54	0.53	0.71	0.23	0.92	-	-	-	-	-
Basal area	241	7.74	0.010	2.28	0.088	0.91	0.47	615	5.87	0.023	2.17	0.10
Species density	267	16.8	0.0004	2.22	0.094 <sup>†</sup>	0.70	0.60	-185	0.54	0.47	2.28	0.088

In models for basal area and species density, flooding was included as a quadratic term. Coefficients (Est.) are included for the effect of flood level.

<sup>†</sup> 0.10 < p; \*p ≤ 0.05; \*\*p ≤ 0.01; \*\*\* p ≤ 0.001

Table 5-3. Summary of linear mixed model results for the effects of flood level, livestock activity (1999-2008), and their interaction on tree stem mortality and recruitment, species loss and gain, change in stem density, and change in basal area over 9 years. Coefficients (Est.) are shown for flood level effects.

Rate of change	Flood level			Livestock intensity		Flood x livestock	
	Est.	F	p	F	p	F	p
Mortality (stem loss)	0.29	0.004	0.95	5.84	0.001**	1.16	0.35
Recruitment (stem gain)	-1.10	10.9	0.002**	0.81	0.52	0.62	0.65
Species gain	-0.99	5.32	0.028*	1.88	0.14	0.87	0.49
Species loss	0.18	0.17	0.68	0.78	0.55	0.95	0.45
Change in stem density	-39.9	5.67	0.024*	1.03	0.40	1.67	0.18
Change in basal area	-20.7	0.002	0.96	0.79	0.54	0.53	0.71

† 0.10 < p; \*p ≤ 0.05; \*\*p ≤ 0.01; \*\*\* p ≤ 0.001

Table 5-4. Tree stand structure and species richness (mean & SD) in the three forest inventories, 1999, 2003, and 2008.

Year	Mean DBH (cm)	Stem density (ha <sup>-1</sup> )	Basal area (m <sup>2</sup> ha <sup>-1</sup> )	Observed species (Mao tau)	Species richness (Chao 1)
1999	23.2 ± 13.9	693 ± 206	33.2 ± 16.3	71 ± 2.45	75.7 ± 4.49
2003	23.7 ± 15.0	680 ± 216	38.2 ± 15.6	70 ± 2.03	72.5 ± 2.9
2008	25.6 ± 15.7	571 ± 201.5	37.2 ± 16.1	69 ± 2.37	74.6 ± 5.35

Table 5-5. Estimated species richness (Chao 1 means & SD) of trees ( $\geq 10$  cm DBH) and seedlings across flood level categories (low = 0-0.60; medium = 0.60-1.3; high = 1.30-2.0 m) and average livestock activity in 1999-2008 for trees and in 2008 for seedlings.

	Flood low	Flood medium	Flood high
Trees	65 $\pm$ 9.2	60.5 $\pm$ 3.5	38.3 $\pm$ 5.4
Seedlings	58.2 $\pm$ 6.4	48.5 $\pm$ 4.0	32.5 $\pm$ 3.2
	Livestock light	Livestock medium	Livestock heavy
Trees	64.4 $\pm$ 4.7	55.6 $\pm$ 4.8	58.5 $\pm$ 12.9
Seedlings	65 $\pm$ 9.9	64.4 $\pm$ 11.2	37.6 $\pm$ 3.9

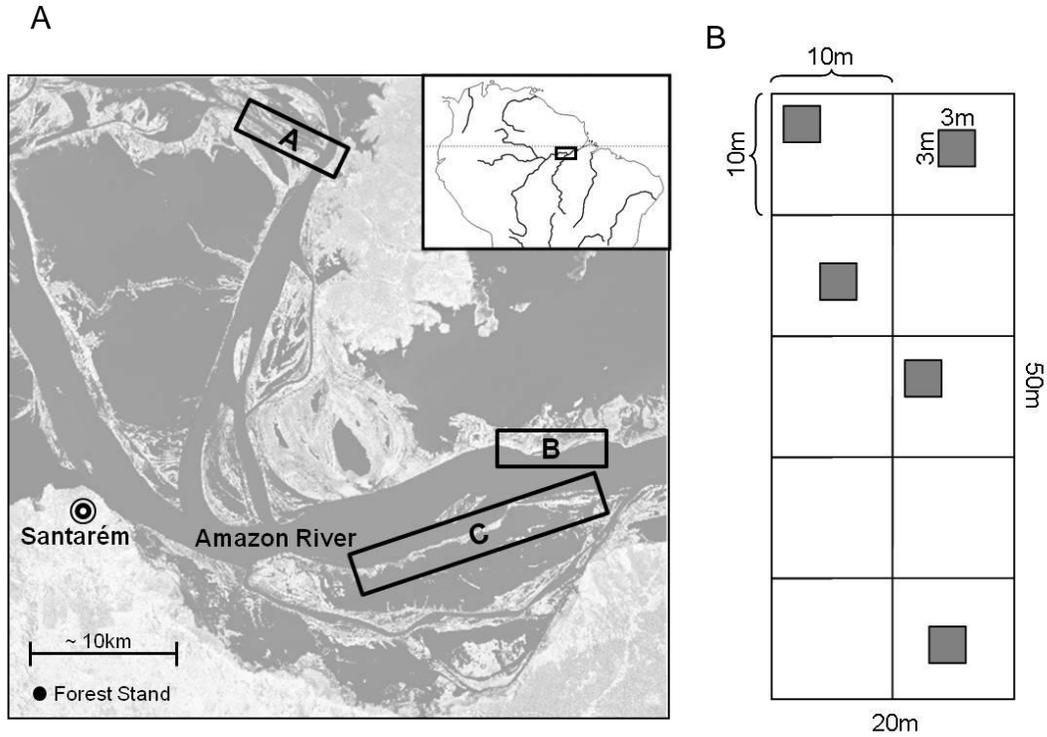
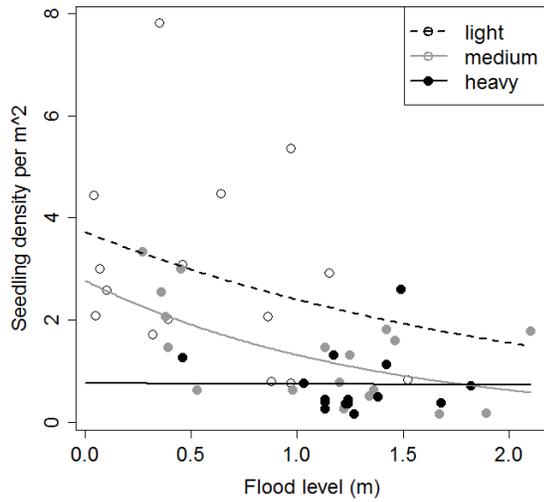


Figure 5-1. Map of secondary floodplain forests stands in Santarém, Pará, Brazil, at the confluence of the Amazon River and the Tapajós River. A) Boxes indicate three locations within which 0.1 ha. plots were established (A: 9 plots; B: 7 plots; C: 27 plots). B) Experimental design of 0.1 ha plots with 5 3 x 3 m seedling subplots (indicated in grey).

A



B

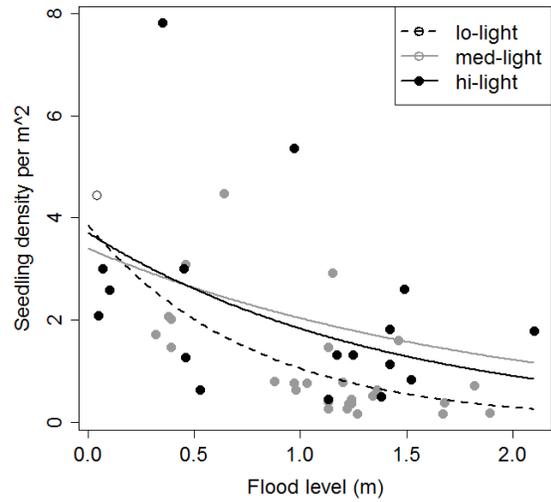


Figure 5-2. Average seedling density across a flood gradient. Seedling density as a function of A) flood level and livestock activity levels in 2008, and B) flood level and light availability (low = 0-5%, medium = 5-10%, and high = 10-35% canopy openness). Points indicate plot level averages of seedling density.

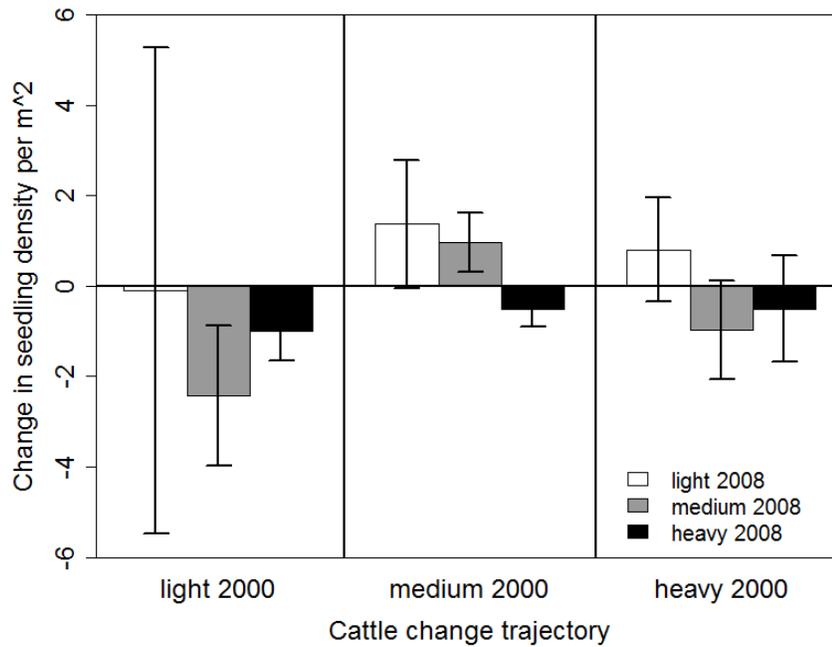


Figure 5-3. Change in seedling density across livestock change trajectories from 1999 to 2008 (means & SD). Bars indicate a given change trajectory from livestock levels in 1999 (x-axis) to livestock levels in 2008 (white, grey, and black bars).

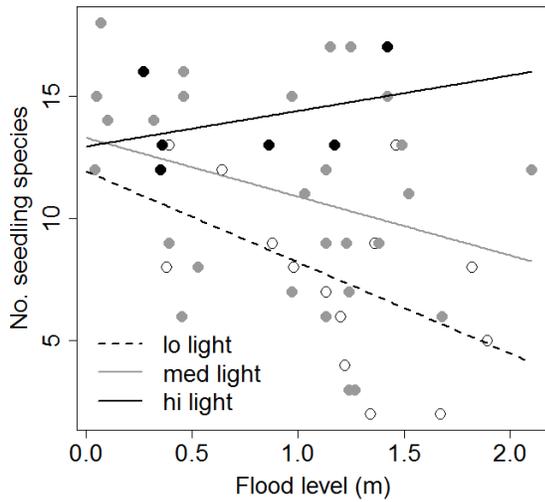
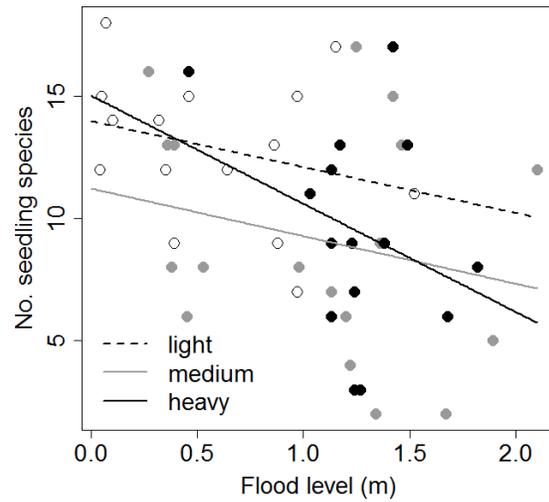
**A****B**

Figure 5-4. Number of seedling species in 45 m<sup>2</sup> across a flood gradient. Species number as a function of A) flood level and light availability (low = 0-5%, medium = 5-10%, and high = 10-35% canopy openness); and B) flood level and livestock activity (light, medium, and heavy) in 2008.

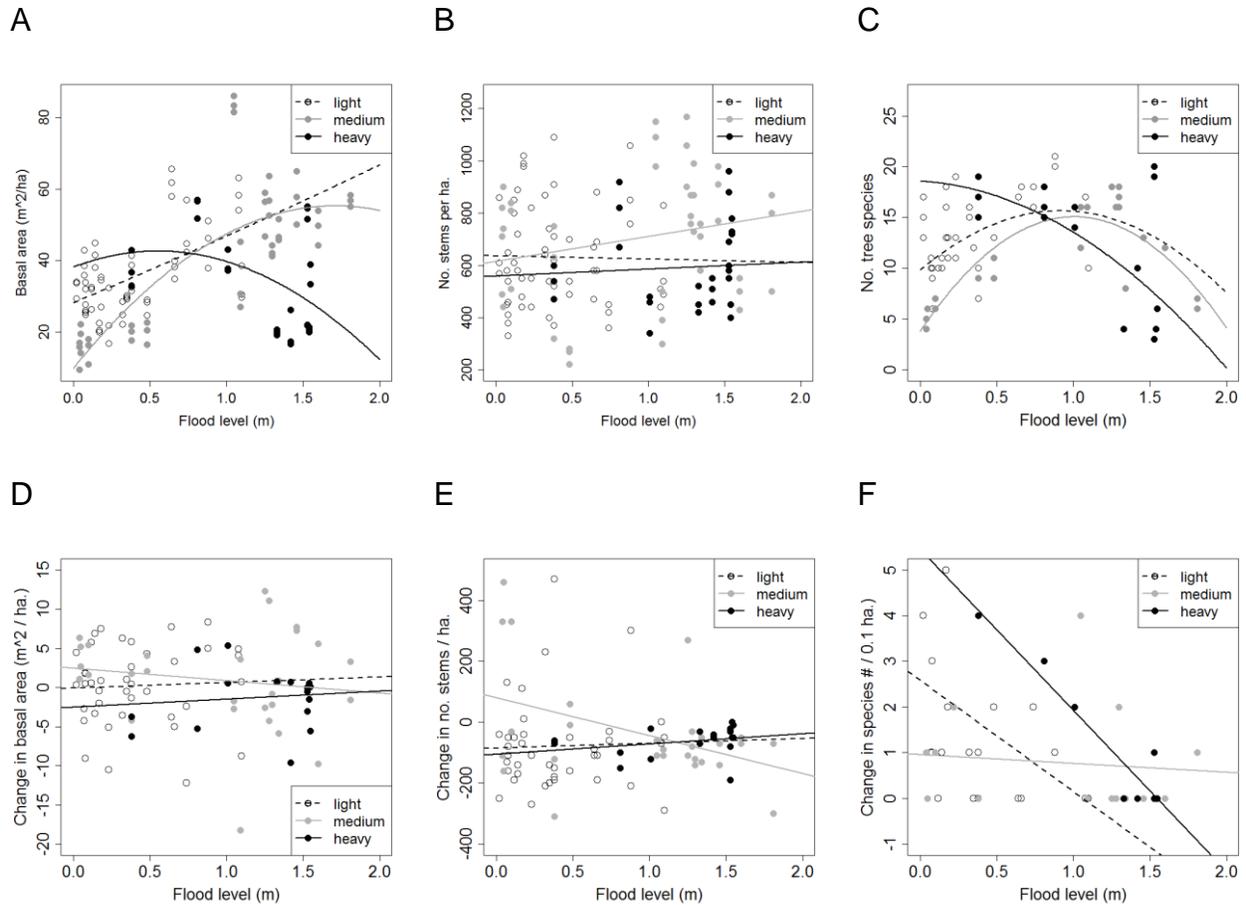


Figure 5-5. Trends in forest stand structure across flood level and livestock activity. A) Basal area, B) stem density  $ha^{-1}$ , and C) species density  $0.1 ha^{-1}$ , across flood level and livestock activity in 1999-2008. Trends in D) change in basal area, E) change in stem density, and F) change in species density from 1999 to 2008 across flood level and livestock activity. Points indicate values for each of 43 plots for each census in 1999, 2003, and 2008.

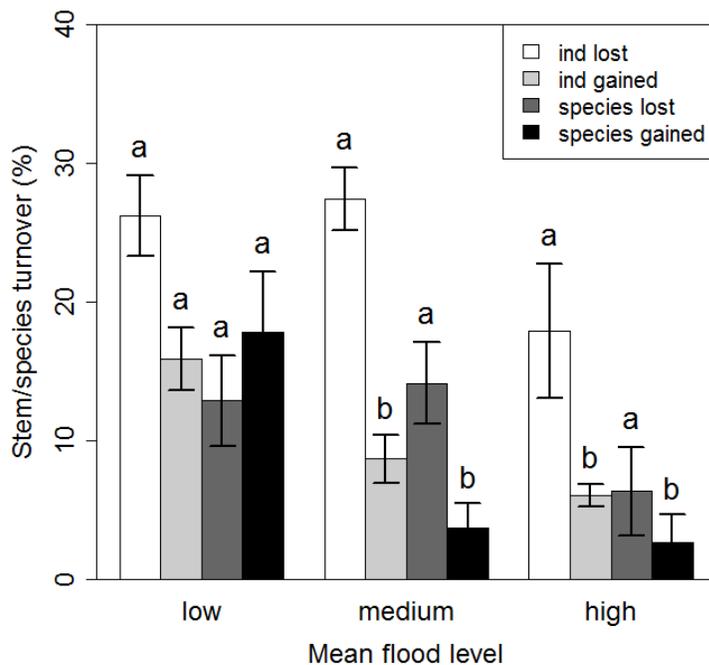
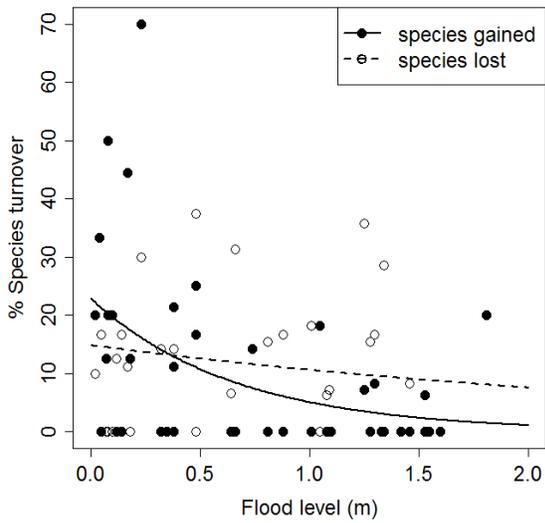


Figure 5-6. Stem and species turnover rates from 1999-2008 comparing percent of trees lost (mortality) and gained (recruitment) and the number of species lost and gained across flood levels (0-0.6 m = high; 0.61-1.3 m = medium; 1.31-1.9 m = high) in 0.1 ha plots (means & SD). Differences based on Tukey HSD tests are indicated by lower case letters.

A



B

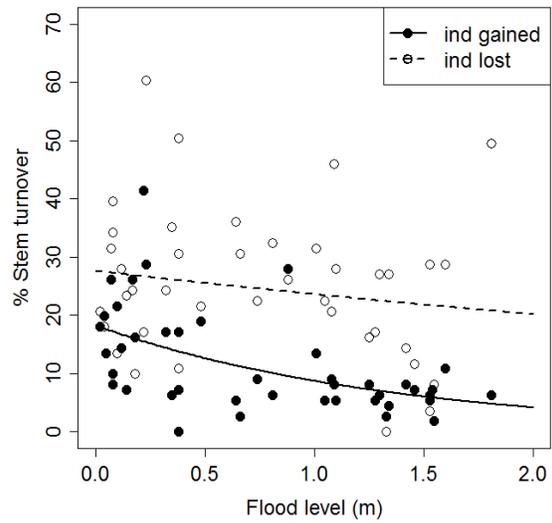


Figure 5-7. Trends in stem and species turnover across the flood gradient. A) Species lost and gained as a function of flood level. B) Stems lost (mortality) and gained (tree recruitment) as a function of flood level.

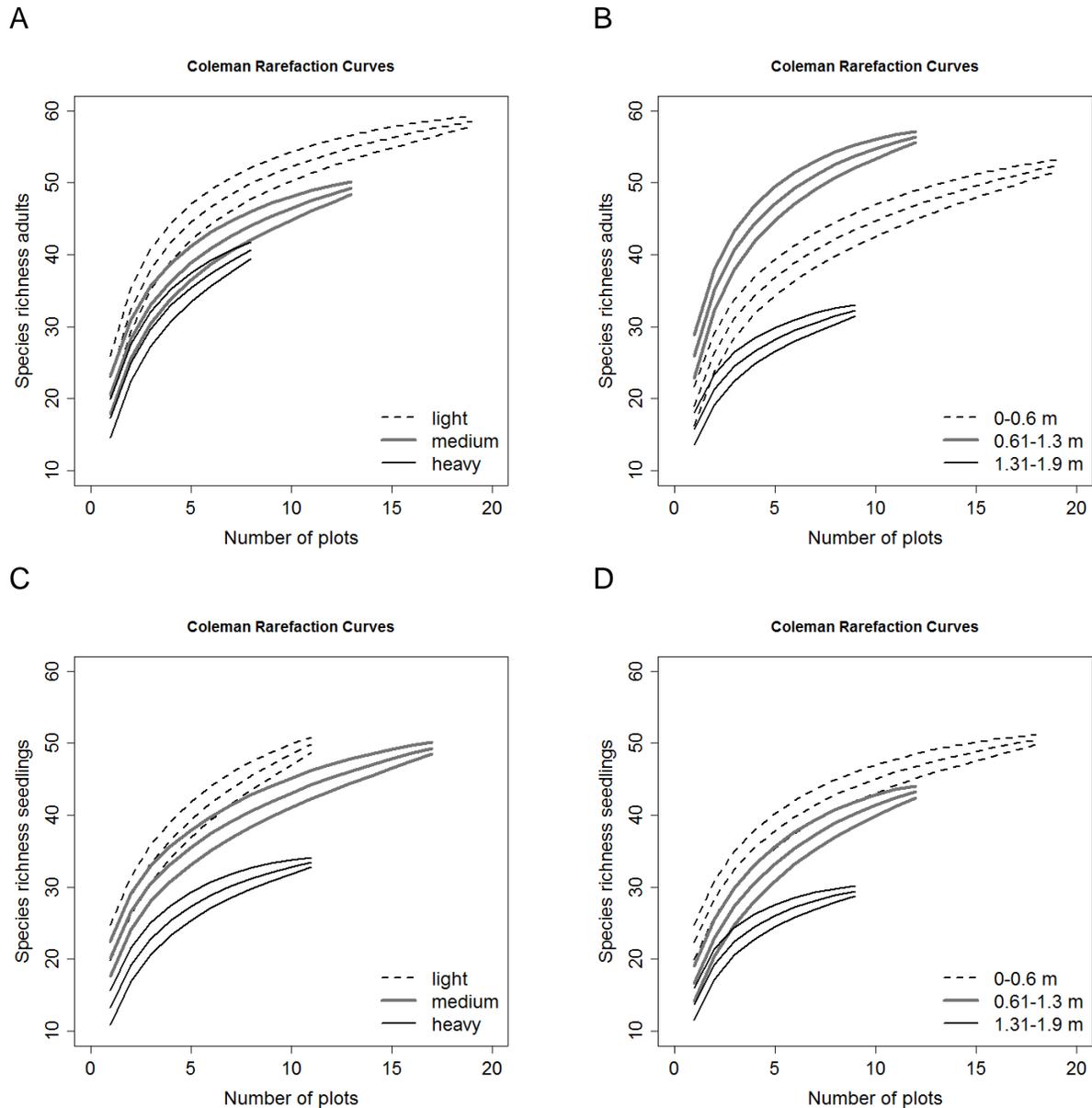
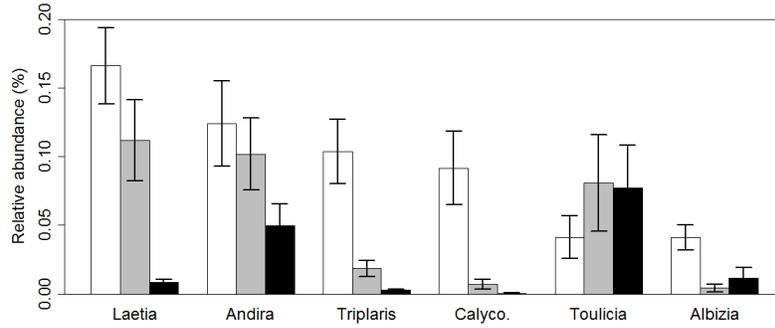
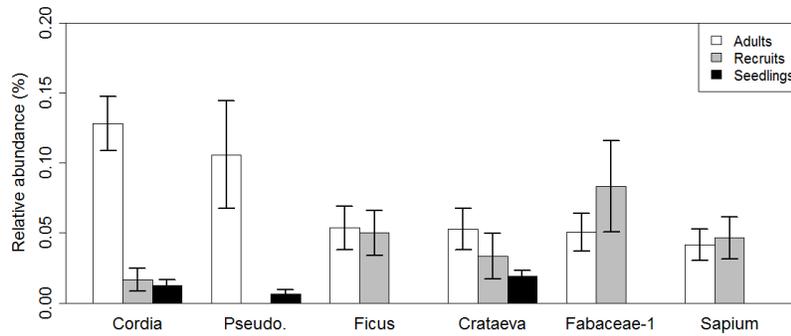


Figure 5-8. Species accumulation curves for seedlings and trees. A) Species accumulation curves of trees ( $\geq 10$  cm DBH) across three livestock levels in 1999-2008. B) Species accumulation curves of trees across three flood level categories. C) Species accumulation curves for seedlings across three livestock levels in 2008. D) Species accumulation curves for seedlings across flood level categories. All values based on Coleman rarefaction values with 95% confidence intervals calculated in EstimateS.

A



B



C

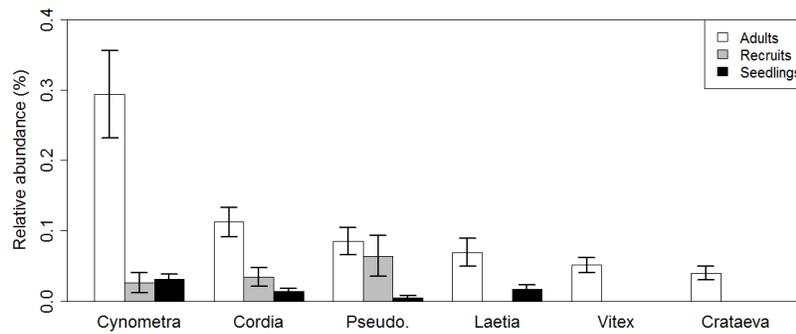


Figure 5-9. Comparisons of relative abundance of the of the 6 most common species of trees, recruits, and seedlings at different flood levels: A) low flood level, B) moderate flood level, and C) high flood level.

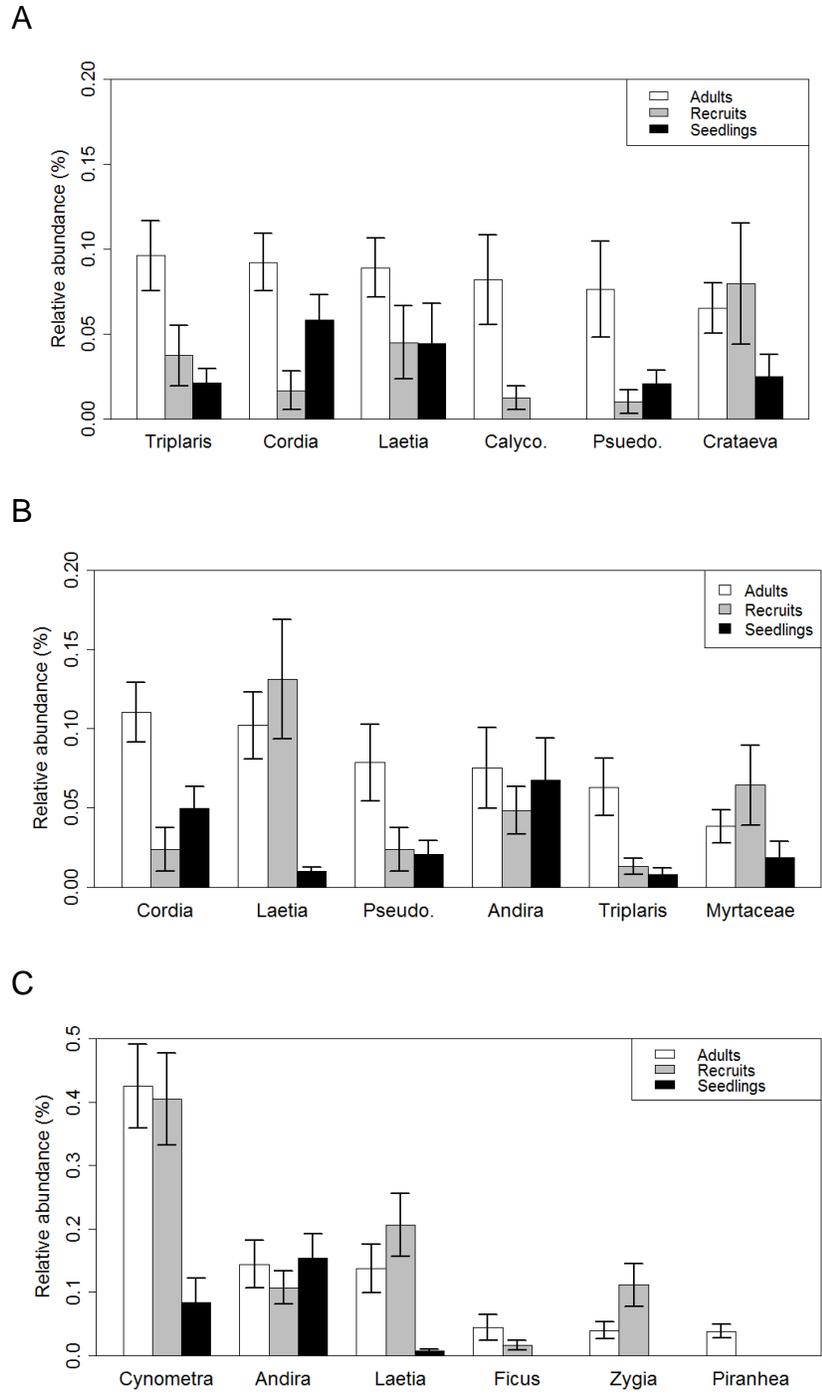


Figure 5-10. Comparisons of relative abundance of the 6 most common species of trees, recruits, and seedlings at different levels of livestock activity: A) light, B) medium, and C) heavy livestock activity.

## CHAPTER 6 ABOVEGROUND BIOMASS AND CARBON SEQUESTRATION IN SECONDARY FLOODPLAIN FORESTS OF EASTERN AMAZONIA

### Overview

Regional carbon budget estimates for the Amazon Basin often exclude the contribution of floodplain forests, which comprise ~4% of land area. Biomass accumulation rates in floodplain forests can double those in upland forests, but few estimates are available to confirm such trends across the Basin. This study fills a gap in ground-based data for aboveground woody biomass (AGB) and biomass accumulation rates in Amazonian floodplain forests in the Dry Corridor. We also test how productivity varies within a floodplain by comparing biomass dynamics across gradients of flood stress, forest age and livestock activity. We estimated average aboveground woody biomass of 15-80 year-old forests as  $\sim 210 \text{ Mg ha}^{-1}$ . Flood level and forest age interacted to affect AGB, which peaked  $> 250 \text{ Mg ha}^{-1}$  in mid-successional forests with moderate flooding ( $\sim 50$ -100 days flooding). In a subset of forests monitored over nine years, average aboveground biomass accumulation was  $\sim 5 \text{ Mg ha}^{-1} \text{ y}^{-1}$ . Biomass accumulation rates showed no correlation with flood level, refuting the hypothesis that productivity should increase with decreasing flood duration. Variation in species composition and livestock activity appeared to explain the slow tree growth and low recruitment that resulted in net carbon losses in some stands. Annual mortality rates averaged 70% of total biomass gains, suggesting relatively high stem mortality. Despite a long history of land-use, carbon sequestration by secondary floodplain forests is an important component of local carbon budgets. These data can improve regional models for C budgets as well as explain local-scale variation in biomass across multiple interacting factors.

## Background

Tropical forests are an important sink for global carbon (Phillips et al. 1998, Baker et al. 2004). Tropical rivers and wetlands, however, can be important sources of carbon via net annual losses from out-gassing of CO<sub>2</sub> (Richey et al. 2002). Floodplain forests are highly productive ecosystems at the transition zone between upland forests and rivers (Junk et al. 1989). Despite comprising only approximately 4% of land area of the Amazon Basin (Saatchi et al. 2007), floodplain forests can sequester carbon at 2-3 times the rate of upland tropical forests (Nebel et al. 2001a, Schöngart et al. 2010). Such high rates of production could help offset net annual carbon losses, but few data are available to incorporate seasonally flooded forests into carbon budget models (Table 6-1; Baker et al. 2004, Saatchi et al. 2007). Further ground-based data for biomass and biomass accumulation rates are needed to understand the role of floodplain forests in source-sink relationships of carbon in tropical watersheds.

Tropical forest biomass and carbon sequestration are affected by regional-scale factors such as dry season duration and extreme climate events such as El Niño/La Niña-Southern Oscillation (Malhi et al. 2004). Regional models for forest biomass suggest that dry regions have lower basal area, which can lead to lower estimations for biomass (Saatchi et al. 2007). Upland tropical forest stands can experience net biomass losses due to increased stem mortality associated with drought (Condit et al. 1995, Nepstad et al. 2007). Trees in the floodplain, however, are unlikely to experience water stress in drought years due to the proximity of the water table, even during exceptionally dry years (Parolin et al. 2009). Seasonally flooded forests should show opposite trends, with increases in biomass accumulation during drought (Schöngart et al. 2010). The decrease in flood levels in drought years can increase the terrestrial

phase for tree growth floodplains, and thus increase diameter increment (Schongart et al. 2004). The Dry Corridor of low rainfall and prolonged dry seasons in the Amazon Basin has been useful for predicting the effects of drought on upland forest biomass (Phillips et al. 2009). Data for floodplain forest biomass and carbon sequestration rates in the Dry Corridor are lacking, making it difficult to understand how floodplain forests differ across regions.

Stand biomass and biomass accumulation rates vary with many local abiotic factors, including environmental stresses such as flooding. The response of forest productivity to flood stress can follow many trends, including that predicted by the subsidy-stress model (Odum et al. 1979). The model suggests that productivity is higher in forests with short-term seasonal floods than in forests with stagnant water and long-term flooding. In stands with short-term seasonal flooding, flooding is not considered a stress to the ecosystem but a subsidy that enhances productivity in comparison to upland forests. This model was developed from observations in cypress swamp forests of the southeastern US (Conner and Day 1976). An alternative hypothesis, which has received more support from empirical data (Megonigal et al. 1997), suggests that the physiological stress of anoxia supersedes the subsidies to production during flooding (Mitsch and Rust 1984). This model also predicts decreasing productivity with increased flooding, but with productivity rates equal to or lower than that of upland forests.

A large area of floodplain forest in the Eastern Amazon is secondary, recovering from deforestation from timber extraction and agriculture (Anderson et al. 1999, Zarin et al. 2001, Wittmann et al. 2006). The rapid growth rates of early-mid successional tree

species in secondary floodplain forests could result in high rates of biomass accumulation (Schöngart et al. 2010). However, secondary floodplain forests also face continual degradation by logging, fuelwood extraction, and trampling by livestock (Sheikh et al. 2006). These local land-use activities could reduce biomass accumulation rates via high stem mortality and poor recruitment (Chazdon et al. 2007).

The goal of this study was to provide long-term data on aboveground woody biomass (AGB) and aboveground biomass accumulation rates in secondary floodplain forests in the Dry Corridor of the Amazon Basin. I measured AGB and biomass accumulation in a network of secondary floodplain forest plots in the Lower Amazon. I addressed the following questions: 1) What are AGB and biomass accumulation rates for secondary floodplain forests in the Dry Corridor and how do they compare to floodplain forests of other regions?, 2) How do AGB and biomass accumulation vary across flood level and forest age?, 3) How do biomass accumulation rates vary across different livestock intensities?

## **Methods**

### **Study Region**

The Amazon Dry Corridor has relatively low rainfall (1200-2200 mm yr<sup>-1</sup>) and prolonged dry seasons of 3-6 months < 100 mm month<sup>-1</sup> (Figure 6-1; Sombroek 2001). Patches of dry forest and savanna within the corridor are relicts of drier periods within the Last Glacial Maximum (Anhuf et al. 2006). The Santarém region of Pará state in Brazil (02°25'S, 54°42'W) lies within the Dry Corridor and has an average rainfall of 2180 mm yr<sup>-1</sup> and 5 consecutive dry months < 100 mm (July-December; Fitzjarrald et al. 2008). In the region, seasonal floods of the Amazon River peak between May and June, rising to an average of 7.5 m a.s.l. (1975-2008, Capitania dos Portos Santarém

2008) and extending up to 40 km from the main channel. Floodplains in the region are a mosaic of natural grasslands, forested levees, lakes, and giant aroid stands of *Montrichardia arborescens*. Forests occupy approximately 15% of the area (M. Crossa, personal communication, June 1, 2007), restricted to higher elevation levees within the floodplain. Historical land uses in floodplain forests include the planting of cacao (*Theobroma cacao*) and rubber trees (*Hevea brasiliensis*) in the 1800s to early 1900s, followed by deforestation for jute (*Corchorus capsularis*) plantations in 1940-1990 (Winklerprins 2006). Forests have regrown on abandoned jute plantations but currently face increasing activity by cattle and water buffalo in the floodplain (Sheikh et al. 2006).

### **Study Design**

A network of 49 plots of 20 x 50 m was established in three levees within the floodplains of the Santarém municipality by P.S. in 1999 to evaluate the effects of cattle and water buffalo on *várzea* forest stand dynamics. The plots were located in three communities of floodplain residents previously associated with the *Várzea* Project of IPAM – Instituto de Pesquisa Ambiental da Amazônia, as well as on land owned by EMBRAPA. This network is among the few semi-permanent system of plots monitoring secondary floodplain forests in the Amazon. By 2008, 43 plots remained due to losses by deforestation (N=2), bank erosion (N=3), as well as changes in willingness to participate by landholders (N=1). In 2008, 6 new plots were added to the network to incorporate older forest stands of  $\geq 80$  y since deforestation. As such, 49 plots were used to estimate forest biomass in 2008, and 43 plots were used to measure change in aboveground biomass over the nine-year study period. Forest age was determined based on informal interviews with landholders in 1999 and 2008. All trees ( $\geq 10$  cm DBH (diameter at 1.3 m height) were measured at the end of the dry season in the low-

water period (December-January) in 1999. Plots were censused again at the same time of year in 2003 and 2008 by C.L.

Plots were classified as light (1), medium (2), or heavy impact (3) of livestock in 1999 and 2008 based on average hoof print density in five 9 m<sup>2</sup> seedling plots (0-10 = light, 11-20 = medium, 21-80 pugmarks = heavy) and herd activity as observed in behavioral studies (Sheikh 2002). Hoof print density was deemed a surrogate variable for herd densities in forests as they remained in soils throughout the low-water season (Sheikh 2002). Average livestock activity over nine years was calculated from the 1999 and 2008 data (light, med-light, medium, med-heavy, and heavy). I calculated flood level as the average water depth in forests during the flood season from 1999 to 2008. Water depth was measured at 10 m intervals in forest plots with a weighted line during peak flooding in June 2006 (river level was 8.6 m a.s.l.). To calculate average flood level over 9 years, I subtracted the difference between levels in 2006 and the average for 1999-2008. Flood depth was thus a relative measure of the difference in maximum water column within plots. Forest plots were located on four different levees within the floodplain, two along the main Amazon channel and two along different branches of the Amazon River (Figure 6-1). To control for differences in stand structure and species composition due to unmeasured variables such as water chemistry and soil structure, levee was considered a random effect in statistical models.

To estimate aboveground biomass and net biomass accumulation, I measured DBH of trees ( $\geq 10$  cm DBH) in forest inventories in 1999, 2003, and 2008. Tree height was estimated visually for each tree, with a sub-sample of standing trees measured with a meter tape to test for accuracy. Wood density values were obtained from previously

published values from species in floodplain forests of the Central and Western Amazon (Wittmann 2006). I calculated total aboveground woody biomass and biomass accumulation rates based on growth intervals in 1999-2004 and 2004-2008. Voucher specimens were collected from a subsample of trees in collaboration with the University of Western Pará of Santarém (UFOPA) and deposited at the INPA-Manaus and UFOPA herbaria. Permission to collect nonthreatened species and deliver to these herbaria was granted by SISBIO, the federal bureau for the within-country collection of biological material in Brazil (Authorization #18177-1).

### **Statistical Analyses**

Aboveground biomass of trees was calculated using allometric regression equations based on wood density, diameter, and height. As allometric equations for trees in floodplain forests have not been calibrated, I used models from *terra firme* tropical forests developed by Cannell (Cannell 1984), as well as models for tropical dry forest and tropical moist forest (Chave et al. 2005). Tropical dry forest allometric equations were developed for trees with severe water stress > 5 mo, and thus may be more adequate for flooded trees with a period of slow growth during annual floods (Schöngart et al. 2010). Of the 74 species recorded, wood density was available for 43 species (Wittmann et al. 2011). Wood densities for 17 of the remaining species were calculated by genus-level estimates for species occurring in *várzea*; 6 species were calculated by genus-level estimates from trees in *terra firme* tropical forests; and 8 species, including unknown morphospecies were estimated by the average wood density of *várzea* trees in Central and Western Amazonia (Schöngart et al. 2010). Carbon was assumed to contribute 50% of biomass (Clark et al. 2001, Saatchi et al. 2007).

Cannell's tropical forest model (Cannell 1984)

$$AGB = 0.06 \cdot WD \left\{ \frac{(\pi \cdot DBH^2)}{4} \right\} \cdot h$$

Dry tropical forest model (Chave et. al 2005)

$$AGB = 0.112 \cdot (WD \cdot DBH^2 \cdot h)^{0.916}$$

Moist tropical forest model (Chave et. al 2005)

$$AGB = 0.0509 \cdot DBH^2 \cdot h$$

Trends in biomass accumulation and loss were observed at two time intervals (1999-2003 and 2003-2008) over a period of nine years. The 43 sites with repeated measurements of DBH were grouped into three age categories to compare biomass trends in stands of different age: 15-25 (N=6); 30-35 (N=21); 45-50 (N=16) years since agricultural abandonment. Forest biomass was compared across flood levels and forest age categories with repeated measures Linear Mixed Models fit by restricted maximum likelihood and an autoregressive correlation structure (Crawley 2007). Biomass was log transformed to achieve normality of model residuals, according to Shapiro-Wilk tests. Due to the polynomial relationship between flood level and biomass, the quadratic term for flooding was included as a quadratic term in models (Crawley 2007). I accounted for heterogeneity in variance of biomass within age categories by using the VarIdent variance structure in Generalized Linear Models (Zuur et al. 2009). Average annual change in biomass was compared across flood levels and forest age categories with Linear Mixed Models fit by restricted maximum likelihood. Differences in biomass and net biomass change between forest age categories were tested *post-hoc* with Tukey's

HSD tests. All analyses were conducted in R 2.9.0 (R Development Core Team 2009) using the the “nlme” package (Pinheiro et al. 2008).

## Results

I identified 2568 of 2852 individuals in the 2008 inventory to species, an additional 216 to genus, and 36 to family; 32 trees were unknown. Wood density among trees averaged  $0.57 \pm 0.16$  SD g/cm<sup>3</sup>, and was highest in forests 30-35 y old (Tukey HSD,  $p < 0.05$ ).

Average AGB of forests 15-80 y old was  $204 \pm 97$  Mg ha<sup>-1</sup> according to Cannell's tropical forest model;  $220 \pm 105$  Mg ha<sup>-1</sup> according to the Dry tropical forest model; and  $211 \pm 87$  Mg ha<sup>-1</sup> according to moist tropical forest model, with no differences among model estimates (Tukey HSD,  $p < 0.05$ ; Figure 6-2A). As such, I hereafter refer to values reported by the moist tropical forests as it provided an intermediate estimate for biomass. Across forest ages, AGB peaked at  $268 \pm 25$  Mg ha<sup>-1</sup> in forest plots of 26-35 y, then tapered off at  $197 \pm 8$  to  $213 \pm 9$  Mg ha<sup>-1</sup> in 80-yr old forest plots (Figure 6-3B). Although no main effect of age was found in generalized linear models, there were interactive effects of forest age with flooding and the quadratic term for flooding (Table 6-2).

Across a flood gradient of 0 to 1.9 m depth, AGB peaked at moderate flood levels (0.7-1.3 m or approximately 100-130 d of flooding). AGB was predicted by a negative quadratic relationship in relation to flood level (Figure 6-2B; Table 6-2). Plots with exceptionally high AGB of 500-570 Mg ha<sup>-1</sup> had large trees 71-149 cm DBH (e.g., *Ficus insipida*, *Triplaris surinamensis*).

Net aboveground biomass accumulation averaged  $4.9 \pm 13.8$  SD Mg ha<sup>-1</sup> y<sup>-1</sup> over nine years. Biomass accumulation ranged from  $10.6$  Mg ha<sup>-1</sup> y<sup>-1</sup> in young forests (15-25

y) to  $2.8 \text{ Mg ha}^{-1} \text{ y}^{-1}$  in late successional forests of 40-50 y old. There were no effects of forest age or flood level on biomass change (Figure 6-2B; Table 6-2). Net change in AGB was not correlated with flood level ( $t_{41} = -1.28$ ,  $p = 0.21$ ,  $r = -0.20$ ).

Plots sustaining heavy cattle activity over time displayed negative changes in AGB over time (Figure 6-3). Heavily impacted stands had low biomass gains in tree growth, but no difference with other plots in terms of biomass lost via mortality or biomass gained via recruitment (Figure 6-3). There was no main effect of average cattle impact on biomass accumulation (Table 6-3), but forests with sustained heavy cattle impacts had lower biomass accumulation than from forest stands with less impact (Tukey HSD  $< 0.05$ ; Figure 6-3).

By measuring the components of net biomass change, I found that 70% of biomass gained was lost to stem mortality on an annual basis. Annual loss in AGB due to stem mortality was  $11.0 \pm 9.3 \text{ Mg ha}^{-1} \text{ y}^{-1}$  or  $2.8 \pm 2.8 \% \text{ y}^{-1}$  of total AGB. The contribution of recruited stems to annual gains in AGB averaged  $1.6 \pm 1.2 \text{ Mg ha}^{-1} \text{ y}^{-1}$  or  $0.22 \pm 0.30 \% \text{ y}^{-1}$  (Table 6-4). The remaining gains in AGB (98%) were attributed to diameter and height growth of standing trees.

## Discussion

### Trends in Aboveground Biomass in Amazonian Floodplain Forest

Secondary floodplain forests were a net carbon sink despite histories of intensive land-use. To our knowledge, I provide the first estimates available for aboveground woody biomass and biomass accumulation in floodplain forests of the Amazon's Dry Corridor. I calculated mean aboveground biomass of forests 15-80 years old as  $\sim 210 \text{ Mg ha}^{-1}$ , comparable to that of less degraded forests of the Central Amazon.

Amazonian floodplain forests, although characterized by seasonal or tidal flooding,

differed widely in aboveground biomass (Johnson et al. 2000). Such differences may be due to a combination of factors, including hydrological regime, climate, and land-use history. Net annual rates of biomass accumulation were lower than those of floodplain forests of similar ages (Table 6-4) but similar to rates in upland forests.

Flood level was a key predictor of forest biomass. Forests reached maximum biomass at moderately flooded sites (see also Mitsch and Ewel 1979, Ferreira 1997). I expected biomass to peak in high elevation forests with low flood levels, as a longer dry period would increase the growth season. The low AGB in high elevation forests may be due to die off of large, low-flood-tolerant species in high flood years (e.g., *Hura crepitans*, *Guarea guidonia*); harvesting of trees for fuelwood (e.g., *Calycophyllum spruceanum*); and the exposure of high-elevation levees to wind and soil erosion. In the Central Amazon, stands of similar species composition and land-use history had peak biomass in mid-high elevation stands flooded 1-2 mo  $y^{-1}$  (Schöngart 2003). However, in the Western Amazon floodplain forests of Peru, biomass was highest in low-elevation *tauhampa* forest flooded 4 mo  $y^{-1}$  (Nebel et al. 2001a). Comparison of biomass trends across the flood gradient is complicated by within-site variation in soil moisture availability, nutrient status, flood regime, and species composition, which all affect biomass. While the subsidy-stress model predicts high biomass in stands with short-term periodic flooding, I contribute to growing empirical evidence that the relationship between flooding stress and forest biomass is site-specific (Mitsch and Rust 1984, Megonigal et al. 1997).

Forest age is a primary predictor of forest biomass, but its effect can be difficult to detect over short time periods (Steininger 2000). The effect of forest age on AGB was

dependent upon flood level, whereby differences between old and young forests were only detected at moderate flood levels. Contrary to the common trend of increasing biomass with age, I found the highest AGB in forests of 30-35 years old. Similarly, a study of Central Amazon floodplain forests showed that AGB peaked at 30-50 y and declined in mature stands (Schöngart et al. 2010). Upland secondary forests approach mature stand biomass as early as 30 years post-agricultural abandonment (Letcher and Chazdon 2009); 72 years (Hughes et al. 1999); or > 80 years (Saldarriaga et al. 1988). The high biomass in younger floodplain forests may be caused by phases of succession characterized by dense stands of fast-growing long-lived pioneers, *Pseudobombax munguba* (Schöngart et al. 2010) and *Triplaris surinamensis* (this study).

I have little evidence to suggest that variation in land-use intensity had visible effects on forest biomass. Biomass in forests sustaining intense livestock activity over time had relatively lower biomass than other stands. While browsing and trampling by livestock can decrease riparian vegetation biomass (Robertson and Rowling 2000, Kauffman et al. 2004), the low biomass in high-disturbance sites may be related to other factors such as soil texture, geomorphology, and species composition.

In the Amazon estuarine floodplain forests recovering from abandoned jute and banana cultivation, AGB of forests 50-60 y old is double the values for the Santarém region (Johnson 1999). The fertility of floodplain forest soils and annual cycles of erosion and deposition are potential mechanisms by which these forests rapidly recover such large amounts of carbon in AGB following disturbance by small-scale agriculture.

### **Changes in Aboveground Biomass**

Estimated carbon sequestration by aboveground woody biomass was approximately half that of the Central and Western Amazon *várzea* forests (Table 6-1).

I expected higher annual biomass accumulation rates than other floodplain forests given the long dry season and high nutrient status of soils (Johnson et al. 2000).

Nonetheless, early successional forests show a net influx of  $\sim 5 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ , which is relatively high considering rates of C sequestration by AGB in early successional upland forests of  $\leq 6 \text{ Mg ha}^{-1} \text{ yr}^{-1}$  (Steininger 2000). Late successional forests  $> 40$  y old show C sequestration rates ( $1.40 \pm 0.62 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ ) equal to that of old-growth upland forests in the Santarém region (Rice et al. 2004). Based on these comparisons, I conclude that while these forests have suffered multiple phases of deforestation and have low biodiversity, they may play an important role for C budgets in the region.

Net change in aboveground biomass may have been low due to high losses to stem mortality of 70% of biomass gained. Similar results were found in a Western Amazon secondary forest, where gross biomass accumulation was  $9.7 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ , of which half was lost annual to stem mortality (Valencia et al. 2009). Mortality in floodplain forests may be related to the death of pioneer species as a natural phase of succession. I observed high mortality of pioneer stems (e.g., *Cordia tetrandra*, *Triplaris surinamensis*) in plots subjected to windstorms and strong currents along the main channel of the Amazon River. Mortality may also be a result of anthropogenic disturbances from long-term cattle and water-buffalo activity within forests, as well as removal of stems by firewood harvesting.

There was no correlation between flood level and biomass accumulation to support a subsidy-stress model for woody production in Amazonian floodplain forests. As found in river-floodplain systems in temperate regions (Megonigal et al. 1997), woody biomass production was highly variable across all flood levels. Such variation

may be attributed to differences in species composition or land-use. Biomass accumulation in secondary forests is known to be a function of many factors, including stand age, length of the growth season, soil moisture availability, nutrient status, disturbance size and disturbance intensity as well as species composition (Johnson et al. 2000). For floodplain forests, I find supporting evidence for decreasing biomass accumulation with forest age, with wide variance within stand age classes. Despite the shorter growth season for trees at lower elevations with sometimes slow-flowing waters, I found no evidence to support lower biomass accumulation in low-elevation forest stands.

Disturbance by large herbivores can limit biomass production in forests (Robertson and Rowling 2000), but I did not find evidence to support this conclusion. Rather, in this study the net loss of biomass in stands with heavy cattle impacts was a result of low tree growth rates, and not high tree mortality or low recruitment (Figure 6-4). Cattle and water buffalo could decrease tree growth rates via soil compaction and root damage, but I have no data to show such an effect. Growth rates are instead likely to be low due to the fact that 5 out of the 6 plots maintaining heavy cattle impacts are dominated by *Cynometra bauhiniifolia*, a slow-growing dense wood ( $WD=0.81$ ) of mid-late successional stages. Given species composition and forest age, I would expect biomass accumulation to be low. Negative change in biomass appears to be attributed to the fact that biomass loss from stem mortality exceeds gains from stem growth and recruitment. Livestock could play a role in causing low recruitment rates.

Finally, it is important to consider the potential sources of error in biomass calculations (Phillips et al. 2000). Among the largest sources of error for biomass

calculation is the selection of the allometric model for biomass estimation (Chave et al. 2004). The allometric equations applied here were developed for *terra firme* forests, as no equations for *várzea* forests are available. Trees of the same species are shorter in the *várzea* than in uplands (Worbes 1997), and thus models based on tapering of trunks in uplands may overestimate biomass for *várzea* species. Although I incorporated height and wood density to increase accuracy, error for biomass estimates using such terms in models may still reach 14% (Nelson et al. 1999). I also suspect that there were overestimates of large trees with DBH > 30 (Nogueira et al. 2006), resulting in biomass estimates of 450-570 Mg ha<sup>-1</sup> for some stands. Allometric equations based on trees from floodplain forests are clearly necessary. In addition, errors in height estimation can be an important source of error in tree measurement component of biomass estimation (Chave et al. 2004). Finally, repeated measurements of DBH are less accurate than dendrometer bands for measurements of diameter growth. In addition, bark thickness, termite nests, vines, knots, etc. can change DBH measurements.

## **Summary**

Floodplain forests may play a small but important role in carbon sequestration in the carbon budgets for Amazonian forests and aquatic habitats. Our results suggest that secondary floodplain forests annually sequester substantial amounts of carbon. I found substantial losses in biomass due to stem mortality, a potential result of both anthropogenic disturbances (e.g., livestock ranching, deforestation, and fuelwood harvesting) and natural disturbances (e.g., extreme floods, windstorms). While total aboveground biomass peaked at moderate flood levels, annual biomass production was not related to flood level, as predicted by the subsidy-stress model. Extreme climate events such as drought and large floods, as well as land conversion for cattle pasture

are among the major threats to forests in the Amazon today (Malhi et al. 2008).

Continual monitoring of floodplain forest response to such events will be important for understanding their resilience to climate change and anthropogenic disturbance and their role in regional carbon budgets for the Amazon.

Table 6-1. Comparison of mean biomass, carbon storage, and carbon sequestration for aboveground woody stems in *várzea* forests of the Amazon Basin (adopted from Shöngart et al 2010).

Location in <i>várzea</i>	Forest age (sample size)	Biomass (Mg ha <sup>-1</sup> )	C sequestration by AWB (Mg C ha <sup>-1</sup> yr <sup>-1</sup> )
Lower Amazon estuary <sup>1</sup> (Ilha Marajó)	-	193 ± 18	-
Lower Amazon estuary <sup>2</sup> (Macapá)	12-15 (1) 20-30 (3) 50-60 (3)	77 ± 21 247 ± (73) 355 ± 12.4	- - -
Lower Amazon <sup>3</sup> (Santarém, this study)	15-25 (6) 30-35 (21) 45-50 (16)	148 ± 62 274 ± 112 188 ± 67	5.3 ± 1.6 2.4 ± 8.1 1.4 ± 6.3
Central Amazon <sup>4</sup> (Manaus)	80 (3) 44 (1) 80 (7)	204 ± 13 258 279	- 3.7 3.6
Central Amazon <sup>5</sup> (Mamirauá)	7 20 50 120 240	18 ± 3 117 ± 9 261 ± 10 230 ± 9 239 ± 11	2.81 ± 0.43 8.45 ± 0.49 7.17 ± 0.58 3.74 ± 0.16 2.73 ± 0.13
Peruvian Amazon <sup>6</sup> (Loreto)	unknown	344-487	7.43 ± 1.5
Bolivia & Peru <sup>7</sup>	old-growth	195-357	0.49 ± 0.1
Estimated regional <sup>8</sup> average for <i>várzea</i>	various	248 ± 23	

Means and SD are shown, with the exception of data from the Lower Amazon estuary (2), which are SE.

<sup>1</sup>(Almeida et al. 2004) 4 plots of 1 ha in Ilha Marajó and on the Rivers Pará and Xingu in the tidal estuary; trees ≥ 10 cm DBH; measurements taken at a single point in time.

<sup>2</sup>(Johnson 1999) 3 1 ha plots 50-60 y old and 4 plots of 10 x 10 m 6-30 y old in Macapá in the tidal estuary of the Amazon.

<sup>3</sup>this study 43 forest plots of 0.1 ha; trees ≥ 10 cm DBH; NPP based on woody biomass

<sup>4</sup>(Worbes 1997) Based on inventory data between 1981-1991 from 6 stands of *várzea* on the Ilha Montrichardia near Manaus on the Amazon River.

<sup>5</sup>(Schöngart et al. 2010) 4 plots of 1 ha in the Mamirauá Biological Reserve, Amazonas state; trees ≥ 10 cm DBH.

<sup>6</sup>(Nebel et al. 2001a): 9 forest plots of 1 ha in the Loreto Dept. of Peru; trees > 10 cm DBH.

<sup>7</sup>(Malhi et al. 2006): Review of 6 plots in Bolivia and Peru, excluding those from Nebel et al 2001.

<sup>8</sup>(Saatchi et al. 2007): Remote Sensing model estimate based on a meta-analysis including plots in floodplain forest in the Western Amazon (Peru, Bolivia, Ecuador, Colombia) and the Eastern Amazon at the mouth of the Amazon River (Marajó Island, Brazil).

Table 6-2. Summary of generalized linear model results for the effects of relative flood level, forest age, and their interactions on aboveground woody biomass in 2008 and net biomass accumulation from 1999-2008. Coefficient estimates are shown for continuous variables.

	Estimate	SE	F-value	p-value
Aboveground woody biomass				
Forest age	6.64	0.62	0.01	0.92
Flooding	4.99	1.17	24.0	<0.0001
Flooding <sup>2</sup>	-1.51	0.45	13.78	0.0006
Age x Flooding	-1.36	0.63	4.64	0.037
Age x Flooding <sup>2</sup>	0.39	0.24	15.05	0.0004
Net biomass accumulation				
Forest age	-	-	0.83	0.44
Flooding	-63.9	351.6	0.48	0.50
Forest age x Flooding	-	-	0.54	0.59

Table 6-3. Summary of generalized linear model results for the effects of relative flood level, cattle activity and their interactions on aboveground woody biomass in 2008 and net biomass accumulation from 1999-2008. Coefficient estimates are shown for continuous variables.

	Estimate	SE	F-value	p-value
Aboveground woody biomass				
Cattle activity	-0.87	0.53	1.00	0.32
Flooding	-1.65	1.61	37.6	<0.0001
Flooding <sup>2</sup>	1.15	0.95	23.0	<0.0001
Cattle × Flooding	1.88	0.85	4.86	0.03
Cattle × Flooding <sup>2</sup>	-1.04	0.49	0.06	0.81
Net biomass accumulation				
Cattle activity	-	--	0.95	0.45
Flooding	-1685	3142	0.61	0.44
Cattle activity × Flooding	-	-	0.30	0.88

Table 6-4. Rates of change in aboveground biomass in forest stands over 9 years (means & SD) by forest age.

	Forest age category		
	15-25 y	30-35 y	40-50 y
Mortality rate (Mg ha <sup>-1</sup> yr <sup>-1</sup> )	5.4 ± 5.8	11.5 ± 8.0	12.5 ± 9.3
Total gain (Mg ha <sup>-1</sup> yr <sup>-1</sup> )	15.5 ± 5.1	16.1 ± 14.3	15.1 ± 9.5
Growth rate (Mg ha <sup>-1</sup> yr <sup>-1</sup> )	13.9 ± 5.4	15.7 ± 14.0	14.5 ± 9.4
Recruitment rate (Mg ha <sup>-1</sup> yr <sup>-1</sup> )	1.65 ± 0.47	0.57 ± 0.78	0.67 ± 0.73
Net biomass change (Mg ha <sup>-1</sup> yr <sup>-1</sup> )	10.6 ± 3.3	4.89 ± 16.3	2.79 ± 12.7
Relative mortality rate (% yr <sup>-1</sup> )	1.8 ± 1.3	2.5 ± 1.6	3.6 ± 4.0
Relative recruitment rate (% yr <sup>-1</sup> )	0.59 ± 0.33	0.11 ± 0.16	0.22 ± 0.34
Relative growth rate (% yr <sup>-1</sup> )	4.6 ± 1.3	2.6 ± 2.0	3.2 ± 2.0

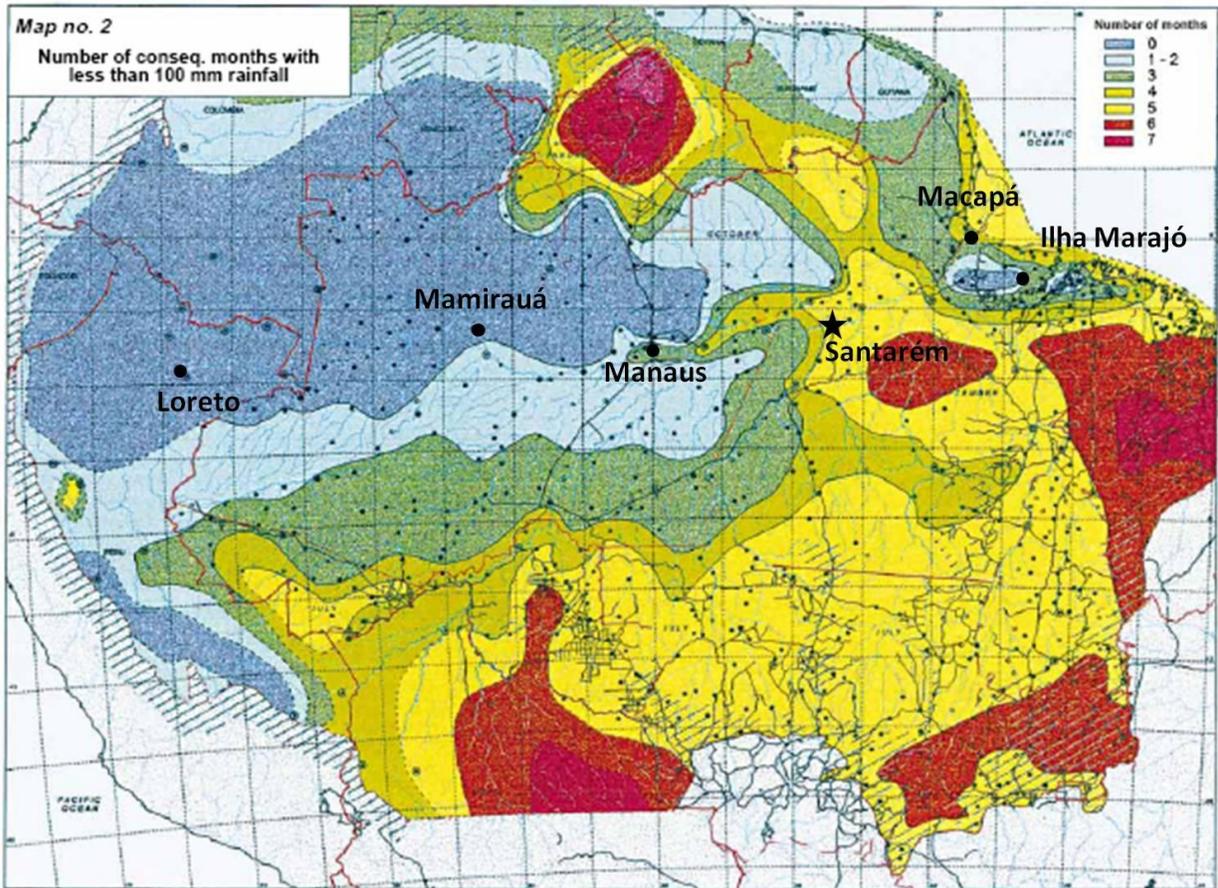


Figure 6-1. Map of the number of consecutive months with rainfall < 100 mm, illustrating the Dry Corridor crossing the Amazon River at 52-58°W. Bold points indicate locations where ground data for AWB of *várzea* forest has been published (Table 6-1); star indicates study location. Map reprinted by permission from Sombroek, W. 2001. Spatial and temporal patterns of Amazon rainfall - Consequences for the planning of agricultural occupation and the protection of primary forests. *Ambio* 30:388-396.

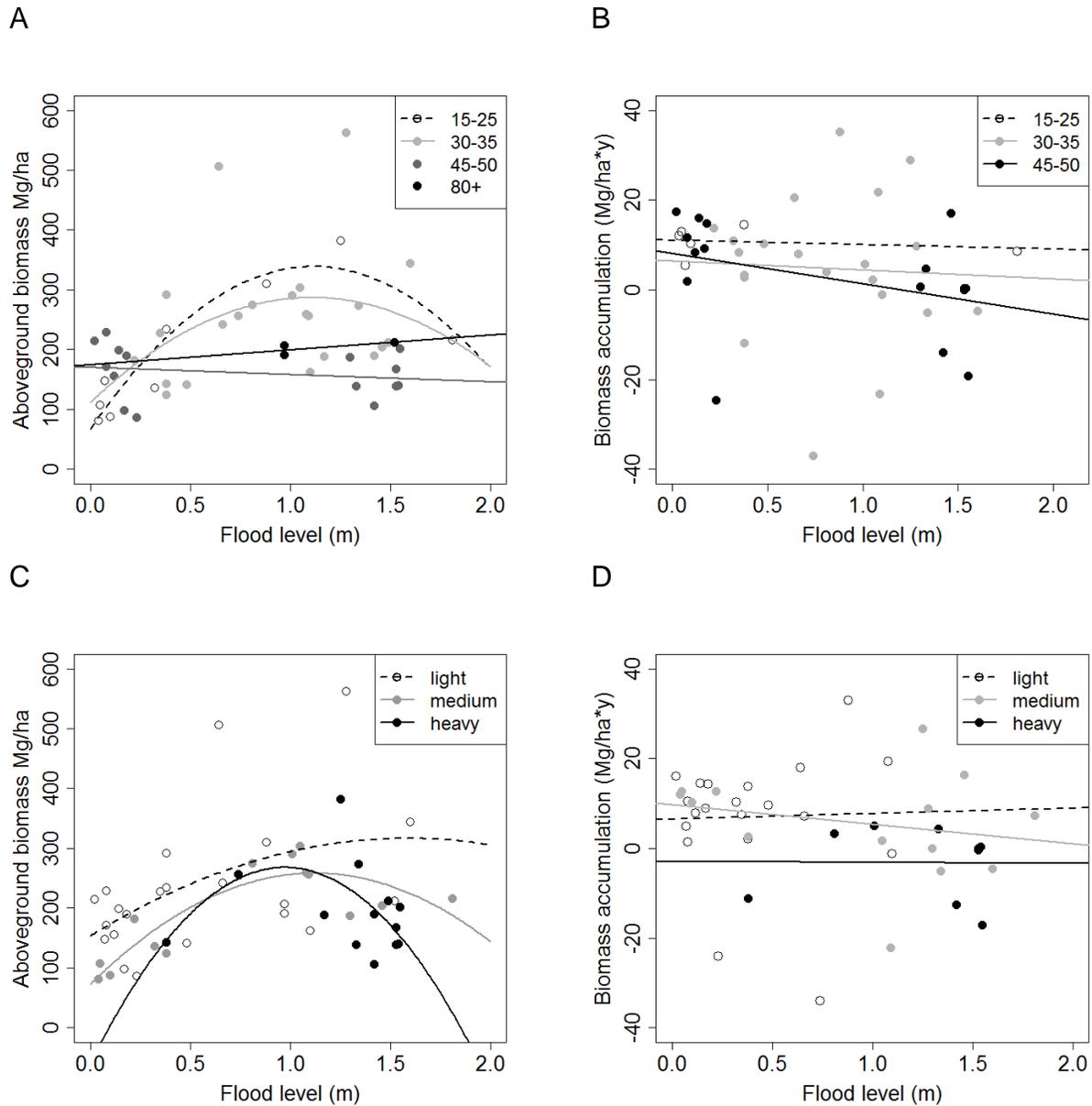


Figure 6-2. Differences in biomass and biomass accumulation across forest age. A) Aboveground biomass across forest age for three model estimates (Cannell, dry forest, and moist forest). B) Annual biomass accumulation across forest age. C) Aboveground biomass across livestock activity levels. D) Annual biomass accumulation across livestock activity levels. Significant differences between means (with SD) to the  $p < 0.05$  level from Tukey HSD tests are shown by letters above bars.

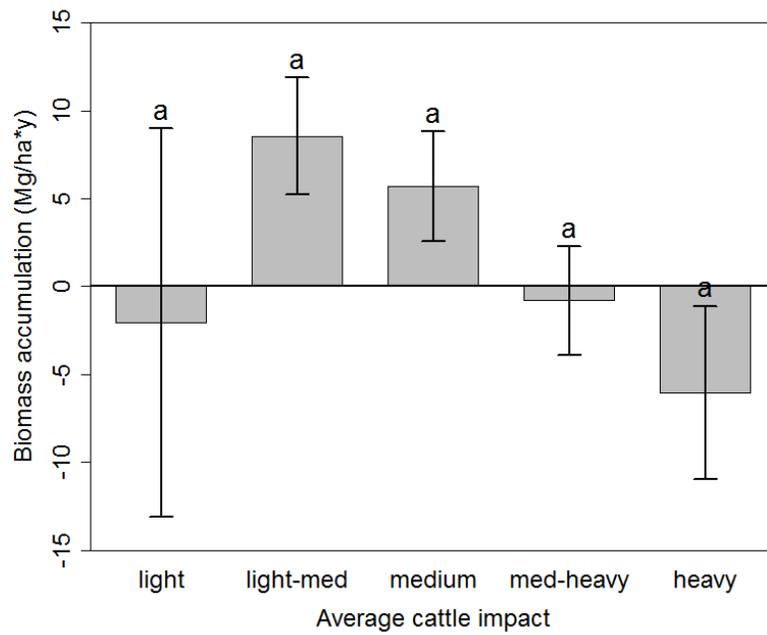


Figure 6-3. Annual biomass accumulation (means & SE) across average cattle impact levels. Lower case letters show significant differences between means within each model estimate (Tukey HSD tests,  $p < 0.05$ ).

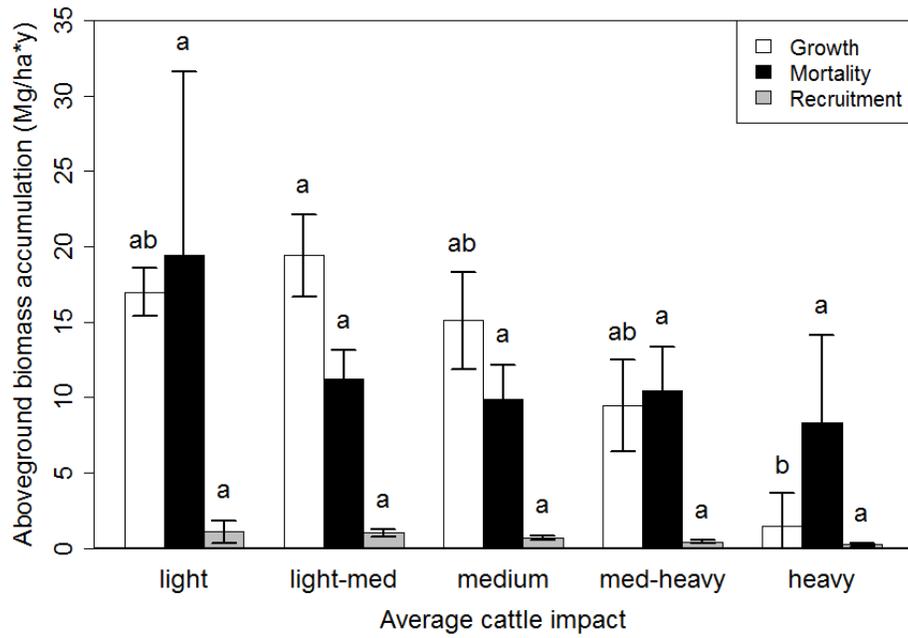


Figure 6-4. Annual biomass accumulation (means & SD) attributed to tree growth, mortality, and recruitment from 1999-2008. Lower case letters indicate differences between means according to Tukey HSD tests ( $p < 0.05$ ).

## CHAPTER 7 CONCLUSIONS

In this research I explored the effects of ecological drivers on regeneration and succession of secondary floodplain forests. My results broaden the understanding of seedling ecology in tropical floodplain forests and may be applied to conservation and management of floodplain ecosystems in Amazonia.

In Chapter 2, I aimed to emphasize the repeated cycles of land-use for agriculture and forest products in Amazonian floodplain forests via a literature search of historic accounts of the *várzea* economy and landscape from Pre-Colombian period through the present-day. Such a history may explain the lack of old-growth stands or no-impact zones in floodplain forests of the Santarém region with which to compare forests with livestock impacts and history of jute plantations. The repeated recovery of floodplain forests from multiple cycles of deforestation suggest remarkable resiliency against disturbance. Although all the forests that were inventoried for this research had been cut for agriculture or silviculture or had been disturbed by livestock, I identified 88 woody species in fewer than 5 ha of forest. Subsequent chapters helped to explain how floodplain tree species recover from such disturbances.

In Chapter 3, I reported germination rates of *várzea* seeds and found evidence for species-specific responses to saturation treatments. My results supported the broader conclusion that the *várzea* is ecologically diverse, with tree species that differ by their phenology and disperse seeds via multiple vectors. I highlighted two common *várzea* species with very different germination syndromes – *Crataeva benthamii*, which has fish-dispersed seeds that tolerate many months of submersion, and *Pseudobombax munguba*, which have wind-dispersed seeds with low tolerance of submersion.

In Chapter 4, I tested the effects of three stressors, flood duration, mechanical damage, and shade on seedling density and species richness, using a common garden experiment. Mechanical damage to stems of planted seedlings decreased survival by ~50% but did not interact with flood duration. Species varied widely in their ability to resprout after mechanical damage. Seedlings experienced two major declines in survival over the course of a year: first, among damaged seedlings, during the dry season and, second, at after flooding. This suggested that damaged seedlings may experience drought-stress in the dry period, a finding observed in other floodplains as well (Lopez and Kursar 2007). Light availability in the understory emerged as a key factor for seedling growth and survival during the first year of establishment.

In Chapter 5, I monitored the dynamics of succession in floodplain forests of different livestock activity levels and age. Flood level, ranging from 0 to 2 m depth, was a major driver of forest stand structure as well as species and stem recruitment rates. Impacts of livestock activity on stand structure and rates of change were undetectable, but increasing livestock density did decrease seedling density and number of species. Light availability and flood level interacted to affect seedling species density, such that seedling species density remained high across the flood gradient with high light availability. Overall, this study showed that for all the factors that can affect the structure of seedling communities and forests, flooding emerges as the most important for explaining temporal trends.

Using the same database from floodplain forests in the Santarém region, I calculated average aboveground woody biomass as 212 Mg ha<sup>-1</sup> with a mean rate of carbon sequestration by aboveground biomass of 2.5 Mg C ha<sup>-1</sup> y<sup>-1</sup> (Chapter 6). My

results suggest that despite land-use histories of deforestation for agriculture and livestock ranching, secondary forests sequester a substantial amount of carbon on an annual basis. Heavily impacted forest stands displayed net carbon loss, a result of slow growth rates of certain tree species.

### **Significance in Ecology**

My dissertation research applied key ecological concepts in plant community ecology to a critical ecosystem, tropical floodplain forests. A major gap in community ecology is how many factors work synergistically to affect tropical forest succession. My results showed how these interactive effects may be evident only in certain phases of tree life history. For example, while livestock activity and flood level interacted to limit seedling density, these effects did not scale up to trees.

Within the growing field of research on tropical seedling ecology, an increasing number of studies are recognizing the importance of seedling recovery from damage as a mechanism for persistence in the forest understory. Prior to this study, I knew of no published data on the ability to resprout among floodplain forest seedlings of the Amazon. I found that species vary broadly in their ability to survive and grow after mechanical damage. Surprisingly, experimental removal of ~50% of seedling biomass had no effect on species flood-tolerance. This finding should open the door to further physiological study as to how floodplain seedlings are able to tolerate such prolonged exposure to anoxia, even when plants have lost all foliar tissue.

Trade-off models are an important concept within plant strategy theory to explain species distributions (Gilbert et al. 2006). These models are founded on the principle that resources are limited, and thus there are trade-offs in the allocation of resources to growth, survival, and reproduction. I found little evidence for a flood-/shade-tolerance

trade-off to explain species survival patterns for Amazonian floodplain forest seedlings. Rather, a few species emerge as tolerant of many stressors, *i.e.*, flooding, shade, and mechanical damage. My findings suggest an escape vs. tolerance model for seedling establishment on the floodplain, whereby seedlings at low elevations are tolerant of prolonged submergence as well as other stresses (Parolin 2002). Such results show how dynamics of regeneration in tropical floodplains can differ from those of temperate floodplain forests (Battaglia and Sharitz 2006).

Perhaps the largest growing area within ecology today is the effect of human activities on climate change and ecosystem processes related to carbon budgets. I provided the first available data for carbon storage and sequestration in secondary Amazonian floodplain forests of the Dry Corridor region. I found that despite the multiple cycles of land-use history, low diversity, and livestock impacts, that forests average  $\sim 210 \text{ Mg ha}^{-1}$  with annual C sequestration rates of  $2.5 \text{ Mg C ha}^{-1} \text{ y}^{-1}$ . These values were comparable to other secondary forests and confirm the important role of successional forests for C sequestration.

In summary, understanding how plant communities are established and change through time and space continues to be a major focus of research in plant community ecology. This dissertation research contributes to the understanding of secondary forest dynamics in response to the interactive effects of stress and disturbance, lending insight as to how the stochastic effects of disturbance change seedling communities (Chase and Leibold 2003). In addition, I contributed to the understanding of carbon uptake by fast-growing floodplain forest species and the role of forested wetlands in the Amazon carbon budget. Ground-based data on forest biomass and tree species

composition contribute valuable information to the debate on the role of secondary forests and wetlands in carbon sequestration. From one of the few semi-permanent networks of floodplain forest inventory plots in the Amazon, the results on biomass accumulation, biodiversity, and regeneration fill a gap in our knowledge of tropical floodplain forest ecology in the Dry Corridor of the Amazon. These results also allow for a more accurate basin-wide understanding of ecological and diversity gradients from the estuary to the West Amazon.

### **Implications for Conservation and Management**

The *várzea* forests of the Amazon face diverse challenges and opportunities for conservation and management of floodplain resources. Each region is distinct in the resources harvested as well as the socio-political and cultural contexts that permit conservation planning and sustainable management to occur. For example, in the floodplains of the Amazon estuary, communities currently face challenges as to how to manage tidal floodplain forests for small-scale timber (Anderson et al. 1995). One opportunity for diminishing the demand on forests for timber is the harvesting of non-timber forest products such as latex, *açaí* fruits (*Euterpe oleracea*) and andiroba oil (*Carapa guianensis*; Fortini et al. 2006).

In the floodplains of the Lower Amazon in the region of Santarém, I have reviewed challenges to forest conservation such as the increasing intensity of cattle and water buffalo (Sheikh 2002) as well as small-scale deforestation for agriculture (WinklerPrins 1999). An opportunity for conserving forests and improving their management is the use of floodplain forests for local fisheries. Approximately 120 species of fish in the Amazon consume fruits from floodplain forest trees (Horn et al. in press), of which 150 woody species serve as food resources (Goulding et al. 1993). In the Santarém region

alone, 27 woody flowering species of 22 families were found in the guts of two characin species, *Colossoma macropomum* and *Piaractus brachypomus*, highly valued both commercially and for local consumption (Lucas 2008). The economic value of these fish that consume forest fruits during the flood season and rely on forests as nurseries is one of the reasons why floodplain forests in the Santarém region are still intact. As such, the sustainable management of the local fishing industry may provide an opportunity for conservation of floodplain forests in the region.

Many species investigated in this research were identified as important food sources for Amazon fishes. Information on the regeneration of these species – seed germination rates, conditions for seedling survival, recruitment of adult stems – are directly applicable to understanding the status of fish-fruit resources and designing plans for sustainable management. In addition, these data may be applied to tree planting projects in the region to recuperate fish abundance in some communities. One local initiative exists in the Santarém region for community-based tree planting project on floodplains degraded by livestock use (McGrath et al. 2005).

At a broader scale, this research provides an example of the synergistic effects of major threats in the Amazon today (Malhi et al. 2008), including the effects of flooding and drought stress on forest regeneration and the mechanisms by which cattle affect forest succession. In monitoring forest change across a period of exceptionally high floods (2006 and 2008), I found the local extirpation of two low-flood-tolerant timber species, *Guarea guidonia* and *Hura crepitans*. In comparing forest stand structure today to that described by elderly residents and naturalists (Chapter 2), I found that other valuable species such as *Carapa guianensis* and *Ceiba pentandra* are also

virtually lost for the region. Landholders that have taken initiatives to enrich floodplain forests with valued species report that large floods kill planted seedlings and saplings of *Carapa guianensis*. Increased extreme events such as drought and high floods are predicted by climate change scenarios for the Amazon Basin (Malhi and Wright 2004). As such, it will become exceedingly important to understand how these supra-annual events affect floodplain forest resources.

APPENDIX A  
LIST OF WOODY SPECIES IN SANTARÉM FLOODPLAIN FORESTS

Table A-1. Species list for woody species recorded in 2008 inventories, ordered by decreasing Importance Value (IV) among trees ( $\geq 10$  cm DBH)

Species	Family	IV
<i>Pseudobombax munguba</i>	Malvaceae (Bombacoideae)	23.07
<i>Ficus insipida</i>	Moraceae	21.38
<i>Laetia corymbulosa</i>	Salicaceae	20.46
<i>Triplaris surinamensis</i>	Polygonaceae	19.83
<i>Cynometra bauhiniifolia</i>	Fabaceae (Caesalpinioideae)	16.83
<i>Cordia tetrandra</i>	Boraginaceae	15.96
<i>Andira inermis</i>	Fabaceae (Faboideae)	15.12
<i>Calycophyllum spruceanum</i>	Rubiaceae	10.45
<i>Luehea cymulosa</i>	Malvaceae (Tilioideae)	9.51
<i>Sapium glandulosum</i>	Euphorbiaceae	8.85
<i>Crataeva benthamii</i>	Brassicaceae	8.75
<i>Ocotea</i> sp.	Lauraceae	7.00
<i>Spondias mombin</i>	Anacardiaceae	6.93
<i>Vitex cymosa</i>	Lamiaceae	6.42
<i>Albizia inundata</i>	Fabaceae (Mimosoideae)	6.32
<i>Neea</i> sp.	Nyctaginaceae	5.40
<i>Swartzia leptopetala</i>	Fabaceae (Faboideae)	4.77
<i>Toulicia guianensis</i>	Sapindaceae	4.39
unknown		4.04
Fabaceae 1	Fabaceae	3.99
<i>Coccoloba ovata</i>	Polygonaceae	3.92
<i>Pterocarpus amazonum</i>	Fabaceae (Faboideae)	3.78
<i>Eugenia</i> sp.	Myrtaceae	3.68
<i>Albizia niopoides</i>	Fabaceae (Mimosoideae)	3.53
<i>Inga cayennensis</i>	Fabaceae (Mimosoideae)	3.49
<i>Lonchocarpus</i> sp.	Fabaceae (Faboideae)	3.42
<i>Ficus</i> sp.	Moraceae	3.40
Myrtaceae 1	Myrtaceae	3.23
<i>Genipa americana</i>	Rubiaceae	3.19
<i>Piranhea trifoliata</i>	Euphorbiaceae	3.16
<i>Pouteria glomerata</i>	Sapotaceae	3.11
<i>Hura crepitans</i>	Euphorbiaceae	3.07
<i>Gustavia augusta</i>	Lecythidaceae	2.56
<i>Talisia cerasina</i>	Sapindaceae	2.40
<i>Garcinia brasiliensis</i>	Clusiaceae	2.29
<i>Lecythis pisonis</i>	Lecythidaceae	2.26
<i>Zygia cataraensis</i>	Fabaceae (Mimosoideae)	2.19

Table A-1. Continued.

Species	Family	IV
<i>Xylosma benthamii</i>	Fabaceae (Mimosoideae)	2.16
<i>Sorocea duckei</i>	Moraceae	1.99
<i>Crescentia amazonica</i>	Bignoniaceae	1.51
<i>Bothriospora corymbosa</i>	Rubiaceae	1.37
<i>Nectandra amazonum</i>	Lauraceae	1.33
<i>Cupania latifolia</i>	Sapindaceae	1.22
<i>Banara cf. nitida</i>	Flacourtiaceae	1.19
<i>Simaba orinocensis</i>	Simaroubaceae	1.18
<i>Zanthozylum compactum</i>	Rutaceae	1.15
<i>Casearea aculeata</i>	Salicaceae	1.14
<i>Trichilia singularis</i>	Meliaceae	1.13
<i>Guazuma ulmifolia</i>	Malvaceae (Byttnerioideae)	1.07
<i>Xylopiya calophylla</i>	Annonaceae	1.06
<i>Maytenus guianensis</i>	Celastraceae	0.95
<i>Crudia amazonica</i>	Fabaceae (Caesalpinioideae)	0.94
<i>Hevea brasiliensis</i>	Euphorbiaceae	0.91
<i>Myrcia cf. deflexa</i>	Myrtaceae	0.89
<i>Connarus incomptus</i>	Connaraceae	0.74
<i>Lecointea amazonica</i>	Fabaceae (Faboideae)	0.70
<i>Tabebuia barbata</i>	Bignoniaceae	0.60
<i>Solanum</i> sp.	Solanaceae	0.59
<i>Inga</i> sp. 1	Fabaceae (Mimosoideae)	0.54
Annonaceae 1	Annonaceae	0.38
<i>Inga stenoptera</i>	Fabaceae (Mimosoideae)	0.38
<i>Cassia grandis</i>	Fabaceae (Caesalpinioideae)	0.36
<i>Pouteria aff. sagotiana</i>	Sapotaceae	0.29
<i>Homalium racemosum</i>	Salicaceae	0.29
<i>Cecropia latiloba</i>	Urticaceae	0.28
<i>Mouriri guianensis</i>	Melastomataceae	0.28
<i>Inga</i> sp. 3	Fabaceae (Mimosoideae)	0.28
<i>Inga</i> sp. 2	Fabaceae (Mimosoideae)	0.27
<i>Faramea</i> sp.	Rubiaceae	0.27

APPENDIX B  
SOILS DATA FOR COMMON GARDEN PLOTS IN CHAPTER 4

The soil texture results agreed with other data collected in agricultural fields in the *várzea* in the same region: Soils were SILT LOAM soils, approximately 75% silt, with very little sand (0.4-13%), and clay (10-33%). Sand content was highest at the high elevation plots (12-13%) and dropped abruptly with decreasing elevation, while clay content increased gradually as elevation decreased (Figure A-1A,C). There seemed to be no trend in silt content across elevation (Figure A-1B). The forest “Mata Grande” had the highest clay content, confirming local residents’ observations. Soil pH ranged from 4.5 to 5.9, with the oldest and least disturbed forest “Mata Doroca” having the lowest pH values. Bulk density ranged from 0.9 to 1.3 g/cm<sup>3</sup>, normal for silt loam soils. Despite the fact that one forest, “Mata Grande” has cattle and water buffalo, the forest was also the lowest elevation, which may have compensated for bulk density. As plots were selected off of cattle trails, soil bulk density was not expected to be above 1.4 g/cm<sup>3</sup>. Soils were collected in the early rainy season January 23-27, 2008.

Table B-1. Soil texture and bulk density in the 21 common garden plots of seedlings.

Forest	Age	Plot	Flood (m)	BD 0-5 cm	BD 5-10 cm	pH	% Sand	% Silt	% Clay
Doroça	80	1	1.2	1.05	0.98	4.6	0.9%	88%	11%
Doroça	80	2	1.7	0.77	0.90	4.5	2.2%	83%	15%
Doroça	80	3	1.7	1.13	1.26	4.9	2.6%	82%	15%
Doroça	80	4	1.8	1.06	1.00	4.7	0.5%	84%	16%
Doroça	80	5	2.3	0.90	1.16	4.9	0.3%	77%	23%
Doroça	80	6	2.5	0.94	1.11	5.0	0.8%	78%	21%
Doroça	80	7	2.5	0.86	1.16	5.2	0.4%	79%	20%
Doroça Means				0.96	1.08	4.8	1.1%	82%	17%
Grande	35	1	1.8	1.01	1.33	5.7	2.2%	75%	23%
Grande	35	2	1.8	1.02	1.25	5.6	2.0%	78%	21%
Grande	35	3	2.1	0.96	1.12	4.7	0.6%	83%	16%
Grande	35	4	2.2	0.96	1.22	5.1	2.0%	66%	32%
Grande	35	5	2.3	1.14	1.27	5.7	2.1%	78%	20%
Grande	35	6	2.5	1.01	1.32	5.2	1.8%	76%	22%
Grande	35	7	2.8	0.88	1.22	5.0	3.3%	78%	19%
Mata Grande Means				1.00	1.25	5.3	2.0%	76%	22%
Santino	80	1	1.0	1.27	1.40	5.2	12.6%	72%	16%
Santino	80	2	1.2	1.13	1.20	5.0	5.2%	81%	13%
Santino	80	3	1.2	1.17	1.33	5.5	13.6%	74%	12%
Santino	80	4	1.5	1.00	1.40	5.0	3.3%	82%	14%
Santino	80	5	1.8	0.82	1.27	5.2	0.9%	79%	20%
Santino	80	6	1.3	1.21	1.35	5.9	2.3%	80%	17%
Santino	80	7	1.2	1.01	1.37	5.6	7.7%	83%	10%
Santino	80	8	1.6	0.77	1.06	5.5	1.4%	82%	17%
Santino Means				1.05	1.30	5.4	5.9%	79%	15%

Table B-2. Soil nutrients and organic matter.

Forest	Age	Plot	Flood (m)	OM	P (mg/g)	N (mg/g)	Ca	Ca+Mg	Al	Cu	Mn	Fe	Zn
Doroça	80	1	1.2	18.3	25.3	28.1	4.7	6.4	2.3	6.2	79.7	1146	10.2
Doroça	80	2	1.7		24.3	28.9	5.5	7.1	2.1				
Doroça	80	3	1.7	18.3	5.6	125.0	4.6	6.8	3.2	6.6	50.6	1033	6.3
Doroça	80	4	1.75	35.6	25.1	31.8	5.4	7.7	2.1	6.9	75.2	1055	10.5
Doroça	80	5	2.3		11.8	33.2	7.0	9.8	2.1				
Doroça	80	6	2.5	22.3	13.3	35.3	6.5	8.8	2.2	6.3	46.0	662	6.6
Doroça	80	7	2.5		23.7	39.1	5.6	7.5	2.3				
Doroça Means				23.6	18.4	45.9	5.6	7.7	2.3	6.5	62.9	974	8.4
Grande	35	1	1.8		18.0	101.9	4.2	5.6	1.1				
Grande	35	2	1.75	32.5	24.6	174.3	5.5	7.4	0.9	6.6	72.5	886	7.3
Grande	35	3	2.05		25.1	42.1	6.0	7.3	2.4				
Grande	35	4	2.15	22.3	6.6	66.6	8.6	11.3	1.8	9.5	63.9	1552	9.0
Grande	35	5	2.3		17.9	101.8	5.6	7.5	1.7				
Grande	35	6	2.5		6.8	84.9	6.6	9.2	1.9				
Grande	35	7	2.75	35.8	6.4	34.7	7.3	10.0	1.9	8.0	49.0	891	8.0
Mata Grande Means				30.2	15.0	86.6	6.3	8.3	1.7	8.0	61.8	1110	8.1
Santino	80	1	1.0		32.8	35.2	4.6	6.0	1.0				
Santino	80	2	1.2		25.5	35.5	5.0	6.5	1.4				
Santino	80	3	1.15	20.3	33.4	28.3	4.4	5.6	1.0	6.9	54.7	960	9.0
Santino	80	4	1.5		27.1	36.3	5.2	6.9	1.0				
Santino	80	5	1.75	16.5	15.5	40.4	7.5	10.0	1.5	9.3	89.9	984	13.9
Santino	80	6	1.3		27.1	39.7	5.6	7.4	1.2				
Santino	80	7	1.2	37.2	29.5	34.5	12.4	14.0	0.0	4.5	89.7	569	8.6
Santino	80	8	1.6		19.3	78.5	5.7	7.7	1.7				
Santino Means				24.6	25.3	41.9	6.5	8.3	1.1	6.9	78.1	838	10.5

Values for organic matter (OM) and nutrient levels were provided by the Soils Laboratory of EMBRAPA in Belém, Brazil.

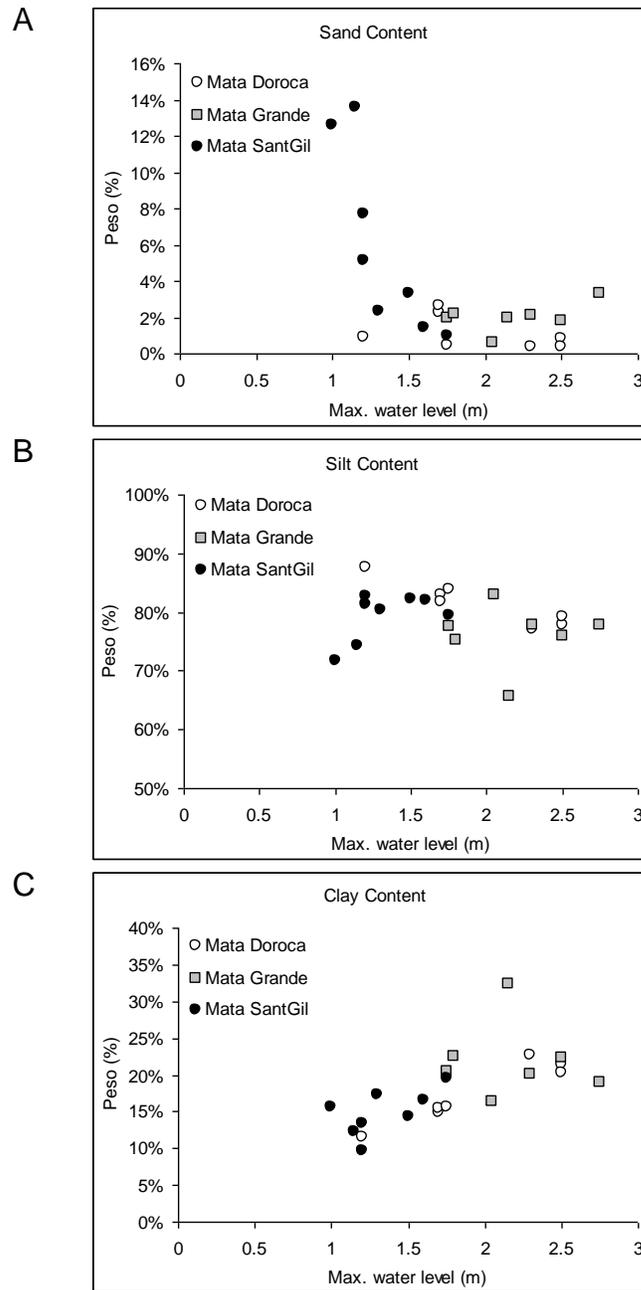


Figure B-1. The relationship between flood level and soil texture in three floodplain forests.

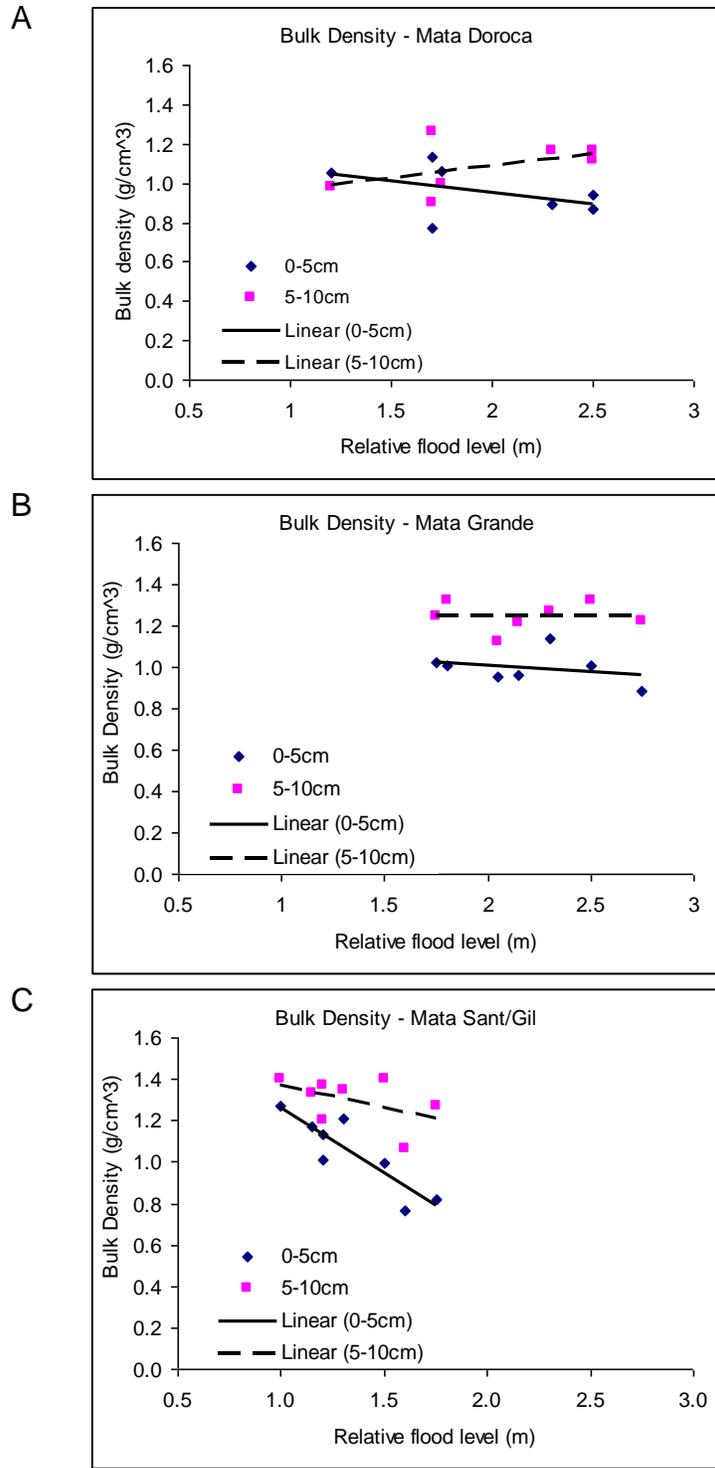


Figure B-2. Bulk density at 0-5 cm (diamonds) and 5-10 cm (squares) in three floodplain forests, Mata Doroca (A), Mata Grande (B), and Mata Sant/Gil (C).

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## BIOGRAPHICAL SKETCH

Christine Lucas was born in Salem, Massachusetts in 1978 in a typical New England snow storm. She grew up on the North Shore of Massachusetts in Beverly as the eldest of two sisters and moved inland to Framingham, MA, where she attended Framingham High School. Christine received her BA in Biology with a minor in Anthropology in 2001 from Vassar College in the Hudson Valley of NY. She then moved to New York City to work at the New York Botanical Garden, an experience which introduced her to colleagues in Brazil. In 2003 she was awarded the Clark Fellowship from Vassar College to conduct research on fruit eating fish and floodplain forest stand dynamics in collaboration with IPAM in Santarém, Brazil. Her interaction with floodplain residents and the *várzea* ecosystem provided the inspiration for her to return as a Ph.D. student. Her experience as a mentor for biology students in Brazil has inspired her to seek out teaching as a profession. Christine joined the Wildlife Ecology and Conservation Department at UF in 2004 as Emilio Bruna's Ph.D. student and a fellow of the Working Forests of the Tropics Program. Christine received her Ph.D. from the University of Florida in the summer of 2011. Christine currently lives in Montevideo, Uruguay and plans to seek new research projects concerning the ecology, conservation, and management of wetland forests world-wide, while continuing to build capacity among young ecologists in the U.S. and Latin America. In her spare time she enjoys doing botanical illustration and dancing.