THE NATURE OF SAVANNAS THAT REPLACE DRY FORESTS IN CHIQUITANIA, BOLIVIA

By

JOSEPH WILLIAM VELDMAN

A DISSERTATION PRESENTED TO THE GRADUATE SCHOOL
OF THE UNIVERSITY OF FLORIDA IN PARTIAL FULFILLMENT
OF THE REQUIREMENTS FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY

UNIVERSITY OF FLORIDA

2010

To Aaron, Ava, and Helen

ACKNOWLEDGMENTS

First and foremost I thank F.E."Jack" Putz for his tremendous investments in my development as a scientist. I will be forever grateful to Hope College Professors Greg Murray, Kathy-Winnett Murray, William Mungall, and Mark Northuis who encouraged me to attend graduate school. I also thank my committee members, Emilio Bruna, Michelle Mack, and George Tanner for their suggestions and guidance in both the developmental and final stages of my dissertation. Thanks also to Botany faculty Kaoru Kitajima, Stuart McDaniel, Chris Baraloto, and Jack Ewel for their support. Departmental staff Kathy Jones, Kim Williams, Denise Caswell, Karen Patterson, and Tangelyn Mitchell helped me navigate the University of Florida system and kept research funds flowing to me in Bolivia.

My parents Jim and Lorraine Veldman, my sister Katie, and dear friend Nathan Geisler gave me the love and support without which this research would mean little. Lin Cassidy and Camila Pizano are my Gainesville family and will forever be my neighbors even if living on different continents. I spent many weekends running at San Felasco with John Engels, Christine Archer, Alfredo Rios, Santiago Espinosa, Franklin Paniagua, Amy Duchelle, Gaby Stocks, Wendy-Lin Bartels, and Peter Derby. Since returning to Florida I have been blessed with new friends Jared Westbrook, Lucas Majure, Meribeth Latvis, Nick Miles and Alejandro Berrio, as well as friends from Bolivia now at the University of Florida: Marlene Soriano and Martijn Slot.

I have been privileged to share offices with a number of graduate students in the Departments of Botany and Biology. My first years at the University of Florida were spent at McCarty Hall in the office of Fire and Chemical Ecology with Morgan Varner and Matt Palumbo. On the 3rd floor of McCarty I also had the camaraderie of Geoff Blate, Bill Grauel, Claudia Romero, Skya Murphy, Ana Eleuterio, Paulo Brando, Camila Pizano, Julia Reiskind and

Ann Wagner. In Bartram Hall I am fortunate to work with Vincent Mejibe, Drew Silver, Yuan Zhou, Alexander Shenkin, Xavier Haro, and Mathew McConnachie.

During time I spent in Ann Arbor, University of Michigan Professor John Vandermeer generously gave me space in his lab; I sincerely appreciate that David Allen, Jahi Chappell, Heidi Liere, Zach Miller, Doug Jackson, Shalene Jha, Aley Joseph, and Senay Yitbarek shared their office, friendship, and ideas. I am also grateful to University of Michigan Professor Robyn Burnham for sharing her excitement for ecology and inviting me to the LOTS discussion group that includes David Marvin and Becca Sonday.

This research was possible because of the hospitality of the Bolivian people - I will forever feel that Bolivia is my second home. I owe a huge debt of gratitude to Bonifacio Mostacedo who encouraged me to pursue research in Bolivia. In Bolivia the people of the *Instituto Boliviano de Investigación Forestal* (IBIF) gave me friendship, guidance, and support: Bonifacio Mostacedo, Marielos Peña-Claros, Zulma Villegas, Marisol Toledo, Lourens Poorter, Geovana Carreño, Juan Carlos Licona, Alfredo Alarcon, Carlos Pinto, Emma Nuñez, Laly Dominguez, Bety Flores, Israel Ibañez, Miguel Ángel Chaves, Mayra Maldonado, Jose Luis Santivañez, Vincent Vroomans, Saskia Grootemaat, Ari Martinez, Skya Murphy, and Margo Stoddard. I additionally wish to acknowledge the friendship of Elibeth Paredo, Remedios Calle, Eva Maria Rivero, Gabriela Gutierrez, and Javier Chambi. I spent much of my time in Bolivia with Lars Markesteijn, fellow doctoral student and biologist, who shared his friendship and ideas about life and ecology.

Field work would not have been impossible without the help of field assistants including: Juan Alvarez, Juan Carlos Alvarez, Israel Melgar, the late Juan Pesoa, Juan Pasavare, and Jose Iraipi. In particular, I am honored to have worked with Don Juan Alvarez of Concepcion who

accompanied me tirelessly for months of field work. Throughout Chiquitania, ranchers and rural villagers gave me a place to camp, food to eat, permission to study their land, and directions. The Colombara family deserves special thanks for the use of Estancia Cacarachi and for providing horses to ride to field sites. Thanks to Don Juan of San Francisco, the residents of San Jose, Don Negro of Concepcion and many others. The portions of this research conducted in selectively logged forest were facilitated by the managers and employees of INPA Parket LTD; in particular I thank Paul Rozenboom, William Pariona, and Daniel Velasquez. Don Wilfredo and Don Raul kept my pick-up truck functioning between trips to the field.

I was fortunate to use the plant collection at the *Herbario del Oriente Boliviano (Museo de Historia Natural Noel Kempff Mercado)* and thank botanists Fabiana Mamani, Daniel Soto, Moises Mendoza, and Daniel Villarroel. Nelson Joaquin of the *Centro de Investigación Agricola Tropical* (CIAT-Santa Cruz) helped me learn about tropical forage grasses.

Financial support for this research came from the Garden Club of America Award in Tropical Botany, a National Science Foundation Doctoral Dissertation Improvement Grant, and a University of Florida Alumni Doctoral Fellowship.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

Abstract of Dissertation Presented to the Graduate School
of the University of Florida in Partial Fulfillment of the
Requirements for the Degree of Doctor of Philosophy

THE NATURE OF SAVANNAS THAT REPLACE DRY FORESTS IN
CHIQUITANIA, BOLIVIA

By

Joseph William Veldman

May 2010

Chair: Francis E. Putz
Major: Botany

Climate change, deforestation, agriculture, logging, drought, and fire are predicted to interact in ways that will render forests of the Amazon Basin susceptible to conversion to savanna, but it remains unclear what sort of savanna will replace forest and the identities of the grasses and tree species that will dominate. I studied savannas that replaced dry forests in the region of Chiquitania in eastern lowland Bolivia, which is on the southern rim of the Amazon Basin in a transition zone between forest and savanna biomes. Using satellite image analysis of a 22,500 km^2 area, I identified 1420 km^2 that was transformed from forest to savanna between 1986 and 2005. The savannas that replaced forest were dominated by one or two native or exotic grasses, and were floristically distinct from native savannas. The trees in recently derived savannas were primarily thin-barked forest species and not fire-tolerant species typical of fire-maintained savannas. Derived savannas had lower native grass and tree diversity than native savannas, occurred on more fertile soils and supported fuel loads that were twice as large. The majority of derived savannas were dominated by either exotic forage grasses in the genus *Urochloa* or by *Guadua paniculata*, a native bamboo. *Guadua* stands were characterized by frequent fires, charred dead trees, and large fuel loads (up to 16 Mg/ha); clearly fire played a role

in their creation. On a positive note, foliar analysis of *Guadua* indicates its potential use as cattle forage.

To better understand the role of land-use practices in promoting savanna expansion into forested areas, I studied grasses in a selectively logged forest. Forest invasion by alien grasses was promoted by selective logging and fire through opening the canopy and creating sites suitable for C_4 grasses, the most abundant of which was *U. maxima*; no native savanna species were found to colonize logged forest. To determine how grass propagules arrived in the forest, I collected seeds falling from logging trucks and demonstrated that grass seeds are carried far into the forest by motor vehicles. This research improves our understanding of how the floristic compositions of forest-replacing savannas are influenced by human-land use, soil fertility, and seed dispersal. Savanna expansion models could be improved by clarifying the sort of savanna that will replace forests and the ecosystem level consequences (e.g., fuel loads) of derived compared to native savannas.

CHAPTER 1
TROPICAL DRY FOREST REPLACEMENT BY SAVANNAS ON THE SOUTHERN EDGE OF THE AMAZON BASIN

Current trends in land-use, fire regimes, and climate change may promote savanna expansion in the Amazon Basin, but what type of savannas will replace forests and which grass species will be involved remains unclear. I used Landsat TM and CBERS-2 satellite images to quantify forest replacement by savanna between 1986 and 2005 in 22,500 km^2 of eastern lowland Bolivia. I then sampled savannas derived from forest and native savannas to compare their grass and tree species compositions, flammability, and soil properties. Savannas replaced 1420 km^2 of forest (8.4% of forest in 1986), a rate comparable to deforestation for agriculture (1200 km^2). Detrended and canonical correspondence analyses (DCA and CCA, respectively) showed native and derived savannas differed both floristically and in soil fertility; native savannas occurred on sandy acidic soils and derived savannas on relatively fertile soils. Whereas native savannas contained a diversity of grass species, the derived savannas were usually dominated by either *Guadua paniculata* (a native bamboo), *Urochloa brizantha* or *U. maxima* (exotic forage grasses), *Imperata brasiliensis* (a native invader of swidden plots), *Digitaria insularis* (a native ruderal), or the native fire-adapted herb *Hyptis suaveolens* (Lamiaceae). Just one of 17 derived savannas resembled native savannas in grass species composition. The trees in derived savannas were not thick-barked species characteristic of savannas environments (e.g., *Curatella americana*) but forest trees (e.g., *Anadenanthera colombrina*) and fire-tolerant palms (*Attalea* spp.). Grasses and herbs in derived savannas on fertile soils produced fuel loads twice as large compared to native savannas. The relationships between soil fertility, grass species composition, and fuel loads could be used to improve savanna expansion models, clarify the sorts of savannas that will expand, and emphasize the differences between native and derived savannas.

Introduction

Vast areas of Amazon forest are expected, or assumed, to be vulnerable to savanna expansion when subjected to the combined effects of climate change, intensification of land-use, and fire. Predictions of savanna expansion are based on climate models that project the Amazon Basin to become too dry to support forests (e.g., Cox et al. 2004), as well as on the effects of logging, road building, and pasture creation on forest flammability and susceptibility to grass invasions (Uhl & Buschbacher 1985; Cochrane et al. 1999; Laurance 2003). These factors do not act in isolation but interact as positive feedbacks between deforestation, drought, tree mortality, fire, and atmospheric carbon dioxide concentrations (Nepstad et al. 2004; Golding & Betts 2008). It is these drivers of deforestation in combination with the grass-fire cycle (D'Antonio & Vitousek 1992), and recognition of savanna as an alternative stable state (sensu Holling 1973; Suding et al. 2004) that have led to expectations of forest replacement by savannas. There remains a great deal of uncertainty about what is meant by savanna expansion, whether savanna will be the ultimate fate of tropical forests subjected to climate change and fire (Mahli et al. 2009) and if so, whether we should expect the expansion of species rich native savannas or dominance by a few invasive grass species.

Savanna definitions are complicated in the Neotropics in part because of the existence of both native savannas and extensive areas dominated by African forage grasses (Daubenmire 1972). Furthermore, the term “savanna” can encompass a huge range of vegetation types that may have little more in common than graminoid-dominated understories and sparse tree cover (e.g., Putz & Redford 2010). Native savannas, such as those of the cerrado biome of South America, are amongst the most species diverse and threatened ecosystems in the world (Oliviera et al. 2002). Climate shifts have influenced the distribution and extent of native savannas for millennia (Mayle et al. 2004). In contrast, modified fire regimes coupled with the introduction of

exotic forage grasses in the Neotropics resulted in the creation of vast areas of physiognomic or "derived" savannas over the last century in areas that were formerly forests (Parsons 1972). A strictly physiognomic definition of savanna ignores the identities of the graminoids and forbs involved, and whether they are native or exotic, naturally regenerated or planted. Nonetheless, there are reasons to consider grass-dominated systems collectively, particularly with respect to the increasing frequency of fires and the grass-fire cycle (Cochrane et al. 1999). I use "savanna" broadly on a physiognomic basis to describe areas with a graminoid or herb-dominated understory and <65% tree canopy cover in full recognition of the fact that areas fitting this definition can be floristically and functionally very different, even if grasses, fire, and sparse tree cover are common features; to make this distinction clear I refer to "forest derived" and "native" savannas.

Studies on the vulnerability of Amazon forests to environmental change have not adequately addressed what sort of savanna will replace forest. In describing the possible outcomes of forest degradation in the Amazon Basin, authors use terms such as savanna-like scrub (Nepstad et al. 1999) or savanna-like vegetation (Nepstad et al. 2008), old fields or scrub savanna (Cochrane & Schulze 1999), and savanna (Hutyra et al. 2005). Another ill-defined term, "savannization," has been used to describe both the spread of native savanna (Cavelier et al. 1998) as well as a range of processes that degrade forest (Borhidi, 1988; Nepstad et al. 1999). Complicating matters, studies that assume that the climate currently associated with savannas can predict future savanna distribution imply that the native savanna biome of South America will shift northward as the Amazon Basin dries (e.g., Hutyra et al. 2005; Mahli et al. 2009); despite this implication, to date there is little evidence that large scale native savanna expansion is occurring.

Determining what sorts of savannas are expanding and what species are involved is critical to understanding ecosystem level consequences of vegetation shifts. Differences between native and exotic grass species can result in substantial differences in their ability to co-exist with trees, invade forest, or drive savanna expansion (e.g., Lippincott 2000; Platt & Gottschalk 2001; Hoffmann et al. 2004). Tree species identity and natural history are important given that thick-barked savanna trees are more fire tolerant than thin-barked forest trees (Hoffmann et al. 2009), and that savanna expansion in areas that lack fire-adapted tree species (i.e., much of the Amazon Basin), are unlikely to maintain tree cover important to ecosystem services (i.e. precipitation; Hoffman et al. 2000). A goal of this study is to determine where savanna has already replaced forest in lowland Bolivia, to identify the grass and tree species involved, and determine the consequences for biodiversity and ecosystem flammability.

The seasonally dry forests of eastern lowland Bolivia represent an appropriate study system for advancing our understanding of the process of forest conversion to savanna. The region known as Chiquitania contains a mosaic of vegetation types dominated by seasonally dry tropical deciduous forest interspersed with native savannas that are western disjuncts of Brazilian Cerrados (Killeen et al. 1990). The forests of Chiquitania are transitional between the more humid Amazonian forest to the north and the drier scrub woodlands to the south (Killeen et al. 2005). On the periphery of the Amazon Basin these forests and are expected to be particularly vulnerable to replacement by savanna due to seasonal drought and high flammability (Hutyra et al. 2005), as well as documented sensitivity to climate change (Mayle et al. 2000). These forests are also subject to the anthropogenic drivers of deforestation and savanna expansion that operate throughout the Amazon. In particular, agricultural conversion, road building, and logging have all contributed to the fragmentation, degradation, and increased fire susceptibility of Chiquitano

dry forest (Steininger et al. 2001). Importantly, the diverse native grass flora of Chiquitania, plus naturalized African forage grasses, permits investigation of the savanna-forming potential of a variety of grass species. Variability in soil fertility makes the region suitable for studying the interaction between soils and savanna grass species composition. Soil fertility is thought to determine native savanna-forest distributions in South America (Hoffman et al. 2009); in Chiquitania, native savannas generally occur on shallow sandy soils or well drained oxisols, whereas forests occur on younger, relatively fertile soils developed from the granite rock of the Precambrium Shield that underlies the region (Killeen et al. 1990). Given the huge range in soil characteristics that occur across the Amazon Basin (Quesada 2009), a better understanding of associations between soil type and grass species assemblages will be important for predicting savanna expansion.

The objective of this study was to determine how much and what kind of savanna has already replaced forest on the southern rim of the Amazon Basin in eastern lowland Bolivia. I used satellite imagery to quantify the extent of forest replacement by savanna between 1986 and 2005. Based on this analysis, I identified and sampled native (old) savannas and newly derived savannas (i.e., areas that changed from forest to savanna between 1986 and 2005) to determine their grass and tree species compositions, to measure fine fuel loads, and to collect soil samples. I use these data to describe forest-replacing savannas, to determine the degree to which they floristically resemble native savannas, to relate soil chemical and physical properties to grass species assemblages, and to suggest ecosystem consequences of native as opposed to derived savanna expansion.

Materials and Methods

Study Area

This research covers 22,500 km^2 of northern Chiquitania bounded by the limits of CBERS-2 satellite scenes and the San Ramon-Trinidad Highway on the southwest (Figure 1-1). Primary towns within the region are Concepción (16° 8' S 62° 1' W; 500 m altitude; population 6,900) and San Ignacio (16° 22' S 60° 57' W; 400 m altitude; population 24,000). The region has a mean annual temperature of 24°C with extreme temperatures of 4 – 37°C; mean annual precipitation is 1160 mm but ranges 799 – 1859 mm (data from *Administración de Aeropuertos y Servicios Auxiliares a la Navegación Aérea* collected in Concepción, 1943-2005). Seven months each year receive < 100 mm precipitation (April through October) and during four months (June through September), potential evapotranspiration exceeds rainfall (M. Peña-Claros, *unpublished data*).

Satellite Image Analysis

To quantify the extent of forest replacement by savanna during 1986-2005, I digitally processed satellite images to create a change trajectory map that identified areas transformed from forest to savanna. Due to the seasonality of the region and the predominance of deciduous trees, I chose images from the early to mid-dry season, a time of year before complete leaf senescence but with many cloud-free days. For the 1986 classification, I used adjacent 1986 Landsat Thematic Mapper (TM) scenes for Path 230 Row 071 and Path 229 Row 071 from 2 July 1986 and 27 July 1986, respectively, available from the Global Land Cover Facility, University of Maryland, USA. The Path 230 Row 071 scene was already orthogeorectified and I obtained an orthogeorectified scene for TM Path 229 Row 071 from 16 July 1988. Due to technical failures in Landsat 7 and limited availability of current Landsat TM scenes, I chose two CBERS-2 (China-Brazil Earth Resource Satellite) scenes from INPE (National Institute of Space

Research), Brazil for Path 172 Row 118 from 24 July 2005 and Path 171 Row 118 from 27 July 2005. The data were projected to WGS84, UTM Zone 20 S, resampled to 30 m x 30 m spatial resolution, and geo-referenced via image-to-image rectification using the orthorectified TM images with a root mean square (RMS) error of < 0.5 pixels.

During June-July 2007 I visited 190 sites distributed across the study region to create a database of Geographic Positioning System (GPS) coordinates and corresponding vegetation descriptions needed to interpret current and historic satellite images. At each 30 x 30 m site (i.e., the size of one Landsat pixel), I measured tree canopy cover at three random points with a spherical densitometer at (Lemmon 1956) and visually estimated the percent ground cover of graminoids (of any height). I also took digital photographs of each site and made notes on current and past land-use practices. Based on this information, I defined each site as forest, savanna, large-scale agriculture, or wetland for classification of the current image (Table 1-1). A point was only assigned to a different class for 1986 than in 2005 when there was convincing evidence that class shift had occurred. For example, a present day pasture that contained standing dead forest trees 50-80 cm in DBH and that looked like forest in the image would be classified as forest for interpretation of the 1986 image.

I used a random selection of half of the training samples to create spectral signatures based on histogram-equalized CBERS-2 Bands 2, 3, 4 and histogram-equalized TM Bands 2,3,4, 5 and then assigned pixels to the four classes using the maximum likelihood model in Erdas Imagine 9.0. (Leica Geosystems, Norcross, Georgia USA). Improved pastures and savannas were the only classes that were not consistently separable based on spectral signatures alone. Large-scale agriculture, including improved pastures and industrial monocrops, were easily distinguished from savannas because ranchers usually clear forests in a manner that

creates regularly shaped borders (Steininger et al. 2001; Martinez M. et al. 2003). I manually edited the classified images to correct areas of large-scale agriculture that would have been classified as savanna based on spectral signature alone. Once each of the images was classified, I used the remaining half of the training samples to perform accuracy assessments. The accuracy results I report are the mean values for the two TM 1986 scenes and the two CBERS 2005 scenes weighted by their proportional contribution to the 1986-2005 change trajectory analysis. I used image subtraction to detect changes in pixel classifications between 1986 and 2005 to show the areas where savanna replaced forest. Prior to overlaying classified images to produce the change trajectory map I created a mosaic of the two adjacent scenes for each year. I used the error matrix produced by the accuracy assessment to correct the total area estimates for each cover class and each trajectory class (van Deusen 1996); both raw (map values) and corrected (unbiased) values for cover classifications are presented.

Savanna Floristic, Fuels, and Soil Analyses

During the mid to late rainy season of 2008 (February and May), I conducted detailed field sampling of areas determined by satellite image analysis to have shifted from forest to savanna between 1986 and 2005. I used a stratified random sample of pixels from across the study region to identify savanna patches > 9 ha that included 20 derived savannas and 12 old (native) savannas (i.e., areas classified as savanna in both 1986 and 2005). I excluded some savannas (~10% of all derived savannas) in roadless portions of the study region. In each of the selected sites, I established five 20-m variable width transects at random locations. Along each transect, I measured ground cover density and vegetation height up to 2 m at 41 points spaced at 0.5 m intervals of the following classes: 1) grass cover by species; 2) other herbaceous plants; 3) woody shrubs; 4) leaf litter; and, 5) bare soil. At the ends and midpoint of each transect, I clipped all standing biomass < 25 mm diameter from 0.5 m x 0.5 m plots in the following classes:

1) graminoids (i.e., Poaceae, Cyperaceae, Juncaceae); 2) other herbs; and, 3) shrubs. I also collected litter from these three plots (0.75 m^2/transect) and sorted the material collected as graminoid litter or litter from all other sources. Grass species present in the these plots but not at the 41 ground cover density points were assigned a cover value of 1%. To obtain more accurate estimates of standing biomass of the native bamboo *Guadua paniculata*, three 1 m^2 clip plots were measured. After weighing biomass in the field, subsamples were dried at 65°C for 48 hr to correct for moisture. At the ends and midpoint of each transect, I estimated tree canopy cover with a spherical densiometer (Lemmon 1956) held at 1.5 m. I identified to species and measured the DBH and height of all trees >5 cm DBH that fell within 4 m of the transect (i.e., 20 m x 8 m). As an indication of the intensity of past fires, I measured the maximum char height on the trunk of each tree (Fry 2008). Although, some grasses (*Guadua paniculata*, *Hyparrenhia rufa*, and *Urochloa maxima*) can exceed 2 m in height, I included grass cover >2 m tall in estimates of ground cover but not for tree canopy cover.

At the midpoints of each of the five transects per site, I measured soil depth to 2 m with a bucket auger, collected soil samples for bulk density determination (0-4 cm) in 6.8 cm diameter tins, and extracted soil cores (0-20 cm, 6.8 cm diameter) for laboratory analysis. When soil depth was < 20 cm, I collected an equivalent volume of soil from multiple shallower cores. I mixed the five soil cores from each site before sending samples for analysis by the soils laboratory of the Center for Tropical Agriculture Research (CIAT- Santa Cruz). Soils were analyzed for: pH (1:5 in water); electrical conductivity (1:5 in water); soluble cations - Ca, Mg, Na, K (atomic absorption (AA) following soil digestion in ammonium acetate; for Ca and Mg soil was additionally treated with lanthanum chloride); interchangeable acidity (titration with potassium hydroxide of soil diluted in potassium chloride); Al (floride titration); available P (modified

Olsen method for pH<5.4, modified Bray and Kurtz method for pH >5.4); total N (Micro-Khejldaljh method), organic material (Walkley-Blach method); and, texture (sedimentation analysis). Cation exchange capacity was calculated as the sum of interchangeable acidy plus the concentration of soluble cations (Ca, Mg, Na, K). Bulk density samples were oven dried at 105°C for 24 hr prior to weighing.

I identified grass species using the nomenclature of Renvoize (1998), with assistance of keys provided therein and by Killeen (1990). Nomenclature departs from Renvoize (1998) for the former *Brachiaria brizantha*, *B. decumbens*, and *Panicum maxima* that molecular data place within *Urochloa* (Aliscioni et al. 2003). Tree nomenclature follows Jardim et al. (2003) and Killeen et al. (1993). Identifications were confirmed at the Noel Kempff Mercado Museum of Natural History Herbarium in Santa Cruz, Bolivia (SCZ) where voucher specimens were deposited. Note that after first mention, species are referred to by their generic name (except where ambiguous).

I used detrended correspondence analysis (DCA) to ordinate savannas based on their grass and tree species compositions. I performed two ordinations, one using percent grass cover by species and a second using tree basal area by species. Only species present in at least two sites were included in the ordinations; the grass and tree DCAs included 52 and 64 species, respectively. I performed both ordinations in R 2.9.0 (the R Foundation for Statistical Computing) using the *decorana* command from the *vegan* 1.15-2 package. Three of the derived savannas sampled did not fit within my definition of savanna in terms of tree canopy cover and herbaceous ground cover. After excluding these wooded areas that were misclassified as derived savanna in the change trajectory map, I analyzed data from n = 12 native and n = 17 derived savannas. To compare how grass and tree species belonging to particular vegetation associations

(forests or savannas) or functional groups (native savanna grasses or exotic forage grasses) were distributed in derived versus native savannas, I classified grasses and trees *a priori* based on species descriptions by Killeen (1990) and Jardim et al. (2003), respectively.

I compared native and derived savanna diversity on the basis of numbers of species of native grasses, savanna trees, and forest trees; the proportions of all trees that were savanna species, forest species, or palms were also compared. To control for the effect of area sampled, I counted the species present on a per transect basis. As such, values for each savanna are the average from five 20-m transects. The number of native grasses includes all species recorded in cover counts or present in three 0.5 m x 0.5 m sub-plots per transect. The number of tree species (>5 cm DBH) were those present in each transect (160 m^2 sampled per transect). To compare numbers of species in native and derived savannas I used Student's t-tests and Mann-Whitney U-tests. I used canonical correspondence analysis (CCA) to relate grass species composition to soil variables measured in native and derived savannas. CCA was performed in R 2.9.0 using the *cca* command from the *vegan* 1.15-2 package. I tested for differences in soil characteristics between native and derived savannas using t-tests. I compared native and derived savanna fuel loads and individual biomass components (i.e., graminoid litter, stand herbs, etc.) using Mann-Whitney U tests.

Results

Satellite Image Change Analysis

The 1986 Landsat TM and 2005 CBERS-2 classifications had overall accuracies of 90% and 89%, respectively, with overall Kappa values of 0.84 and 0.84 (Table 1-2). The 1986 and 2005 classifications differed in accuracy for forests and savannas such that there was high confidence in pixels classified as forest in 1986 and high confidence in pixels classified as savanna in 2005 (Table 1-2). In the 1986 classification, user's accuracy (or consumer's risk, the

probability that a classified pixel is indeed that cover class; van Deusen 1996) for forest (100%) was greater than for savannas (76%), whereas in the 2005 classification user's accuracy for forest (84%) was less than savanna (91%). These values signify high confidence that areas classified as derived savanna in the change trajectory map are areas of former forest. The trade-off for confidence in derived savanna detection is that the analysis provides a conservative estimate of savanna formation and overestimates succession from savanna to forest. After correcting for this trade-off, I estimate that between 1986 and 2005, total forest cover declined from 83% of the study area to 68%, savanna increased from 14% to 22%, and large-scale agriculture increased from 2% to 9% (Figure 1-3). Of the 17,700 km^2 classified as forest in 1986 in the change trajectory analysis, 4.5% (800 km^2) changed to savanna by 2005 and 5.4% (959 km^2) was converted to large-scale agriculture (Table 1-3); both of these estimates are conservative and error-corrected values are 7.6% (1420 km^2) and 6.4% (1200 km^2), respectively. Some 2000 km^2 was classified as savanna in both 1986 and 2005 and was defined as native (old) savanna for the floristic studies that follow.

Savanna Floristics

Field sampling and subsequent DCA performed on grass species data showed two kinds of native savannas: typical *cerrado* and areas dominated by *Guadua*. Native savannas were clustered together on DCA axis-1 (Fig 4a); 10 of 12 native savannas were floristically distinct from the derived savannas, a position in ordination space that reflects the DCA scores of native *cerrado* grasses compared to the scores of other species (Figure 1-4b,c). The two native savannas that were not closely grouped with the *cerrados* contained the native bamboo *Guadua paniculata*, either as the dominant grass species or in lower abundance along with *cerrado* grasses. Derived savannas were considerably more dispersed in ordination space than native savannas (Figure 1-4a). The positions of most derived savannas corresponded with the species

scores of the following dominant grasses: *Guadua*, *U. brizantha* and *U. maxima*, *Imperata brasiliensis*, and *Digitaria insularis* (Figure 1-4c). With the exception of a single derived savanna that had a grass flora floristically similar to the *cerrados*, the only derived savannas that clustered near native savannas were *Guadua*-dominated.

The tree DCA revealed a distinct cluster of native savannas but little grouping of derived sites (Figure 1-5a). The site scores for native savannas corresponded to the species scores of *Curatella americana* (Dilleniaceae), *Qualea grandiflora* (Vochysiaceae), *Caryocar brasilensis* (Caryocaraceae), *Diptychandra aurantiaca* (Caesalpinoideae), and other trees considered to be characteristic of savanna by Jardim et al. (2003; Figure 1-5b,c). In contrast, the derived savannas typically contained a few remnant forest tree species such as *Anadenathera columbrina* (Mimisoideae; a dominant forest species), palms in the genus *Attalea* (*A. phalerata A. speciosa*, Arecaceae), or woodland-forest species (e.g., *Astronium urundeuva,* Anacardiaceae) that occur across a range of habitat types. Whereas the grass ordination revealed two types of native savannas (*cerrados* and those with *Guadua*), the analysis based on tree species composition showed all native savannas as part of one distinct cluster. None of the derived savannas clustered amongst the native savannas, but four sites had DCA-1 scores similar to native savanna. These sites clearly differed from native savannas along DCA-2 based on the presence of *Anadenathera*, *Astronium*, *Attalea speciosa*, and *Magonia pubescens* (Sapindaceae).

Native savannas had more native grass species and a greater number of savanna tree species than derived savannas, whereas derived savanna contained more forest tree species (Figure 1-6). The average numbers of native grass species per transect were 5.7 ± 0.6 and 1.7 ± 0.3 for native and derived savannas, respectively (mean±1SE; Figure 1-6a). Median savanna tree species richness values per transect (160 m^2) were 2.5 (range 1.2 – 5.8) and 0.4 (range 0 – 7.2)

for native and derived savannas, respectively (Figure 1-6b). Mean forest tree species richness values per 160 m^2 were 0.6 ± 0.1 and 1.3 ± 0.3 for native and derived savannas, respectively (mean±1SE; Figure 1-6c). The relative proportions of savanna trees, forest trees, and palms differed between native and derived savannas with native savannas composed primarily of savanna tree species and derived savannas containing higher proportions of forest trees. In native savannas, 83% and 14% of trees were savanna and forest species, respectively, compared to derived savannas where 22% and 72% of trees were savanna and forest species, respectively (Figure 1-7). Relative abundance of palms did not differ between savanna types, but maximum abundance of palms was greater in derived savanna. In addition to these comparisons, grass and tree species listed in order of their respective DCA-1 scores (Figure A-1; Figure B-1) shows the limited number of species shared by derived and native savannas.

There were exceptions to the trend of high native grass diversity in native savannas and low savanna tree diversity in derived savannas. One exception was a single derived savanna located in the transition zone between forest and native savanna. This savanna had the highest mean tree species richness of any site sampled (7.2 savanna and 4.4 forest tree species/transect) and was the only area identified as recently derived savanna in the satellite analysis that was similar to diverse native savanna in grass and tree species composition; it is possible that this site was misclassified as having shifted from forest to savanna. The exception to the relatively high grass species richness in native savannas was a site where *Guadua* appeared to exclude most other grasses and that contained few trees (only 1.4 savanna and 0.6 forest tree species per transect).

The majority of the native savannas sampled (11 of 12) and one of the newly derived savannas (1 of 17) contained a diversity of grass species typical of *cerrado* vegetation (Killeen et

al. 1990; Killeen & Hinz 1992a). The most abundant species were the native grasses *Elionurus muticus*, *Trachypogon spicatus*, *Thrasya petrosa, Paspalum stellatum,* and the naturalized African forage grass *Hyparrhenia rufa.* In lower abundances but frequently present in *cerrado* were the native grasses *Andropogon selloanus*, *Axonopus barbigerus*, *A. marginatus*, *P. erianthum*, and *Schizachyrium sanguineum*. Of the 77 grass species encountered in this study 36 occurred exclusively in *cerrados*.

The most common forest-replacing savannas (7 of 17 derived savannas) were dominated by *Guadua*. On the basis of their nearly arboreal habit, bamboos are commonly lumped by ecologists with woody plants or are considered a vegetation class of their own. In this study I included bamboo-dominated vegetation within the broad definition of savanna. *Guadua*, the most common bamboo of this region, produces large quantities of fine fuel and resprouts readily following fires (Veldman 2008). *Guadua* stands, which dominate ten of thousands of hectares in the region (Killeen 1990), can be characterized by frequent fires and severely charred or dead trees (Veldman 2008). Although *Guadua* can grow up to 7 m tall, most stands form grass canopies of only 2-5 m. Given its interactions with fire in Chiquitania, it seems appropriate to include *Guadua* within my conceptual frame-work of grass-fire feedbacks influencing forest-to-savanna conversion.

Four exotic forage grasses of African origin were among the most common species encountered in this study. *Urochloa*-dominated savannas (*U. brizantha*, *U. decumbens*, and/or *U. maxima* occurring alone or in mixed swards) accounted for six of 17 derived savannas. Another African pasture grass, *Hyparrhenia,* is widely naturalized in *cerrados*, but rarely occurred in derived savannas. Two of the derived savannas located on abandoned swidden plots contained monodominant stands of *Imperata brasiliensis*. *Imperata* is a rhizomatous native grass that was

a frequent component but never abundant in native savannas. A third area of long-fallowed swidden agriculture was dominated by the native annual herb *Hyptis suaveolens* (Lamiaceae). *Hyptis* formed a canopy of 1.5 to 2.5 m tall and appeared to exclude most other plants including grasses; the only trees interspersed with *Hyptis* were palms with charred trunks indicative of intense fires. *Digitaria insularis*, a native ruderal, was abundant on a single site where it grew on the ash of burnt slash along the border of a *Urochloa* pasture; *Digitaria* was also present in the fallowed swidden plots dominated by *Imperata*.

Fuel Loads and Fire History

Compared to native savannas, derived savannas had higher biomass values for standing graminoids, graminoid litter, and other litter, but the two savanna types did not differ in standing herb or shrub biomass (Figure 1-8). Total fuel loads (biomass <25 mm diameter) in derived savannas (median 8.0 Mg/ha; range 3.5-20) were twice that of native savannas (median 3.6 Mg/ha; range 2.7-9.2; Figure 1-9). Median fuel loads of standing graminoids, standing herbs, and graminoid litter (woody shrubs and other litter excluded) were 6.2 Mg/ha (range 0.8 – 20) and 2.4 Mg/ha (range 0.7 – 7.5) in native and derived savannas, respectively (Figure 1-8). Maximum char heights in native savannas (2.0 ±1.4 m) exceeded those measured in derived savannas (0.8 ± 0.9 m; mean ± 1SD, t-test, $p = 0.009$, $n = 12, 17$, respectively). All native savannas and 16 of 17 derived savannas contained charred trees. Both native and derived savannas contained similar densities of standing dead trees ~26 trees/ha.

Soil Fertility and Grass Species Composition

Concentrations of plant essential nutrients (N, K, Ca, and Mg), cation exchange capacities, electrical conductivities, organic matter, pH, and silt were greater in derived savannas than native savanna (Table 1-4). Native savanna soils were more often sandy, with high Al, acidity, and bulk density (Table 1-4). Savanna types did not differ in clay content, Na concentration, or soil

depth. CCA of savanna grasses and soils showed very similar clustering of sites and species compared to DCA of grass species only (Figures 1-9, Figure 1-4 respectively). CCA-1 appears to represent a soil fertility gradient with most native savannas (*cerrados*) occurring on infertile soils and derived savannas occurring on fertile soils (Figure 1-9).

Discussion

Over a twenty year period (1986-2005) in eastern lowland Bolivia, savannas replaced forests at approximately the same rate as deforestation for large-scale agriculture. These new savannas were dominated by a native bamboo, a few exotic forage grasses, or native invaders of fallowed swidden plots. In rare cases, savanna expansion resulted in high native grass and tree diversity, but these high diversity transitions zones along native savanna-forest margins accounted for a small fraction of total forest to savanna conversion. The large difference in species richness and floristic composition between native and newly derived savannas underscores the contrasting biodiversity implications of native savanna expansion compared to forest-replacement by derived savannas.

Of the species that dominated forest-replacing savannas, *Guadua*, *Imperata*, *Urochloa* spp., and *Hyptis* appear to represent alternative-stable states maintained by positive feedbacks with fire, or in the case of *Hyptis*, a combination of fire and allelopathy. Many bamboo species interacted with fire (Keeley & Bond 1999) and bamboo stands are thought to be an alternative stable state to broadleaf forest in both temperate (e.g., *Arundinaria gigantea*; Gagnon & Platt 2008) and Neotropical (e.g., *Guadua sarcocarpa* and *G. weberii*; Griscom & Ashton 2003, 2006) regions. Pasture grasses in the genus *Urochloa*, introduced from Africa as cattle forage, are widespread across the Neotropics (Parsons 1972). In the study region, *U. brizantha* and *U. maxima* are the most common planted pasture species, are roadside weeds, and invade disturbed forest in areas that receive motor-vehicle traffic (Veldman & Putz 2010). Both *U. maxima* and *U.*

brizantha are bunch grasses whereas culms of *U. decumbens* spread laterally and root at the nodes. All three species form dense canopies, with *U. maxima* (2-3 m tall) typically exceeding the heights of *U. brizantha* and *U. decumbens* (1-1.5 m tall). Because these forage grasses are both intentionally planted and accidentally introduced (Veldman et al. 2009), it is difficult to ascertain the genesis of all *Urochloa* stands in this study. *Urochloa*-dominated areas included pasture margins, where annual fires probably contribute to pasture expansion, as well as roadsides where fires and grazing are common but grasses may have been planted or simply colonized. *Imperata*, a native rhizomatous grass, is described by Killeen (1990) as "a serious pest in banana and coffee plantations" and Renvoize (1998) mentions *Imperata* stands as one type of anthropogenic savanna in lowland Bolivia. In northern Bolivia, *Imperata* abundance in small scale agriculture plots was reported to increase with repeated slash-and-burn cycles (Sools 2007), and in Peru *Imperata* invasion of swidden plots followed by repeated fires was considered critical step in the conversion of forest to savanna (Scott 1977). An ecologically similar congener of Asian origin, *I. cylindrica,* has changed fire-regimes, replaced native vegetation from southeast Asia to the southeastern United States (e.g., Lippincott 2000), and is considered one of the most invasive plants in the world (MacDonald 2004). *Hyptis,* an herb native to the Neotropics, is invasive in India were it colonizes shifting agriculture sites and was observed to enhance dry-season fires (Murthy et al. 2007). Additionally, *Hyptis* is reputedly allelopathic and limits the germination and growth of both grasses and trees (Totey et al. 1994; Mokat et al. 2005).

Soil fertility helps to explain differences between native and derived savanna grass species composition (Table 1-4; Figure 1-9)**.** Consistent with previous studies in the region (Killeen et al. 1990; Killeen & Hinz 1992a), I found native savannas to occurr on nutrient-poor acidic soils. In

contrast, derived savannas occurred on relatively fertile soils normally associated with forests – not surprising for sites that were forests within the last two decades. The absence of native savanna grasses in most derived savannas may be due to dispersal limitation, a competitive disadvantage on fertile soils, or both. Native savanna grasses adapted to infertile soils are probably unable to take advantage of nutrients available in more fertile sites, whereas grasses with high potential growth rates (e.g., *Guadua* and *Urochloa* spp.) are physiologically ill-equipped for infertile soils, but exploit disturbed forest soils that tend to be richer in nutrients (Grime et al. 1997). An apparent consequence of productive grasses and herbs growing on fertile soils, derived savannas had fuel loads that were twice as large compared to native savannas.

Imposed over the region's vegetation and underlying soil characteristics are human-land uses. As such, we should expect the determinants of derived savanna grass species compositions to be more complicated than simply soil fertility and fire history – factors that define native savanna-forest boundaries (Hoffmann et al. 2009). When people clear forests for agriculture they prefer the most fertile soils. When people establish pastures they intentionally introduce exotic forage species. In some cases savanna formation may be driven by complex socio-political factors: in one derived savanna *U. brizantha* and *U. maxima* were clearly planted, but never grazed, presumably as a way to lay claim to the land or otherwise show that it was being put to productive use – a case of savanna formation resulting from issues related to land-tenure.

The use of climate data from South American's native savannas to predict savanna expansion into the Amazon Basin (e.g., Mahli et al. 2009) may be inappropriate because derived savanna species are not functional equivalents of the species found in old-growth native savannas (i.e., derived savanna grasses produce greater fuel loads). Additionally, underlying environmental gradients (i.e., soil fertility) and human-activities favor a few grass species over

cerrado grasses. Native savannas may expand in areas with low soil fertility, but when savannas expand onto fertile forest soils we should expect them to be composed of a few grasses and herbs species that produce large fuel loads. Differences in fuel loads are relevant given the differences in fire-tolerance between tree species characteristic of forest compared to savanna (Hoffmann 2009); in lowland Bolivia and throughout much of the Amazon Basin, forest trees are susceptible to even low-intensity fires (Pinard & Huffman 1997). Given that most of the trees I found in derived savannas were forest species unlikely to survive repeated grass-fueled fires, maintenance of tree cover may depend on whether savanna tree species are able to colonize.

Forest replacement by species-poor savanna is just one sort of vegetation shift in lowland Bolivia. Although this study focused on places transformed from forest to savanna, selective logging, fires, and swidden agriculture can result in a variety of derived vegetation states (Putz & Redford 2010). One such outcome is liana dominance, a state transition that may be favored by the increased competitiveness of lianas under increasing atmospheric concentrations of CO_2 (Foster et al. 2008) or in response to forest fires (Pinard et al. 1999). Although my data support other reports that swidden fallows are invaded by fire-promoting grasses and herbs (Scott 1977; Killeen, 1990; Renvoize 1998; Sools 2007), savanna is not the only fate of abandoned agricultural land. Indeed, the remote sensing analysis showed 10% of the area classified as large-scale agriculture in 1986 had regenerated to forest by 2005.

This study was conducted in a region that contains native savannas, but in forests that are far from native savannas, the likelihood of native savanna expansion seems less likely, at least over decadal time scales. Although it is clear that repeated fires can push forests into a severely degraded state (e.g., Barlow & Peres 2008), the presence of one or more forest-invading and fire-promoting grasses is likely a trigger that promotes forest-to-savanna conversion. Data collected

in forests that are currently far from propagule sources of invasive grass species may be quite different than those subjected to the synergistic effect of disturbance plus invasion by savanna-forming species. Clearly more needs to be known about the biology of the grasses, herbs, and trees that dominate recently derived savannas as compared to those characteristic of native savanna. Species differences in fine fuel production, heights, soil nutrient requirements, seed production, capacity for vegetative expansion, and drought resistance could result very different vegetation-climate-fire interactions in the Amazon Basin.

Conclusion

The derived savannas that replaced tropical forest in this study had low grass and tree species diversity, were floristically distinct from native savannas, were usually dominated by one or two species of grasses, and contained remnant forest tree species. The distinction between diverse native savannas and low-diversity derived savannas is important given the threatened status of the native savannas of South America and predictions that Amazonian forests are increasingly susceptible to savanna expansion. Soil fertility should be considered when predicting which grass species are likely to replace forests; fertile soils are more likely to be colonized by a few highly productive native or exotic species rather than native savanna grasses. Species identities are important because grass species with high growth rates are capable of producing large fuel loads on fertile soils. As research on large-scale tropical forest-savanna dynamics progresses, we ought to be explicit about what sort of savanna is involved.

Table 1-1. Tree canopy cover and graminoid cover of training samples (used for the satellite image classification) and native and derived savannas included in the savanna floristic study. Values are mean percent±1SD.

		n	Tree Canopy Cover (%)	Graminoid Cover (%)
Training Sample Classes				
	Forests	81	89 ± 10	6 ± 12
	Savannas	63	18 ± 18	79 ± 16
	Large-Scale Agriculture	34	4 ± 6	85 ± 18
	Wetlands/Water	12	-	-
Floristic Study Sites				
	Native Savannas	12	22 ± 14	51 ± 16
	Derived Savannas	17	30 ± 19	50 ± 23

Table 1-2. Accuracy assessment of classified images used in the 1986 to 2005 change trajectory analysis.

	TM 1986		CBERS 2005	
Class	Producer's Accuracy (%)	User's Accuracy (%)	Producer's Accuracy (%)	User's Accuracy (%)
Forest	87	100	95	84
Savanna	96	76	78	91
Large-Scale Agriculture	83	100	92	97
Water	100	86	83	100
Overall Accuracy	90		89	
Overall Kappa Statistic	0.84		0.84	

Table 1-3. Area of change trajectory classes from 1986 and 2005. Raw totals are the sum of all pixels as indicated by the change trajectory analysis that was used to identify native and derived savannas for field sampling. Error-corrected totals were adjusted based on the results of the accuracy assessment to more accurately reflect true transition class values.

			Map Totals		Error-Corrected Estimates	
Trajectory (1986-2005)	Trajectory Class Synonyms	Color Figure 1-3	km^2	% of Study Area	km^2	% of Study Area
Forest – forest	old growth forest	gray	15963	71.1	14182	64.9
Forest – savanna	derived savanna	yellow	800	3.6	1418	6.5
Forest – large-scale agriculture	agricultural conversion	white	959	4.3	1196	5.5
Savanna – forest	forest succession	gray	1713	7.6	1115	5.1
Savanna – savanna	native (old) savannas	brown	1986	8.9	2579	11.8
Savanna – large-scale agriculture	agricultural conversion	white	481	2.1	440	2.0
Large-scale agriculture – forest	forest succession	gray	42	0.2	62	0.3
Large-scale agriculture – savanna	persistent agriculture	white	50	0.2	148	0.7
Large-scale agriculture – large-scale agriculture	persistent agriculture	white	176	0.8	366	1.7
Water (in any year)		black	268	1.2	340	1.6

Table 1-4. Soil variables measured in native (n = 12) and derived (n = 17) savannas listed in increasing order of CCA-1 axis scores relating savanna grass species and soil variables. Significant differences noted for $p<0.05$ (t-tests).

Soil Variable	Native Savannas (mean ± 1SD)			Derived Savannas (mean ± 1SD)			*p*	CCA-1
Bulk Density (g/cm^2)	1.25	±	0.11	1.03	±	0.10	***	-0.84
Acidity (cmol/Kg)	0.9	±	0.7	0.1	±	0.1	**	-0.69
Al (cmol/Kg)	0.5	±	0.7	0.0	±	0.0	*	-0.61
Sand (%)	63	±	10	51	±	17	*	-0.40
Clay (%)	17	±	8	17	±	4	ns	0.00
Na (cmol/Kg)	0.10	±	0.02	0.12	±	0.05	ns	0.12
Depth (m)	1.3	±	0.7	1.5	±	0.6	ns	0.26
P (mg/kg)	1	±	0	5	±	6	*	0.28
K (cmol/Kg)	0.16	±	0.07	0.30	±	0.15	**	0.34
Silt (%)	21	±	11	31	±	16	*	0.39
pH	5.2	±	0.5	6.4	±	0.6	***	0.44
Electrical Conductivity (µS/cm)	19	±	9	75	±	52	***	0.48
Cation Exchange Capacity (cmol/Kg)	2.5	±	0.7	6.6	±	3.4	***	0.51
Ca (cmol/Kg)	0.9	±	0.4	4.5	±	2.6	***	0.56
Mg (cmol/Kg)	0.5	±	0.3	1.5	±	0.8	***	0.61
N (%)	0.09	±	0.04	0.17	±	0.05	***	0.64
Organic Matter (%)	1.0	±	0.6	2.3	±	0.4	***	0.81

Figure 1-1. Study location in eastern lowland Bolivia. The shaded area corresponds to the intersection of the Landsat TM (1986) and CBERS-2 (2005) satellite images analyzed to detect forest replacement by savanna.

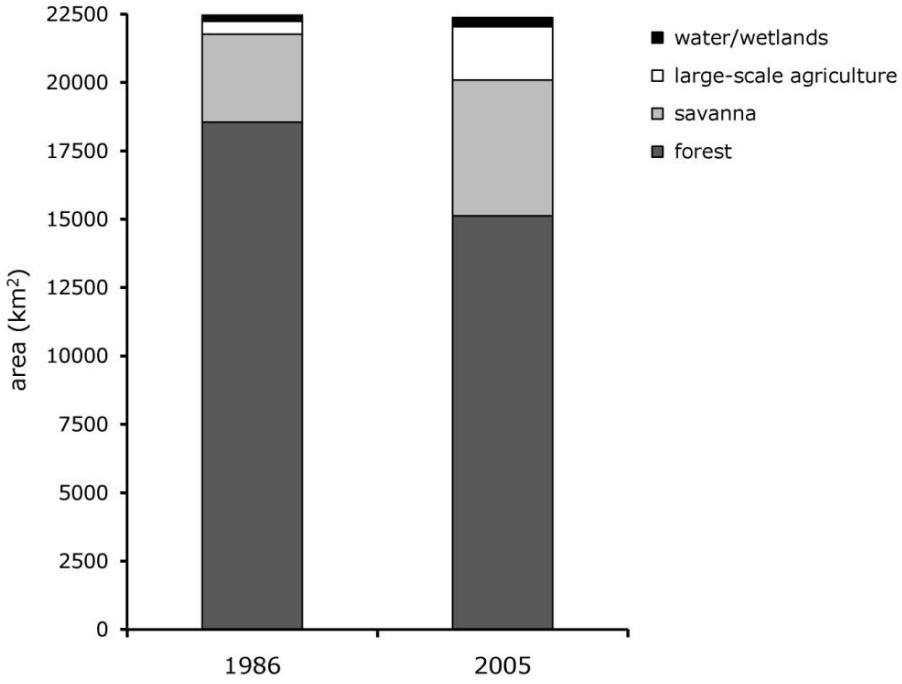

Figure 1-2. Land-cover class distributions based on error-corrected area totals for the 1986 (Landsat TM) and 2005 (CBERS-2) classifications.

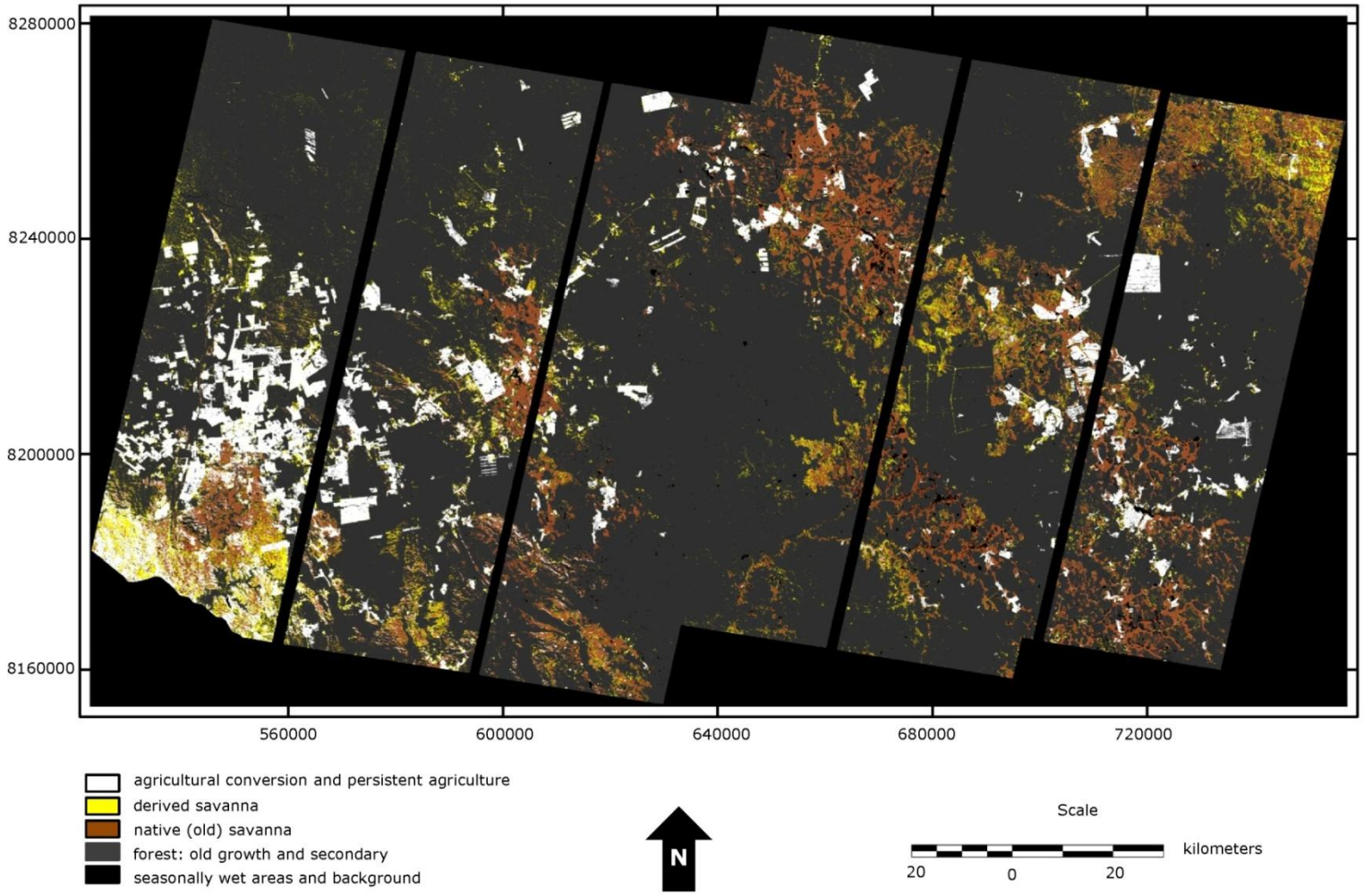

Figure 1-3. Modified change trajectory map created from classified 1986 (Landsat TM) and 2005 (CBERS-2) images used to identify forest-replacing (derived) savannas and native (old) savannas. Trajectory classes other than forest-savanna and savanna-savanna have been grouped in the color coding for visual simplification; see Table 1-3 for clarification of color groupings. Axes are labeled with UTM coordinates for WGS 84 Zone 20 south. The four unclassified strips that transect the map correspond to pixels of low CBERS-2 image quality that were excluded from the analysis.

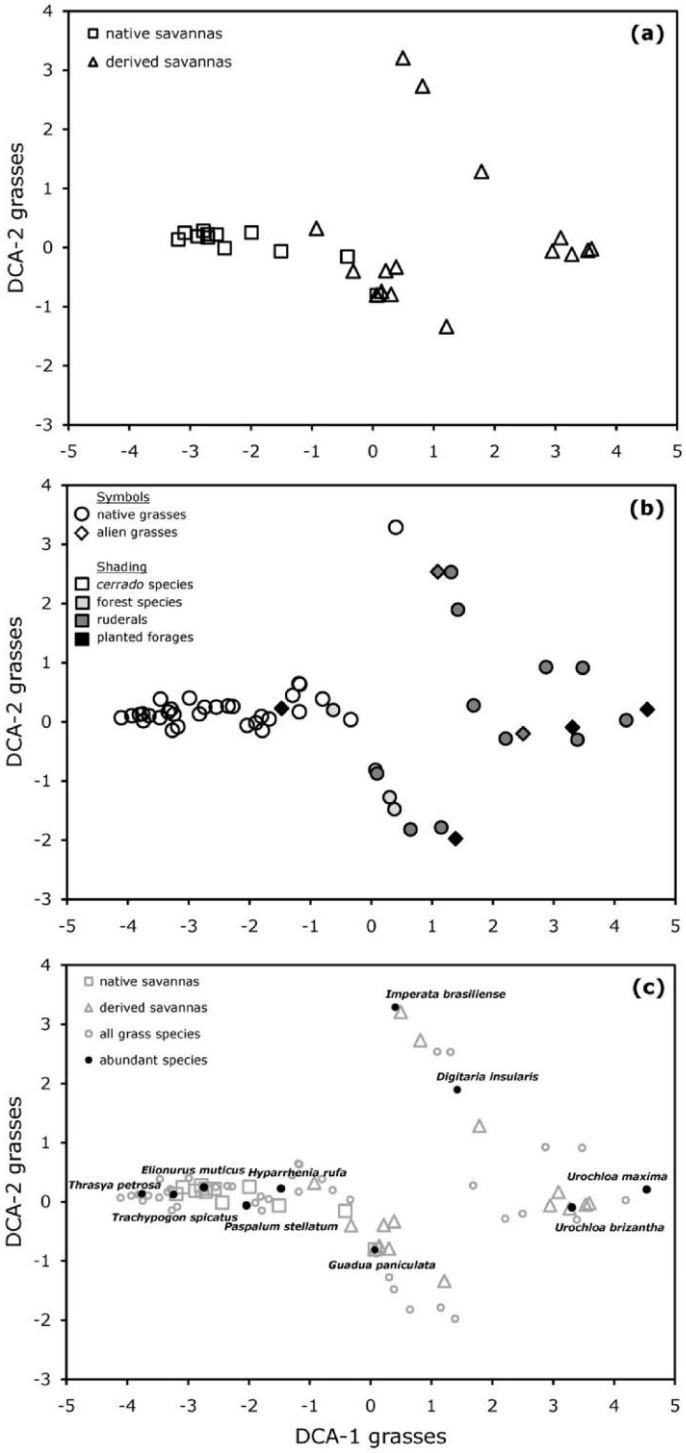

Figure 1-4. Detrended correspondence analysis of grass cover by native and exotic species in native and derived savannas. Ordination plots display the scores for sites and species along the first two DCA axes. (a) Ordination of 52 grass species present in at least two sites. (b) Ordination of sites; n = 12 native savannas, and n = 17 derived savannas. (c) Composite ordination of sites and species with the ten most abundant grasses species noted.

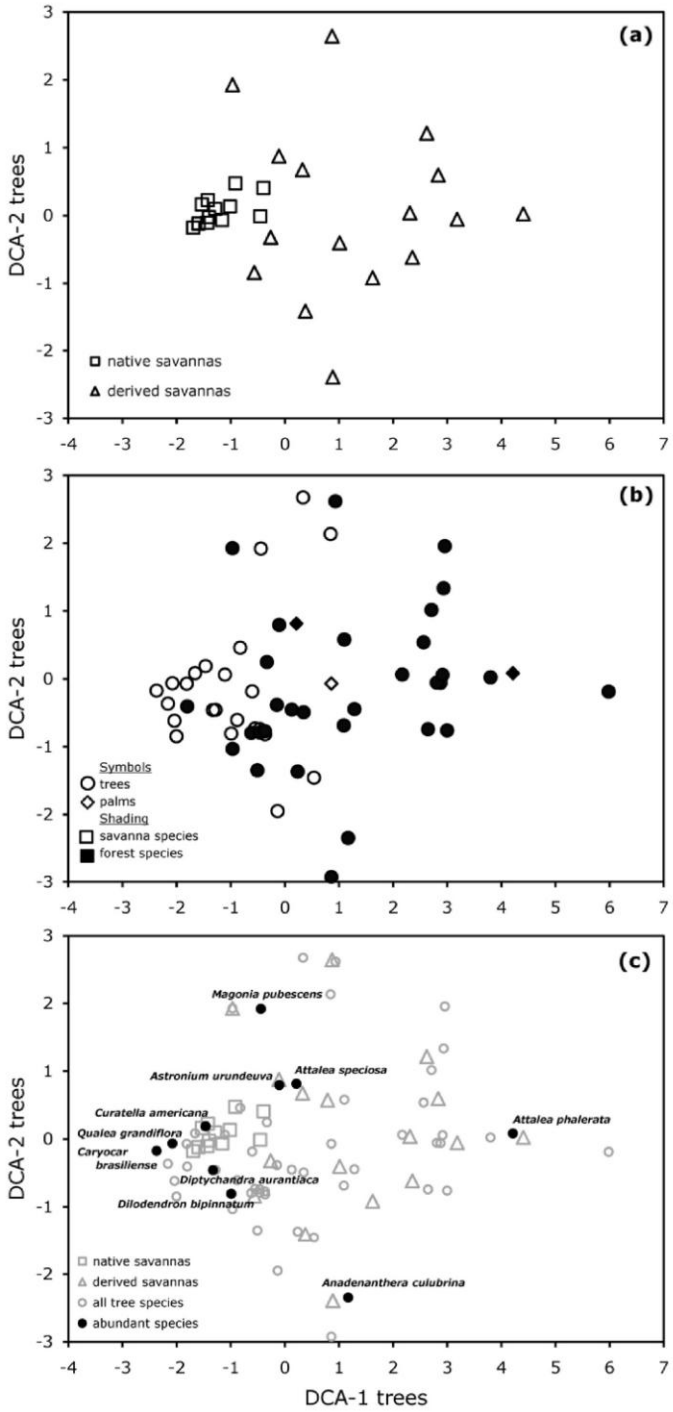

Figure 1-5. Detrended correspondence analysis of tree species by basal area in native and derived savannas. Ordination plots display the DCA scores for sites and species along the first two DCA axes. (a) Ordination of sites; n = 12 native savannas, and n = 17 derived savannas. (b) Ordination of 64 tree species present in at least two sites; shading of species characteristic of savanna or forest is based on Jardim et al. (2003). (c) Composite ordination of species and sites with the ten most abundant tree species noted.

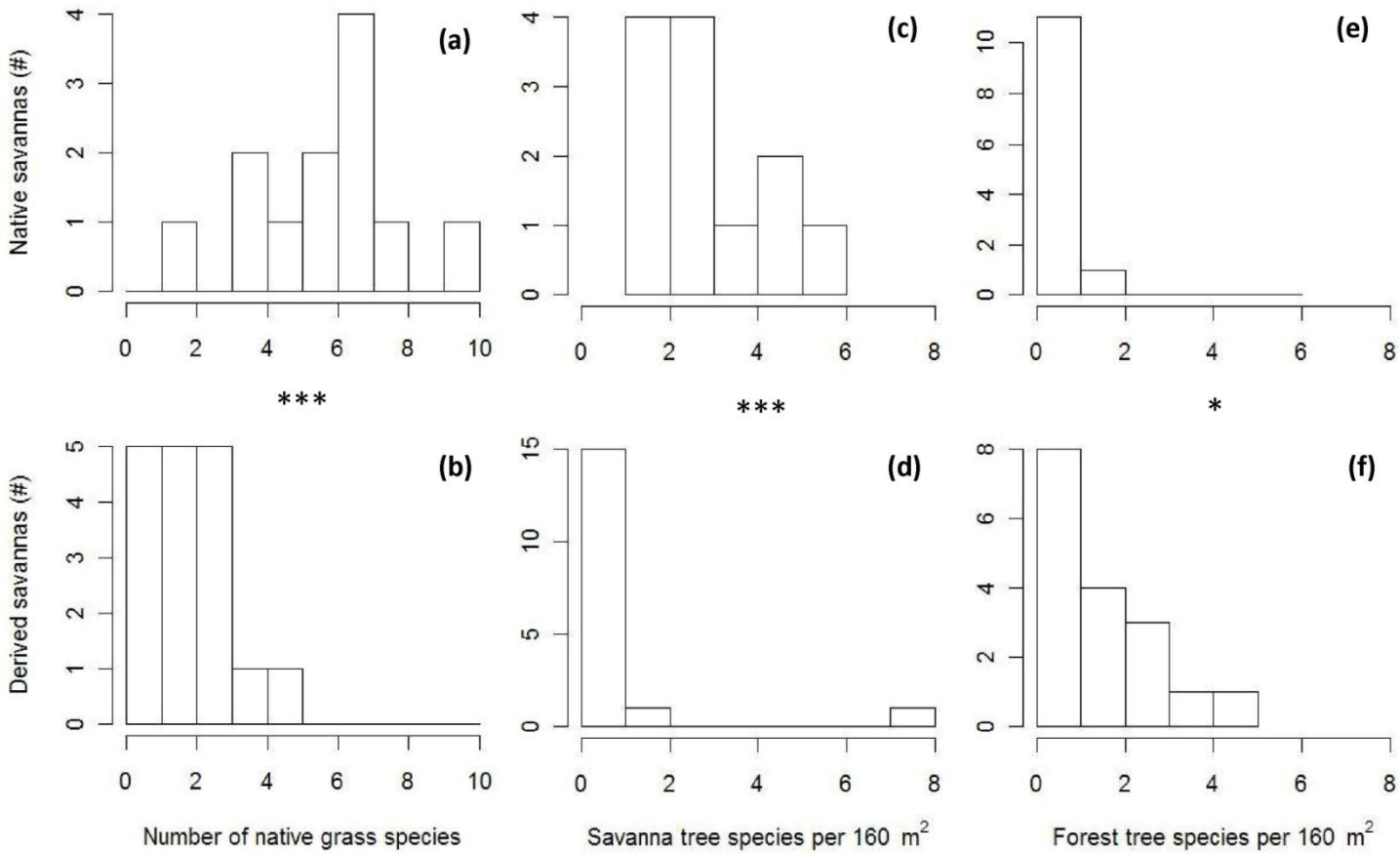

Figure 1-6. Frequency distributions of numbers of native grass and tree species in native (n = 12) and derived (n = 17) savannas. (a-b) mean number of native grass species present per transect; native and derived savannas differ at $p < 0.001$ (t-test). (c-d) mean number of savanna tree species present per transect; native and derived savannas differ at $p < 0.001$ (Mann-Whitney U-test). (e-f) mean number of forest tree species present per transect; native and derived savannas differ at $p < 0.05$ (t-test). Trees >5 cm DBH were counted in 20 m x 8 m transects and are classified as savanna or forest species; palms were excluded from the analysis.

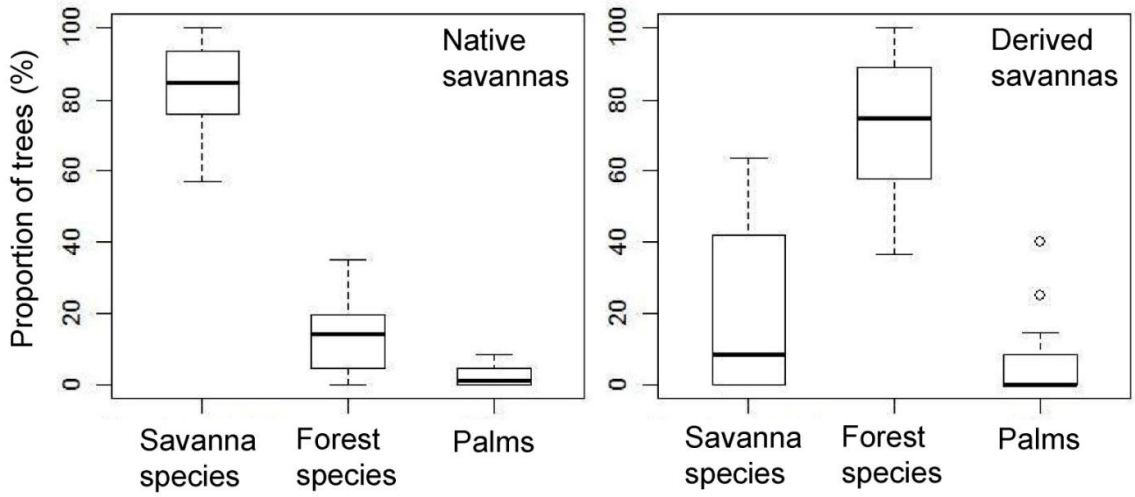

Figure 1-7. Proportion of savanna tree species, forests tree species, and palms in native (n = 12) and derived (n = 17) savannas. Native and derived savannas differed in proportions (% of total stems >5 cm DBH) of savanna and forest species (t-tests, p<0.001).

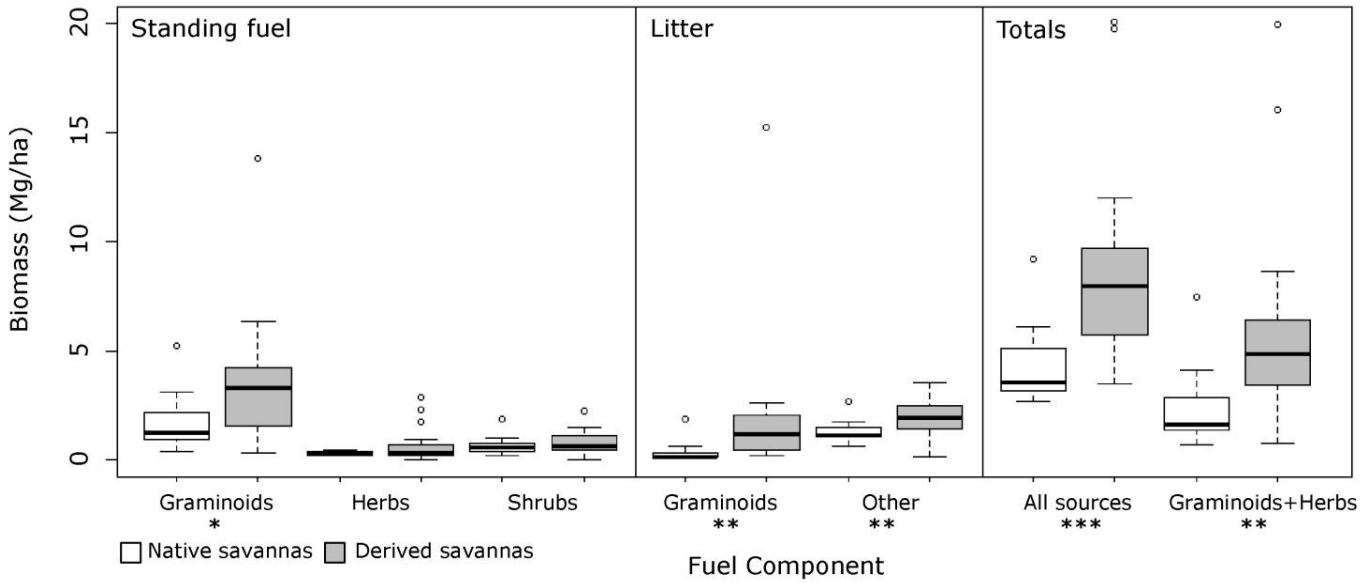

Figure 1-8. Fuel loads produced by graminoids (Poaceae and Cyperaceae), herbs, and shrubs in native and derived savannas. Fuel loads are dry weights of biomass <25 mm diameter. Graminoid + Herbs includes standing graminoid fuel, standing herb fuel, and graminoid litter. Asterisks denote differences between native (n = 12) and derived (n = 17) savannas at p <0.05 (Mann-Whitney U tests).

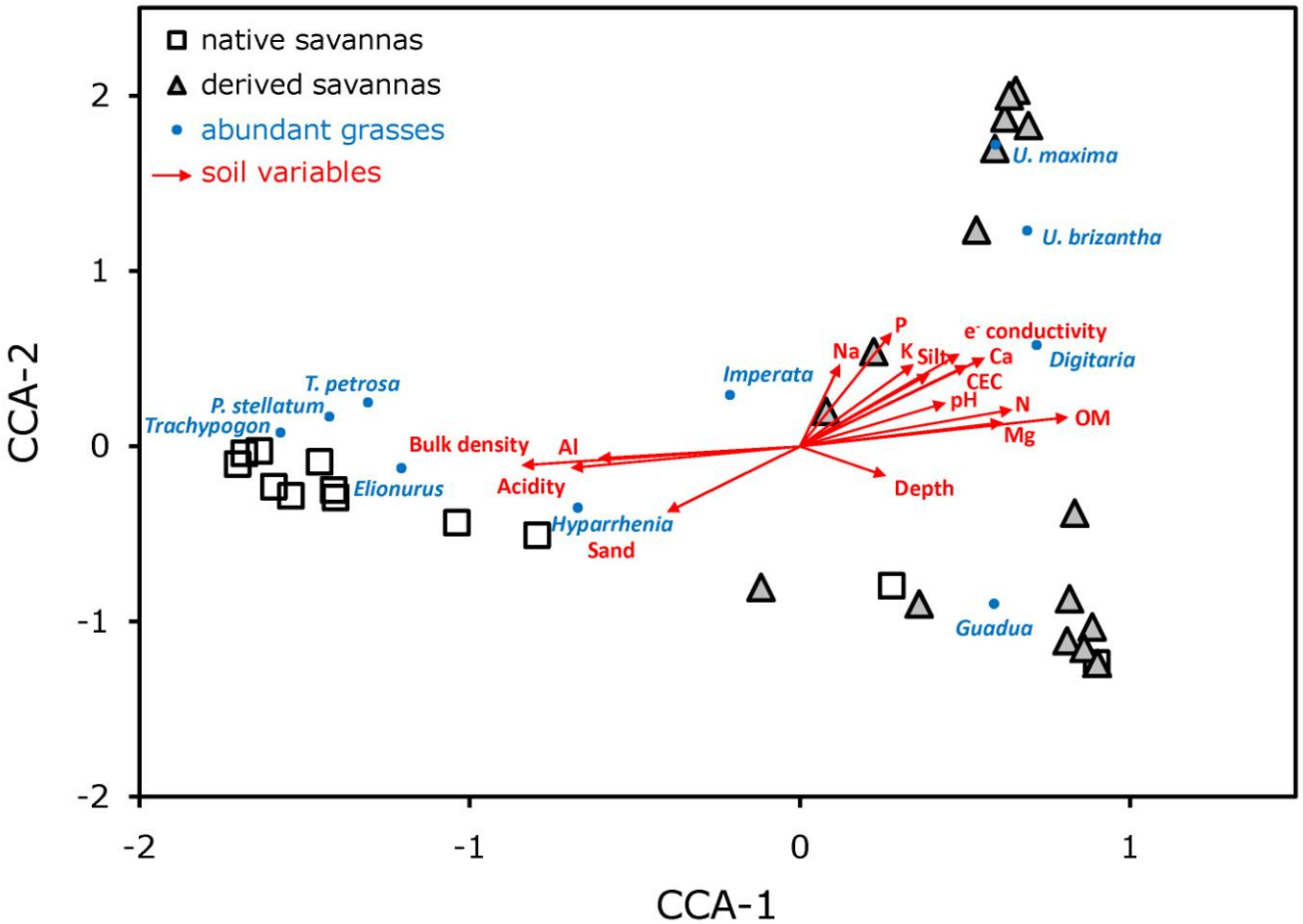

Figure 1-9. Canonical correspondence analysis of grass cover by (native and exotic)species and soil variables measured in native (n = 12) and derived (n = 17) savannas. Ordination plots display the scores for sites, species, and soil variables along the first two CCA axes. All grasses were included in the CCA but only the 10 most abundant species are displayed.

CHAPTER 2
SELECTIVE LOGGING AND FIRE AS DRIVERS OF ALIEN GRASS INVASION IN A BOLIVIAN TROPICAL DRY FOREST[1]

Logging is an integral component of most conceptual models that relate human land-use and climate change to tropical deforestation via positive-feedbacks involving fire. Given that grass invasions can substantially alter fire regimes, I studied grass distributions in a tropical dry forest 1-5 yr after selective logging, and experimentally tested the effect of forest fire on populations of invasive grasses. In unlogged forests and in microhabitats created by selective logging I found a total of four alien and 16 native grass species. Grasses covered 2% of unlogged and 4% of logged forest, with grass cover in logged forest concentrated in areas directly disturbed by logging; log landings and roads had relatively greater grass cover (37% and 17%, respectively) than did skid trails (10%) and felling gaps (8%). Total grass cover and grass species richness increased with canopy openness and were greatest in sites most severely disturbed by logging. The grass flora of these disturbed areas was composed mostly of native ruderal species (e.g., *Digitaria insularis, Leptochloa virgata*), a native bamboo (*Guadua paniculata*), and *Urochloa (Panicum) maxima*, a caespitose C_4 pasture grass introduced from Africa. *Urochloa maxima* formed monodominant stands (up to 91% cover and 2-3 m tall) and grew on 69% of log landings and 38% of roads. To better understand the potentially synergistic effects of logging and fire on the early stages of grass invasion, I tested the effect of a 12-ha experimental fire on *U. maxima* populations in a selectively logged forest. Three years after the fire, the area covered by alien grass in burned forest increased five-fold from 400 m^2 (pre-fire) to

[1] Reprinted with permission from: Veldman, J. W., B. Mostacedo, M. Peña-Claros, and F. E. Putz. 2009. Selective logging and fire as drivers of alien grass invasion in a Bolivian tropical dry forest. Forest Ecology and Management **258**: 1643-1649.

1660 m^2; over the same period in a logged but unburned (control) area, *U. maxima* cover decreased from 398 to 276 m^2. Increased canopy openness due to fire-induced tree mortality corresponded with the greater magnitude of grass invasion following fire. Selective logging of this dry forest on the southern edge of the Amazon Basin promotes alien grass invasion; when coupled with fire, the rate of invasion substantially increased. Recognition of the grass-promoting potential of selective logging is important for understanding the possible fates of tropical forests in fire-prone regions.

Introduction

The combined effects of road building, logging, increased intensity of land use, climate change, and fire in the Amazon Basin are predicted to result in widespread replacement of forest by savanna (e.g., Nepstad et al. 1999; Cox et al. 2004; Hutyra et al. 2005). Such projections are based on positive feedbacks between deforestation and climate change (Shukla et al. 1990; Betts et al. 2004), vegetation disturbance and fire (Cochrane et al. 1999), and drought and fire (Nepstad et al. 2004). A critical step in the process of forest conversion to savanna (i.e., to an open-canopied ecosystem with grass dominance of the understory), is invasion of forest by savanna grasses. Unfortunately, the factors that control grass invasions and their consequences for tropical forests are not well understood.

Given the increasing susceptibility of tropical forests to fire (e.g., Hutyra et al. 2005; Golding & Betts 2008), it is important to recognize land-use practices the promote grasses. Forests generally recover, albeit slowly at times, from severe degradation and even from outright destruction (Uhl et al. 1988). In contrast, a forested area pushed into the alternative stable state of grass dominance (i.e., another stability domain *sensu* Holling 1973) faces huge obstacles to recovery of its forested condition primarily due to the effects of grasses on fire regimes (D'Antonio & Vitousek 1992). Most grasses produce large amounts of fine fuel, resprout readily

from basal meristems, and thrive in frequently burned areas (e.g., Daubenmire 1972). As such, we may view tropical forest conversion to savanna in light of disturbance-regime shifts from one of very rare fires to one of frequent fires that favor grasses and limit forest regeneration [e.g., Mack & D'Antonio 1998; see also Bond (2008) for a comprehensive review of factors influencing the balance between grasses and trees].

Logging figures prominently among land-uses that degrade tropical forests in ways that might contribute to grass invasions and subsequent forest conversion to savanna. Logging opens canopies, disturbs soil, and otherwise renders forests more prone to fire (Uhl & Buschbacher 1985; Laurance 2003; but see Blate 2005). Tropical dry forests may be at particular risk of grass invasion following logging due to their naturally open canopies, severe seasonal limitations on water availability, and slow tree growth rates. Tropical dry forest susceptibility to grass invasion is evident in Guanacaste, Costa Rica where forests have largely been converted to derived savannas of the African grass *Hyparrhenia rufa* (Daubenmire 1972), and in Hawaii where invasion of dry forest by another African grass, *Melinis minutiflora*, drastically altered ecosystem functions (Mack & D'Antonio 2003).

In this study I investigated forest invasion by grasses in eastern lowland Bolivia where agricultural conversion, road building, and logging all contribute to the fragmentation, degradation, and fire susceptibility of the region's tropical dry forests (Steininger et al. 2001). My primary objectives were to determine if disturbance by logging promotes forest colonization by grasses, and to identify which grass species invade logged forests. To this end, I present data on the identities and distributions of native and alien grasses in a tropical dry forest 1-5 yrs after selective logging. In light of the grass-fire cycle, I hypothesized that the rate of alien grass invasion is amplified by forest fires. To test this hypothesis I evaluated the effect of a 12-ha

controlled burn on the population growth of the introduced African pasture grass, *Urochloa maxima* (formerly *Panicum maximum* and *Megathyrsus maximus*) in a partially grass-invaded area of selectively logged, seasonally dry tropical forest on the southern rim of the Amazon Basin.

Methods

Study Site

This research was carried out in the Bolivian region of Chiquitania in selectively logged areas of the 30,000 ha private property of INPA Parket Ltd. (hereafter INPA). The region contains a mosaic of vegetation types dominated by tropical deciduous dry forest (bosque seco Chiquitano) interspersed with native savannas floristically related to the Brazilian cerrados (Killeen et al. 1990; Jardim et al. 2003). These dry forests, in the transition zone between more humid Amazonian forest to the north and drier savannas and scrub woodlands (Gran Chaco) to the south, are thought to be particularly vulnerable to replacement by savanna due to seasonal drought, high flammability (Hutyra et al. 2005), and sensitivity to climate change (Mayle et al. 2000). Although a history of fire is thought to have influenced eastern Bolivia's dry forests (Killeen et al. 2005), most trees do not develop bark thick enough to withstand even low-intensity fires (Pinard & Huffman 1997). Indeed, anthropogenic forest fires are considered among the greatest challenges to forest conservation in the region (Steininger et al. 2001).

INPA (16° 15' S 61° 40' W; elevation 440 m) has a mean annual temperature of 24°C (extreme temperatures range from 4°C to 37°C) and receives an average of 1160 mm of precipitation annually (range 799 – 1859 mm, data from Administración de Aeropuertos y Servicios Auxiliares a la Navegación Aérea at Concepción collected 1943-2005), with seven months each receiving < 100 mm (April through October) and four months (June through September) during which potential evapotranspiration exceeds rainfall (M. Peña-Claros,

unpublished data). Between 2002-2006, 900 ha yr-1 of INPA were selectively logged at an intensity of 4 trees ha-1.

A single road accesses the property from the town of Concepción, 40 km to the west, and passes through a matrix of forest fragments, native savannas, cattle pastures, and small farms before entering the continuous forests of INPA. These nearby agricultural lands are frequently burned and are sources of fires that threaten the property annually. Due to fire suppression efforts by forest managers, no wildfires occurred on the property for the last 20 years (1987-2007, M. Peña, pers. obs.).

Grass Species Distributions

To determine the effect of forest disturbance by logging on grass colonization, I studied the identities and distributions of grasses within a 2,600 ha area of INPA that was selectively harvested between 2002-2006 using reduced-impact logging techniques. Using a map of the property that showed the locations of roads and log landings as well as year of harvest, I randomly selected 16 log landings to sample during the mid rainy season (February and March 2007). From these landings I located one example of each of the following microhabitats: primary skid trails; felling gaps; logging roads; and, forest patches with no signs of logging activity [n = 16 per microhabitat; N = 80 (16 x 5 microhabitat types)]. Sampling included areas 1, 2, 3, 4, and 5 yr post-logging (n = 4, 3, 4, 2, and 3, respectively). In each microhabitat I randomly located a single 10 x 3 m plot to sample grass cover, grass species presence/absence, and forest canopy openness. I selected microhabitats such that all plots were a minimum of 100 m from one another but were never >250 m from the landing. To estimate ground cover density within each plot, I classified 33 evenly spaced sample points in a 3 x 11 point grid as grass by species, other vegetation, or no plant cover. Canopy openness was measured at the center and

endpoints of the central axis of each plot using a spherical canopy densiometer (Lemmon 1956) held 1.3 m from the ground.

I identified all grass species according to Killeen (1990) and comparisons with herbarium specimens at the Museo Nacional de Historia Natural Noel Kempff Mercado in Santa Cruz, Bolivia (USZ) where voucher specimens were deposited. I classified each species' photosynthetic pathway as either C_3 or C_4 based on Killeen & Hinz (1992b) and Guissani et al. (2001). Nomenclature departs from Killeen (1990) for *U. maxima* and *U. brizantha* (formerly *Panicum maximum* and *Brachiaria brizantha*, respectively). Molecular data show both species should be together in *Urochloa* (Guissani et al. 2001; but see Simon & Jacobs (2003) who classify *U. maxima* as *Megathyrsus maximus*). Note that after first mention, species are referred to by their generic names except where ambiguous.

Alien Grass Responses to Fire

I used a 12-ha controlled burn to test the effect of fire on the population growth of *U. maxima* in a partially grass-invaded area of selectively logged forest. Although *U. maxima* was generally limited to roads and log landings, a portion of INPA (one harvest unit of 100 ha) had substantial populations growing on skid trails probably because skidders re-used grass-invaded log landings and entered the forest along grass-invaded roads. In 2005 I mapped two separate grass-invaded skid trail networks that were selectively logged the previous year; both networks supported similar *U. maxima* populations at the start of the experiment (see description below). One skid trail network fell within an area assigned to be burned in a 12-ha prescribed fire and the other network served as a control for comparison; as such, I established two unreplicated treatments: logged+burned and logged only.

The implementation and replication of large-scale fire experiments that simulate wild-fire events are difficult and often cost-prohibitive in remote tropical forests. Most studies of tropical

forest responses to fires are from areas that burned as a result of wild-fires and do not include pre-fire data (e.g., Cochrane & Schulze 1999). Well-designed, albeit unreplicated, studies on tropical forest fires that combine pre- and post-fire data from experimentally burned and control plots can yield important results on vegetation responses to fire (e.g., Balch et al. 2008). I used a BACI (before-after-control-impact) designed experiment (Smith 2002), to study the population growth of *U. maxima* in two areas of selectively logged forest, one experimentally burned and the other an unburned control.

Before the fire, I estimated the extent of *U. maxima* cover along skid trails and in felling gaps by measuring the width and length of each patch of *U. maxima*, calculating the area of an ellipse, and then summing the total of all patch areas to determine total cover. Additionally, I measured tree canopy openness with a spherical densiometer (Lemmon 1956) held above each grass patch. Although *U. maxima* is a bunch grass with short rhizomes, it is difficult to unambiguously distinguish between ramets and genets in dense stands (particularly after the first year of establishment); therefore, I measured the area covered by each patch as opposed to attempting to determine the number of individuals. Patches were neither replicates nor representative of intrinsic ecological units. They were rather, a convenient way to measure *U. maxima* cover by identifying areas of continuous grass cover that adhered to an eliptical shape. In 2005, before the experimental burn, the *U. maxima* population in the logged+burned treatment covered a total of 400 m^2 with 113 patches measured ranging 0.06 - 190 m^2 (median = 0.8); the control treatment (logged only) contained 398 m^2 of *U. maxima* with 150 patches ranging 0.05 - 24 m^2 (median = 1.3). After the initial censuses, I returned annually to measure both the burned and unburned (control) populations of *U. maxima* during the first three years after the fire (i.e., up to 4 yr post-logging).

The 12-ha controlled burn was conducted in the late dry season (September 2005) during the height of the fire season. The plot was burned using a backing fire ignited with drip-torches along 350 m of a logging road and a head fire ignited along a bulldozed fire-break on the other edge of the plot. Fire behavior varied as a result of the heterogeneous conditions created by selective logging microhabitats. The fire was extremely intense in felling gaps (~10% of the burned area) but was otherwise a low intensity surface fire. *Urochloa maxima* present before the fire represented only 0.3% of the entire burn area and presumably contributed little to the overall fire behavior or intensity at the 12-ha scale. As such, this experiment tested the effect of fire on the early stages of *U. maxima* invasion – well below the abundance threshold at which grass fuel loads determine fire regimes.

Data Analysis

I compared microhabitats on the basis of canopy openness, grass cover, and grass species richness with ANOVA followed by Tukey *post-hoc* tests. All values are based on a single equal sized plot for each microhabitat (n = 16). Ground cover percentages were square root transformed before analysis to normalize distributions. I used linear regression to relate grass cover and species richness to canopy openness across all sites (N = 80). Regression analysis was also used to relate *U. maxima* cover to native plant cover on log landings where the alien grass had non-zero values for cover (n = 8); I defined native plant cover as the sum of native grass cover plus cover by non-grass vegetation. Frequencies of occurrence of each species were calculated from presence/absence data for each microhabitat type and reported as percentages. I used analysis of covariance (ANCOVA) to test the main effects of time since logging (co-variate) and microhabitat (fixed factor) on total grass cover. I used canopy openness measurements and species presence/absence data to calculate logistic regression curves for each grass species. The calculated slopes from these regression were used as a disturbance affinity

metric (DA) for each species. The steeper the slope the more a species prefers open canopy sites; species that occur almost exclusively in undisturbed, closed canopy forest have negative slopes. Because a combination of water limitation and variation in light availability among microhabitats is likely to influence the distributions of grass with different photosynthetic pathways, I compared mean DA values of C_3 (n = 8) and C_4 (n = 12) species using a Student's t-test. All analyses were performed using SPSS 12.0 statistics software (SPSS Inc. Chicago, Illinois USA).

Due to the low logging intensity (4 tree ha^{-1}) and the use of reduced impact logging techniques disturbed microhabitats cover only a small portion of logged stands. Felling gaps (9%), skid trails (9%), roads (1%) and log landings (0.2%) combine to cover about 19% of harvested areas. In addition to the microhabitat-specific results, I calculated grass cover percentages for harvested forest as a whole weighted by the proportional area of each microhabitat.

I did not perform statistical analysis on the fire effects data because the treatments were not replicated in this BACI designed experiment. Instead, I report the total area covered by *U. maxima* in each yearly census. Canopy openness estimates for each population represent the weighted mean canopy openness values for all grass patches (weighted by patch size). As such, canopy measures are indicative of canopy openness where *U. maxima* was growing, not the forest as a whole.

Results

Grass Species Distributions

I encountered 20 grass species 1-5 yr after logging in this tropical dry forest (Table 2-1). Species included representatives from three sub-families (Bambusoidea, Chloridoideae, and Panicoideae), a wide range of growth forms, and species with C_3 and C_4 photosynthetic pathways. Sixteen of these species are native to eastern lowland Bolivia and four are exotic. Of

the alien species, *U. maxima* and *U. brizantha* were introduced from Africa and are widely planted as cattle forage in the Neotropics. The other exotics, *Sorghum halapense* and *Cynodon nlemfuensis*, are pantropical weeds present at low frequencies and never abundant in my samples. None of the native species are characteristic of the region's diverse savannas and savanna woodlands (Killeen & Hinz 1992a) but instead are either common roadside weeds (i.e., native ruderals) or forest grasses (Killeen 1990; Table 2-1).

Grass cover and species richness increased with increasing severity of logging disturbance. Canopy openness, one indicator of disturbance severity, was greater in all logging microhabitats compared to unlogged forest (Figure 2-1a). Across microhabitats the greatest mean grass cover and mean number of grass species were on log landings (37% cover, 3.3 species) and roads (17% cover, 4.2 species; Figure 2-1b,c). Both grass cover and species richness positively correlated with tree canopy openness across all sites (Figure 2-2a,b). Grass cover across microhabitats was independent of time since logging (ANCOVA, for time since logging, $F = 0.06$, $P = 0.81$).

Although grass cover was typically greater in more disturbed sites, the distributions of individual species differed substantially (Table 2-1). Disturbance affinities ranged from -6.3 for *Pharus lappulaceus*, a forest grass that did not occur in highly disturbed sites, to 9,9 for the exotic *Cynodon* which, like the other alien species, occurred only on roads and log landings. Grasses with C_4 photosynthesis had greater mean disturbance affinities than C_3 grasses (5.5 and -0.15, $P < 0.001$, Student's t-test). *Urochloa maxima,* the most abundant alien grass encountered, formed monodominant stands (up to 91% cover) and was present in 69% of log landings and 38% of roads (Table 2-1). Regression analysis of log landings that had non-zero values for *U. maxima* cover yielded a non-linear negative relationship between alien grass cover and native

plant cover: [native plant cover] = -18.15 ln[*U. maxima* cover] + 86.84 (R^2 = 0.79, P = 0.003, n = 8). In addition to *U. maxima,* the native ruderals *Leptochloa virgata* and *Digitaria insularis*, and the native bamboo *Guadua panicultata* (a giant rhizomatous grass with woody culms) were abundant on log landings (Table 2-1). Unlike *Leptochloa* and *Digitaria*, *Guadua* occurred at low frequency in all microhabitats including unlogged forest. *Guadua* was never abundant with the exception of a single log landing where it grew to 4 m tall and covered 75% of the plot.

Roads had the highest grass species richness (mean 4.2, maximum 9 species per 30 m^2 plot, Figure 2-1c); 18 of the 20 grass species recorded were present on at least one road (Table 2-1). In addition to the exotic *U. maxima*, common grasses on roads were the native ruderals: *Leptochloa, Panicum millegrana*, and *Axonopus compressus*.

I encountered only four grass species and sparse grass cover (2.4%) in unlogged forest. Of the forest grasses, three are Bambusoideae: *Pharus lappulaceus* is a small (50 cm tall) understory species present in 69% of plots; *Guadua* and *Chusquea ramosissima* – a liana-like climber with woody culms, were rare in unlogged plots. Also rare in unlogged forest was *Lasiacis sorghoidea*, a caespitose Panicoideae with C_3 photosynthesis, which typically grows 1-2 m tall. *Lasiacis* occurred in all microhabitats but reached high abundance in areas of intermediate disturbance severity with maximum cover in gaps and on skid trails of 21 and 49%, respectively.

Alien Grass Responses to Fire

During three years of monitoring after burning 12 ha of partially grass-invaded forest*, U. maxima* cover increased from 400 m^2 to 1660 m^2 (a 315% increase; Figure 2-3a). Over this same time period, the control population in unburned forest decreased from 398 to 267 m^2 (a 31% reduction). As such, there was six times more alien grass in the burned forest than in the unburned forest three years after the fire (4 yr post-logging). Canopy openness measured in the

burned and unburned forest corresponded with changes in *U. maxima* cover (Figure 2-3). Canopy openness in the burn treatment remained at its pre-fire post-logging level of roughly 60% during all three years of monitoring. In contrast, mean canopy openness in the unburned forest decreased steadily each year dropping from 47 to 20% during 4 yr post-logging. Inter-annual changes in grass cover were not consistent for either the burned or the unburned forest (Figure 2-3a). After increasing three-fold in the first year, grass cover in the burned forest decreased slightly during the second year only to be followed by another increase during year three. Grass cover in the control area decreased over the course of the study but this decrease occurred after it doubled during the first year of monitoring (i.e., the second year post-logging).

Discussion

Grass Species Distributions

The absence of alien grasses in unlogged forest and their abundance in the most disturbed sites in selectively logged stands suggests a strong link between logging and grass invasion in this forest. Positive effects of the severity of logging-induced forest changes on grass cover are not surprising given that disturbance is an important factor influencing ecosystem invasibility (e.g., Hierro et al. 2006), and that graminoids are widely recognized for their adaptations to disturbed environments (Chapman 1996).

The most abundant grass encountered was *U. maxima*, an alien species with C_4 photosynthesis. While a host of morphological (e.g., seed size) and physiological (e.g., drought tolerance) adaptations might contribute to the invasiveness of *U. maxima*, I expect that photosynthetic pathway (i.e., C_3 vs. C_4) is especially important: two consequences of logging-induced canopy openness are increased light availability and increased water stress (e.g., Ashton 1992) – conditions in which C_4 photosynthesis is advantageous. Indeed, a comparison of the disturbance affinities of C_3 versus C_4 grasses showed that C_4 grasses favored open microhabitats

created by logging disturbances whereas C_3 species tended to be more common in closed canopy sites. In tropical dry forests where water stress typically limits plant establishment and survival (e.g., Gerhardt 1996; Khurana & Singh 2001), C_4 grasses appear poised to take advantage of resources liberated by low intensity reduced-impact logging – but only if seeds arrive at suitable recruitment sites.

In the seasonally dry tropical forest I studied, *U. maxima* dominated sites heavily disturbed by logging (log landings and roads) but did not invade undisturbed forest. Roads and log landings are not solely areas of severe soil and canopy disturbance, but are also sites frequented by logging trucks that make repeated trips into the forest. Given the documented potential for motor vehicles to disperse seeds long distances (von der Lippe & Kowarik 2007), and the fact that alien invasive and native ruderal grasses commonly occurred far (>500 m) from parent populations in this forest, logging traffic probably plays a critical role in dispersing grass seeds during the timber harvest.

Forest invasion by alien grasses is problematic largely because of their effect on forest flammability. *Urochloa maxima* can grow 2-3 m tall and produces fine fuel loads of up to 17 Mg ha^{-1} (standing biomass plus litter, J. Veldman, unpublished data).

With the exception of *Guadua* (a native bamboo), *U. maxima* is the only species in this forest that formed monodominant stands that appeared to exclude native plant species. Primarily because of its high productivity, *U. maxima* was introduced to South America from the Guinea Coast of Africa during the 18th century and is a preferred forage grass throughout the Neotropics (Parsons 1972). The species is still cultivated for forage in the Chiquitania region, but *U. brizantha* is more commonly used. Interestingly, *U. brizantha* is not nearly as invasive as *U.*

maxima in INPA, even though both species are abundant in pastures and along roads leading to the property.

The only native grass that produces fuel loads comparable to *U. maxima* is *Guadua*. Although rare in this study, *Guadua* flourished on one log landing (75% cover), and amongst all species was second only to *U. maxima* in maximum percent cover. Large (100-1000 ha) monodominant *Guadua* stands are common throughout the region (Killeen 1990), and are characterized by bamboo canopies 2-7 m tall, fuel loads of up to 16 Mg ha^{-1} (standing bamboo biomass plus litter), a nearly annual fire regime, low tree density and tree basal area, and charred standing dead trees (Veldman 2008). Vigorous resprouting from rhizomes coupled with production of large quantities of fine fuel makes native bamboo-domination a plausible outcome for forests subjected to canopy disturbances and fire (e.g., Gagnon & Platt 2008). Surprisingly, most forestry research in Bolivia has been conducted in areas with little or no *Guadua* despite the fact that *G. sarcocarpa* and *G. weberbaueri* form monodominant stands that can limit forest succession in other parts of the Amazon basin (Griscom & Ashton 2003, 2006). In contrast to *U. maxima* which can produce 1300 seeds m^{-2} annually (Veldman & Putz 2010), rare seed production by *Guadua* probably explains why this mast fruiting bamboo was not a more frequent colonizer of disturbed sites.

Increased grass cover in logging-affected microhabitats (which account for 19% of harvested stands) translates to a small (but two fold) increase in total grass cover between unlogged (2%) and logged forest (4%). This modest increase in grass cover belies the extent of grass invasion and the spatial distributions of grasses following logging. Grass colonization of roads and log landings results in a network of grassy clearings (log landings) connected by grass-invaded corridors (roads) throughout the forest. Alien grasses in these sites are of consequence

because they extend into all parts of the forest; in my study site 100% of selectively logged areas fall within 500 m of a logging road or log landing.

In the absence of further disturbance, the presence of grasses should be temporary because they will be out-competed by the regenerating forest. Nonetheless, re-entry by logging machines or forest fires can stimulate further expansion of grass populations. Even grass populations that are initially small can serve as propagule sources for larger invasions if roads or log landing are re-used. For example, *U. maxima* invaded skid trails in a portion of INPA apparently because skidders re-used grass-invaded log landings and entered the forest along grass-invaded roads thereby dispersing seeds into the forest. This invasion of skid trails not only provides anecdotal evidence that grass populations can expand due to additional disturbance, but also afforded a site to study the effect of fire on grass-invaded forest.

Alien Grass Responses to Fire

An experimental burn in grass-invaded forest demonstrated that forest fires can increase the extent and duration of alien grass invasion following selective logging; three years after the fire, the combination of logging and fire resulted in an invasion six times larger than logging alone (1660 m^2 versus 276 m^2). Increased light availability due to fire-induced canopy tree mortality (e.g., Cochrane & Shultz 1998) may explain much of the positive effect of fire on alien grass population growth. Both burned and unburned forests had open canopies before the fire as a result of selective logging, but whereas the burned forest canopy showed no signs of recovery, the unburned forest canopy closed substantially. In addition to light availability, the creation of suitable establishment sites following the fire appears to have contributed to *U. maxima* population growth. The high intensity fire that consumed woody debris in felling gaps created large ash-covered clearings throughout the burn plot. Despite no alien grass recruitment in these gaps during the first 2 yr post-fire, in the final census (i.e., 3 yr post logging) I found twelve new

grass patches in burned gaps that totaled 240 m^2 and accounted for 65% of the increase in *U. maxima* compared to the previous year.

As well as increasing the spatial extent of the invasion, the fire increased the duration of grass cover. Under any conceivable scenario of grass population decline and forest canopy recovery beyond three years post-fire (4 yr post-logging), grasses in the unburned area will disappear long before they do in the burned forest. It is unclear exactly how long alien grasses can persist in the absence of additional disturbance. My analysis of grass cover across microhabitats 1-5 yr post-logging showed no effect of time. Consequently, a longer period of forest recovery would be needed to detect substantial declines in grass cover. I can, nonetheless, use the unburned forest data (4 yr post-logging, Figure 2-3a) as well as data from the grass distribution study (up to 5 yr post-logging) to deduce that grasses can persist for at least five years and quite possibly 6-10 years after logging even without fire or re-entry by loggers.

Conclusions

Selectively logged areas in a tropical dry forest in eastern lowland Bolivia are colonized by both native and alien grasses, especially in areas that are also burned. These grass species should not be confused with the native grass flora that composes the species-rich native savannas (*cerrados*) of central South America. Rather, the grasses that colonized logged forest are mostly invasive pasture grasses together with a few common native ruderals and bamboo. I identified two grasses with high potential to respond to disturbance from logging and fire. One of them is *U. maxima,* an alien grass that is already ubiquitous in Neotropical agricultural landscapes; the other one is *Guadua paniculata*, a well-known native bamboo that was relatively rare in my study site. The increased cover of these two grasses following selective logging, combined with their impressive fine fuel production, underscore the need for fire suppression in forests under timber management. This study was conducted in a forest that was logged at a relatively low

intensity, and has been protected from wild-fire in recent history. In poorly managed forests or in areas harvested at greater intensities the implications for forest degradation are far greater.

Understanding the vegetation changes that result from human disturbances is important at both local and global scales if we want to develop better forest management methods and improve vegetation dynamic models to predict the fates of tropical forests. Land-uses that promote grasses over trees, whether intentionally (i.e., pasture establishment) or unintentionally (logging), substantially affect ecosystem flammability, carbon storage, nutrient cycling, evapotranspiration, and forest regeneration. Most of these factors are incorporated in models, both conceptual (e.g., Cochrane 2003) and quantitative (e.g., Cox et al. 2004; Golding & Betts 2008) that predict alarming fates for Amazonian forests. Models currently under development should also incorporate the grass-promoting potential of logging and fire and pay particular attention to the different forest fates that are possible under scenarios with and without invasive native and exotic grasses.

Table 2-1. Grass cover in five forest microhabitats 1-5 yr after selective logging. Alien species are marked by asterisks. Species are listed in decreasing order of affinity for logging disturbance as estimated from the slope of logistic regression equations relating species presence/absence data to canopy openness in 30 m2 plots (*N* = 80). Disturbance affinities (DA) for species present in < 5% of plots are listed in parentheses. Microhabitats are listed in increasing order of logging disturbance. Percentages for mean cover, maximum cover, and frequency in each microhabitat are listed, respectively (*n* = 16 per microhabitat).

			Unlogged forests			Felling gaps			Skid trails			Log landings			Roads		
Species	C_3/C_4	DA	mean	max	freq.	mean	max	freq.	mean	max	freq.	mean	max	freq.	mean	max	freq.
*Cynodon nlemfuensis**	C_4	(9.9)	-	-	-	-	-	-	-	-	-	-	-	6	0.2	3	6
Digitaria insularis	C_4	7.3	-	-	-	-	-	-	-	-	6	4.9	27	44	0.2	3	25
*Sorghum halepense**	C_4	(7.2)	-	-	-	-	-	-	-	-	-	0.2	3	6	0.2	3	6
*Urochloa brizantha**	C_4	(7.2)	-	-	-	-	-	-	-	-	-	0.4	6	6	0.4	6	13
Chloris dandyana	C_4	6.3	-	-	-	-	-	-	-	-	-	0.6	9	13	-	-	19
Leptochloa virgata	C_4	6.1	-	-	-	-	-	-	-	-	-	5.5	27	56	3.8	27	75
*Urochloa maxima**	C_4	5.8	-	-	-	-	-	-	-	-	-	16	91	69	2.5	18	38
Digitaria bicornis	C_4	5.5	-	-	-	-	-	-	-	-	-	0.4	6	25	-	-	6
Panicum trichoides	C_3	4.6	-	-	-	-	-	-	-	-	6	1.1	9	25	1.3	6	50
Paspalum paniculatum	C_4	3.8	-	-	-	-	-	-	-	-	-	0.2	3	6	0.4	3	50
Setaria poiretiana	C_4	(3.3)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6
Setaria vulpiseta	C_4	(3.3)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6
Panicum millegrana	C_3	3	-	-	-	-	-	-	-	-	6	-	-	25	3.0	15	44
Acroceras excavatum	C_3	1.6	-	-	-	0.4	3	19	0.6	6	31	1.9	15	31	1.3	9	25
Axonopus compressus	C_4	0.9	-	-	-	-	-	-	-	-	-	-	-	-	3.2	39	25
Lasiacis sorghoidea	C_3	0.6	0.6	6	13	5.5	21	38	7.8	49	69	0.8	12	25	0.6	3	31
Guadua paniculata	C_3	0.3	-	-	13	0.2	3	13	0.9	9	13	4.7	75	6	0.4	6	6
Olyra latifolia	C_3	(-1.1)	-	-	-	-	-	6	-	-	-	-	-	-	-	-	6
Chusquea ramosissima	C_3	-3.9	0.9	6	19	1.5	24	6	0.4	6	13	-	-	-	-	-	-
Pharus lappulaceus	C_3	-6.3	0.8	6	69	0.8	6	25	0.2	3	50	-	-	-	-	-	-

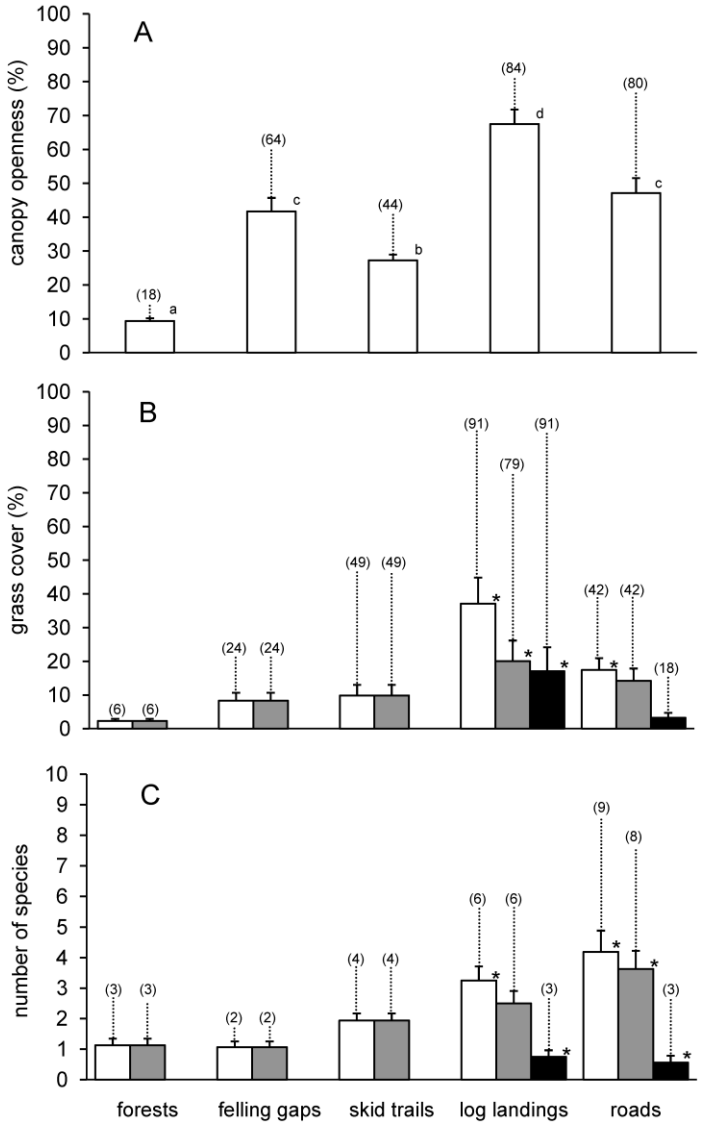

Figure 2-1. Canopy openness, grass cover density and species richness in five microhabitats arranged in order of increasing disturbance by selective logging, 1-5 yr after harvest. A) Canopy openness; habitats labeled with different letters differ at $P < 0.05$ (ANOVA, *post hoc* Tukey, $n = 16$). B) Grass ground cover and C) grass species richness. Total, native, and alien grasses are denoted by white, gray, and black bars respectively; asterisks mark habitats that differ from forests in grass cover or species richness at $P < 0.05$ (ANOVA, *post hoc* Tukey, $n = 16$). Columns and error bars indicate mean+1SE for sixteen 30 m^2 plots per microhabitat type; values in parentheses denote maximum values.

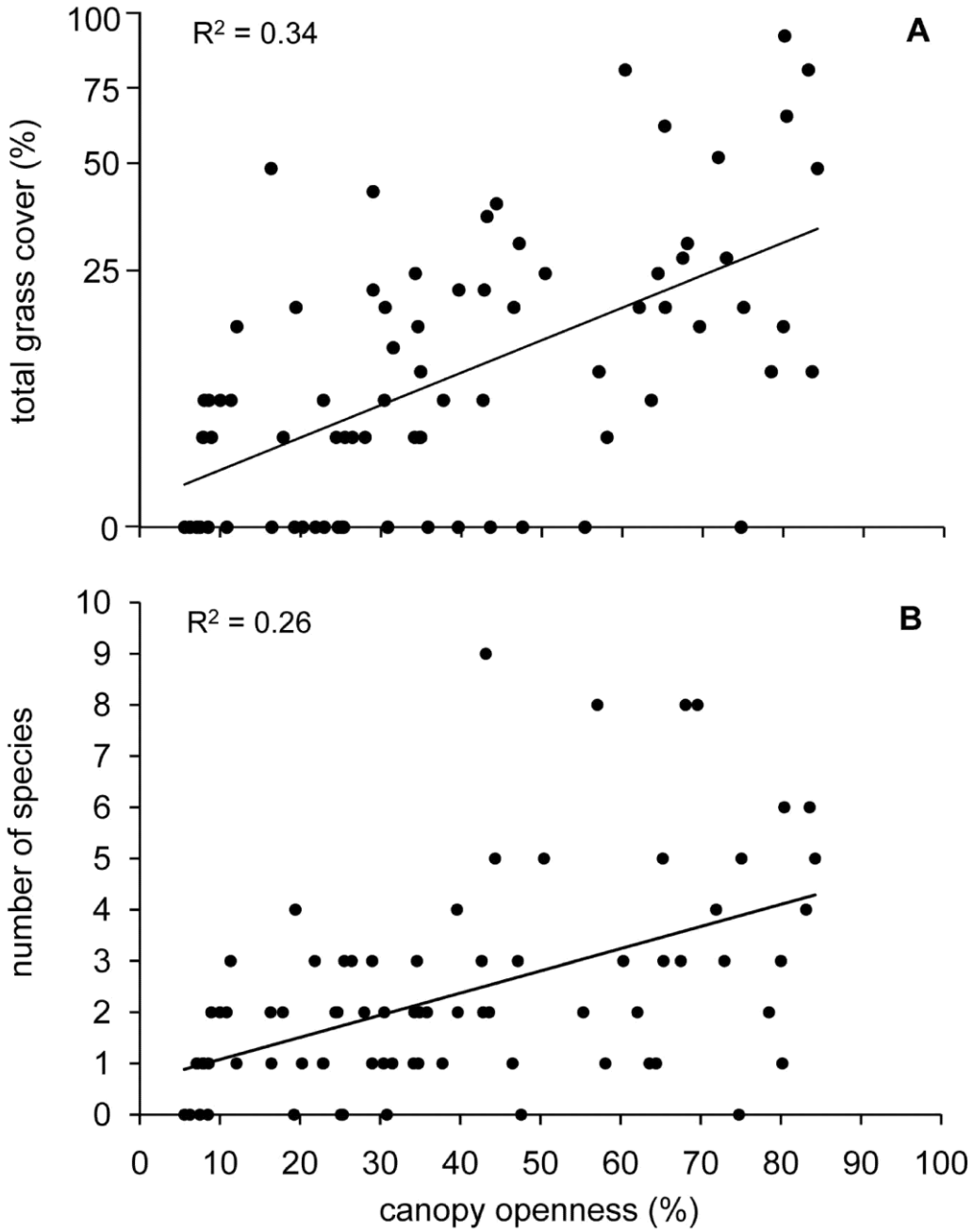

Figure 2-2. Grass cover and species richness in relation to tree canopy openness 1-5 yr after selective logging for all habitats combined ($N = 80$). A) Grass cover: [total grass cover]$^{-2}$ = 0.0631 [canopy openness] + 0.476, $P < 0.001$; note that the grass cover data were square root transformed before analysis. B) Grass species richness based on species presence/absence data: [number of species] = 0.043[canopy openness] + 0.644, $P < 0.001$).

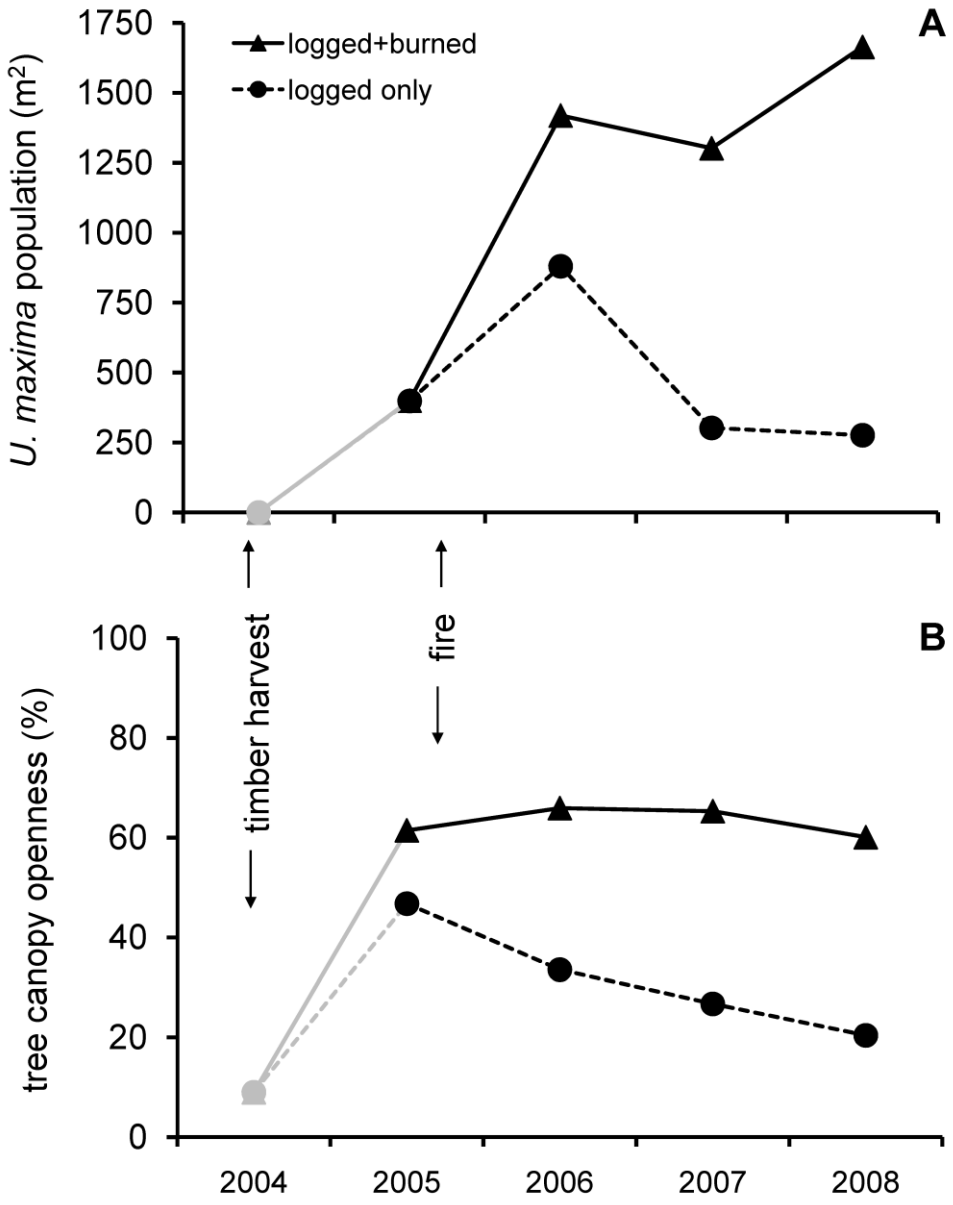

Figure 2-3. Responses of alien grass populations and tree canopy cover to an experimental fire in a selectively logged Bolivian tropical dry forest. Black triangles and circles denote measurements during the three year study; in gray, pre-logging (2004) values are inferred from data measured in unlogged areas of the forest. A) Total *Urochloa maxima* cover before and 3 yr after an experimental fire in grass-invaded selectively logged areas. B) Canopy openness measured above grass patches in the burned and unburned grass-invaded areas.

CHAPTER 3
LONG-DISTANCE DISPERSAL OF INVASIVE GRASSES BY LOGGING VEHICLES IN A TROPICAL DRY FOREST[2]

Predicting responses of vegetation to environmental factors in human-altered tropical ecosystems requires an understanding of the controls on plant population expansion across landscapes (i.e., long-distance dispersal) as well as of factors affecting recruitment at local scales (i.e., microsite conditions). I studied the roles of light availability, habitat type, soil disturbance, and seed dispersal in a selectively logged forest in lowland Bolivia where the exotic forage grass *Urochloa* (*Panicum*) *maxima* is abundant on roads and log landings but does not invade felling gaps or unlogged forest. Shade-house trials and seed addition experiments with *U. maxima* revealed that this C_4 grass thrives in high light but also grows in partial shade (10% full sun; but not 1% full sun), and that felling gaps, but not undisturbed forest, are suitable for grass establishment. To determine if seed dispersal by logging vehicles explains the discrepancy between actual and potential grass recruitment sites, I collected grass seeds that fell from trucks onto log landings located long-distances (>500 m) from established grass populations. Trucks dispersed an estimated 1800 alien grass seeds per log landing during the early dry season; automobiles also transported seeds of grass (135 seeds /vehicle). The seeds collected (and relative abundances) were the exotics *U. (Panicum) maxima* (97%) and *U. (Brachiaria) brizantha* (2%), and the pan-tropical weeds *Sorghum halapense* (1%) and *Rottboellia cochinchinensis* (0.2%). Grasses invade this forest where disturbance coincides with seed

[2] Reprinted with permission from: Veldman J.W., and F. E. Putz. 2010. Long-distance dispersal of invasive grasses by logging vehicles in a tropical dry forest. Biotropica (*in press*).

dispersal by motor vehicles, while dispersal limitation apparently prevents invasion of many sites otherwise suitable for grass recruitment (i.e., felling and natural gaps).

Introduction

There is lagging (but growing) awareness of novel tropical ecosystems (Lugo 2009) and complex vegetation transitions (Putz & Redford 2010), as well as increasing recognition that ecosystems resulting from human activities have not been adequately studied (Hobbs et al. 2006). Although novel disturbances can simply result in altered abundances of native species, plant invasions can cause drastic changes in community compositions, ecosystem functions, or both (e.g., Mack & D'Antonio 1998). As scientists consider the effects of environmental change on tropical vegetation (e.g., Barlow & Peres 2008), it will be important to understand the biology of not only the pool of species present in native plant communities, but also the species (native or exotic) that are likely to expand their current ranges (Higgins & Richardson 1999).

Range shifts, migrations, and biological invasions cannot occur if propagules do not reach suitable establishment sites or if suitable sites are lacking. To conceptualize the suite of factors that limit recruitment, many studies are conducted within a framework of barriers or filters, physical or biological in nature, that a species must pass through in order to invade (e.g., Parendes & Jones 2000). Numerous human activities break down these barriers by creating conditions suitable for invasive plant establishment (e.g., increased resource availability via disturbance) or by enhancing propagule dispersal (e.g., Hodkinson & Thompson 1997). Ecosystem-altering human activities that both create appropriate establishment sites and enhance propagule dispersal of invasive species demand particular attention.

Roadways represent a familiar example of the coupling of human-mediated dispersal and the creation of novel environments. Roads are essentially corridors of repeatedly disturbed habitat (Gelbard & Belnap 2003) along which plant propagules are transported by motor vehicles

(Clifford 1959; but see Christen & Matlack 2006). Roadside floras are often dominated by non-native species, and studies from high-traffic urban areas demonstrate that motor vehicles disperse a disproportionately large number of seeds of invasive species (von der Lippe & Kowarik 2007).

Although it is plausible that long-distance seed dispersal by motor vehicles occurs in remote regions of the tropics, the effects of roads on plant migrations have received little attention in the tropical conservation literature (but see Corlett 2009). Perhaps this disregard is based on the perception that tropical forests resist plant invasions (Levine 2002), or that in comparison to promoting wild-fires, logging, hunting and, ultimately, agricultural conversion (Angelsen & Kaimowitz 1999; Nepstad et al. 2001), any roles roads play in plant invasions seem secondary.

Roads that extend into forests in advance of agricultural frontiers are usually constructed for selective logging (Uhl et al. 1991). In addition to increasing forest access to people, logging opens forest canopies, disturbs surface soils, and renders forests more fire prone (Uhl & Buschbacher 1985; Laurance 2003; but see Blate 2005). Of these disturbances, exposed mineral soil and increased light availability are thought to be important for the establishment of invasive grasses from seed (Setterfield et al. 2005), and fires can further exacerbate grass invasions (D'Antonio & Vitousek 1992). Indeed, both native and alien grasses were reported to colonize a Bolivian tropical dry forest in areas most severely disturbed by selective logging and fire (Veldman et al. 2009), but how grass propagules arrived at the invaded sites remains unclear.

I investigated factors expected to influence patterns of alien grass invasion following selective logging in a tropical dry forest in eastern lowland Bolivia where alien grasses regularly colonize roads and log landings but not other anthropogenic microhabitats created by selective logging (i.e., not felling gaps and skidtrails) or unlogged forest (Veldman et al. 2009). The

aggregation of alien grasses on sites most severely disturbed by logging might reflect habitat specialization due to microsite conditions, but could also be due to high propagule pressure from seeds dispersed by logging vehicles. I conducted a seed addition experiment, along with a shade house study to determine the microsite requirements for grass establishment and to determine if microsite availability limits grass establishment in felling gaps and unlogged forest. To determine whether long-distance dispersal by logging vehicles contributes to grass invasion in this forest, I collected debris falling from logging trucks and inspected automobiles to look for invasive grass seeds. The results of these studies should yield a more complete picture of how grasses invade selectively logged tropical forest, inform strategies to mitigate invasive seed dispersal, and, draw attention to motor vehicles as dispersers of plant propagules in remote tropical regions.

Methods

Study Site

This research was carried out in a seasonally dry tropical forest owned by a vertically integrated logging and parquet flooring manufacturer (INPA Parket Ltd., hereafter INPA) located in a region of eastern lowland Bolivia known as Chiquitania. The study site (16° 15’ S 61° 40’ W; elevation 440 m; mean annual precipitation 1200 mm) covers 30,000 ha of Forest Stewardship Council certified forest of which 900 ha/yr has been harvested since 2002 at an intensity of ~4 trees/ha. The majority of timber is extracted during the dry season (May to October), during which trees are felled, skidded to log landings, loaded onto flatbed trucks (18 m long with 14-18 wheels) and transported 40 km to a sawmill in the town of Concepción (population 6,000).

An indirect consequence of logging in INPA is forest invasion by grasses, the most abundant of which is the African forage grass *Urochloa maxima*. Alien grass distributions are

generally limited to roads and log landings (i.e., the most severely disturbed microhabitats); in a survey of selectively logged areas within INPA, alien grasses were not encountered in unlogged forest, felling gaps, or skid trails (Veldman et al. 2009). A single road provides access to INPA from Concepción and traverses a landscape mosaic of fragmented forests, swidden agriculture plots, cattle ranches, and native savannas. These anthropogenic and semi-natural areas, and the roadside itself, are presumably sources of grass propagules that invade INPA. Alien grasses occur in even the most remote portions of the property that were logged extending some 30 km from the forest entrance.

Shade House and Seed Addition Experiments

I conducted two experiments to assess the establishment requirements of *U. maxima*, and thereby to determine if there are suitable establishment sites in the forest where *U. maxima* does not typically invade (i.e., the degree to which *U. maxima* is microsite as opposed to dispersal limited). To assess the viability of seeds used in the experiments (seeds were purchased 2 wks before the experiments from the *Union Centro Veterinario* in Santa Cruz), I scattered 50 seeds into each of 12 - 10 x 14.5 cm plastic trays lined with paper towels, maintained water in the trays at the saturation point for the paper, and counted/removed germinated seeds daily for 2 wks. An average of 48% of the seeds germinated, of which 97% germinated within the first 7 d.

To estimate the light requirements of *U. maxima*, I assessed seed germination and 1 mo seedling survival (i.e., emergence *sensu* Setterfield et al. 2005) under a range of light conditions in shade houses during the early rainy season (October-November 2005); shade houses were located in Santa Cruz at the Bolivian Institute for Forestry Research (IBIF; Poorter & Markesteijn 2008). I filled 48 plastic trays (10 x 14.5 cm) 2 cm deep with forest soil and placed them in one of four light treatments: 0, 1, 10, or 70% full sun (n = 12 per light treatment); light

intensities were measured with a LI-COR model LI-250 light meter (LI-COR, Lincoln, Nebraska USA). I saturated each tray with water and after the water drained (i.e., the soil reached field capacity), I scattered 50 seeds on the soil surface; the soil was then maintained at about field capacity during the entire experiment. I counted the number of plants in each tray after 7 days to assess initial germination, and then counted and harvested entire plants after 1 mo; seedlings were washed and oven dried to constant weight at 60° C before weighing. I compared seedling survival and plant biomass between light treatments by ANOVA and Tukey *post hoc* tests. All analyses were performed using SPSS 12.0 statistics software (SPSS Inc., Chicago, IL USA).

To investigate how soil disturbance and microhabitat conditions influence *U. maxima* establishment, I sowed seeds in experimental plots in an area of selectively logged forest. In the early rainy season (October 2005), I randomly selected twenty felling gaps and adjacent areas of closed canopy forest within a 100 ha area that was harvested during the preceding dry season. In each felling gap and forest I established plots of either mechanically scarified or untreated soil in a 2 x 2 factorial complete block design with soil treatment and microhabitat as factors and gap-forest pairs as blocks (n = 20 blocks). In each felling gap and forest, I scattered 100 seeds on each of two scarified and two untreated sub-plots of 0.1 m^2 such that 200 seeds were sown per 0.2 m^2 per treatment per block. For the scarified (i.e., disturbed surface soil) treatment I used a machete to remove all litter and plants and to expose a 1.5 m^2 area of mineral soil prior to scattering 100 seeds in the center 0.1 m^2 of each scarified area. I measured canopy cover over each sub-plot using a spherical canopy densiometer held 1.3 m above the ground (Lemmon 1956). After 1 mo I counted the grass seedlings, collected the above and below-ground grass biomass, and weighed the plants after oven drying at 60° C.

I used a two-way ANOVA to test for main effects of soil treatment, microhabitat, and their interaction, on the number of seedlings, total grass biomass, and biomass per individual; blocks were treated as a random effect and Tukey *post hoc* tests were used to compare means among treatments. To reveal which sites in the seed addition experiment were suitable for grass establishment, as opposed to those with plants so small they were unlikely to survive, I counted the plots that had a mean per plant biomass > 3 mg. This biomass cut-off was based on the results of the shade house experiments in which the minimum biomass measured for plants exposed to 10% full sun was 3 mg/individual; 10% full sun was the minimum sunlight exposure required for high grass survival and growth. I compared the frequency of 'suitable establishment sites' among treatments with Chi-square.

Seed Rain from Logging Vehicles

During the early dry season (May 2008) we sampled alien grass seed rain falling from logging trucks (n = 8), and collected seeds from automobiles (n = 3) on three different log landings in the forest. Log landings are large (~700 m^2) clearings where logs are organized and loaded onto trucks; abandoned log landings are often colonized by grasses. New log landings are appropriate sites for studying long-distance seed dispersal by motor vehicles because they are the primary destination of trucks and automobiles entering the forest. I verified that each log landing used in this study was accessed by a newly created road and was at least 500 m from previously logged forest, pre-existing roads, or existing alien grass populations with a geographic positioning system (GPS) and a map of the property. In addition I searched for grasses within 3 m of the road (200 m x 6 m sampled) leading away from each log landing to confirm that alien grasses were not present.

To estimate the number of seeds dispersed by trucks to log landings I randomly positioned 12 plastic tarps (115 x 74 cm each) totaling 10.2 m^2 beneath each truck immediately

after it arrived at the landing. As timber was loaded onto the trucks, dirt and seeds were dislodged and fell onto the tarps. After each truck was loaded, I removed the 12 tarps and combined the material collected into a single sample. In addition to the seed rain from log loading, I collected debris that workers swept off truck beds. Flatbed trailers can accumulate bark and soil that is removed before log loading; I collected this debris onto a 5 x 5 m tarp as it was swept off the trailer. I did not ask forest managers to clean the truck beds for the sake of this study and did not anticipate this source of seed rain.

I estimated the number of seeds carried by automobiles by collecting all soil and other debris that I were able to dislodge by hand using brushes and wooden spatulas from one randomly selected front and one rear wheel well from each car sampled. I also collected seeds present on the removable interior floor mats from the passenger compartments. In comparison with the truck data, which represent a true estimate of seed rain (von der Lippe and Kowarik 2007), I do not know what proportion of the automobile seed is deposited on log landings – a limitation of all studies that collect seeds attached to motor vehicles (e.g., Clifford 1959; Zwaenepoel et al. 2006).

To determine the number of alien grass seeds in the truck and automobile debris I manually sorted through the samples to separate seeds from other material. For samples too large to process in their entirety, I analyzed a series of sub-samples. For samples up to 2.5 kg, the sub-samples comprised at least 10% of the total sample fresh weight; for larger samples a minimum of 0.25 kg was sub-sampled. I identified the seeds to species and determined the number of full seeds (as opposed to empty caryopses) in the samples by cutting each seed with a razor blade and inspecting it under a dissecting microscope. I report only the number of full seeds collected. I chose visual inspection of the samples rather than germination trials to assess the numbers and

identities of grass seeds carried to log landings by vehicles because the seeds of the most common alien grasses in this forest are relatively large (3-6 mm) and are easily separated from soil and other debris. Furthermore, grass seedlings are extremely difficult to identify to species whereas seed characteristics are often diagnostic. Finally, required seed dormancy periods can be long and vary even within species (Usberti & Martins 2007) making reliable germination trials lengthy.

Based on the number of seeds that fell onto tarps (10.2 m^2) during log loading I calculated total seed rain per truck by extrapolating to the area of each truck (~48 m^2). To calculate total seed rain densities in seeds/m^2 for log landings I assumed 10 truck visits per landing and 700 m^2 as the area of each landing. To calculate the number of seeds per vehicle for passenger cars I extrapolated from the two tires/wheel wells sampled to four and used the total number of seeds from the interior floor mats. By sampling only tires and wheel wells I underestimate the total number of seeds carried on the exterior of vehicles. Likewise, more exhaustive cleaning of vehicle interiors would certainly yield higher seed numbers than the floor mats alone. On the other hand, because I do not know what proportion of the seeds attached to automobiles is deposited in log landings, my estimates of alien grass seed rain on log landings are conservative insofar as they only include seeds that fell from logging trucks.

To estimate the production of seeds readily available to passing vehicles, I counted the seeds of *U. maxima*, the most invasive grass in INPA, along 200 m of road abandoned 1 yr prior to my study. The compact soil of the road, lack of traffic, and scarce rain during the period of seed production (early dry season) made it possible to collect fallen seeds from the surface of the roadbed as an estimate of total availability. I collected seeds from 12 – 50 x 50 cm plots in June

2008 (soon after seed shattering) and counted the number of full seeds, as described above. I used these data as an estimate of potential *U. maxima* seed rain onto grass-invaded roads.

Results

Conditions Required for Grass Establishment

In shade houses, mean initial (7 d) germination rates were equal among treatments, but were lower than in seed viability trials (33-38% and 48%, respectively). *Urochloa maxima* emergence (*i.e.*, germination and survival to 1 mo) was equal under high light (70% full sun; 38% survival) and moderate shade (10% full sun; 38% survival); few seedlings survived for 1 mo under deep shade (1% full sun; 3% survival) and none survived without light (Figure 3-1a). Although emergence did not differ between 70 and 10% full sun, the seedlings in high light were nearly four times larger than those grown in moderate shade (19 and 5 mg/plant, respectively); the few seedlings that survived 1 mo in 1% full sun appeared moribund and weighed only 0.5 mg/plant (Figure 3-1b). Although not as large as those grown in 70% full sun, plants in 10% light were clearly maintaining positive carbon balances as evidenced by their growth and apparent vigor. The minimum biomass measured for any of the 12 flats under moderate shade was 3 mg/individual. In the *in situ* studies that follow, I used this value (3 mg/plant) as a cut-off to separate suitable establishment sites from plots with plants that are so small that they are unlikely to survive.

In the seed addition experiment, canopy openness values for plots located in closed canopy forest (n = 20) and felling gaps (n = 20) were 8 ± 2% and 61 ± 13% (mean ± 1SD), respectively. Overall, *Urochloa maxima* emergence was low; only 1.8% of all seeds sown survived for 1 mo. The individuals that did survive were overwhelmingly those sown in closed canopy forest plots on scarified soil (10.5 seedlings/0.2 m^2 of 200 sown; Figure 3-2a); but despite the between treatment differences in numbers of seedlings, total grass biomass did not differ

(Figure 3-2b). This result was partly because of high variability in total grass biomass values for felling gaps (i.e., many plots with no emergence), but was primarily due to the huge discrepancy in plant sizes between gaps and forests; seedlings in gaps were eight times larger than plants growing in the shaded understory (Figure 3-2c). In felling gaps, 35% of untreated soil plots and 20% of scarified plots had plants > 3 mg/individual; in contrast only 5% of scarified plots and none of untreated soil in the forest had a per plant biomass that indicated the site was suitable for grass establishment (Figure 3-2d).

Seed Dispersal by Logging Vehicles

Log trucks were estimated to have dispersed 1800 alien grass seeds per log landing in the early dry season (Table 3-1). The majority of seeds came from flatbed cleaning (1750 seeds/log landing). The seed rain during log loading was more modest: 5 seeds per truck visit or 50 seeds/landing. Automobiles carried alien grass seeds attached to tires and wheel wells (50 seeds/vehicle) and on interior floor mats (90 seeds/vehicle; Table 3-1).

Alien grass seeds collected from vehicles on log landings included three species known to colonize selectively logged forest (*U. maxima*, *U. brizantha*, and *Sorghum halapenses;* Veldman et al. 2009), and another exotic grass, *Rottboellia cochinchinensis,* not previously documented in INPA. The majority of seeds were *U. maxima* (97%) followed by *U. brizantha* (2%), *S. halepense* (1%), and *R. cochinchinensis* (0.2%). Both *U. maxima* and *U. brizantha* are highly productive African grasses planted as forage throughout the Neotropics (Parsons 1972). *Sorghum halepense* and *R. cochinchinensis* are large (2-3 m tall) pantropical weeds that are common along roadsides in Chiquitania, particularly on wet sites. The number of *U. maxima* seeds collected from the surface of a grass-invaded road was estimated as 1270 seeds/m^2, equivalent to ~8000 seeds/m of road.

Discussion

Although logging opens forest canopies and disturbs soil – factors generally thought to influence the success of grass invasions (e.g., Setterfield et al. 2005) – it appears that canopy openness is more important to establishment of *U. maxima* in this forest. Soil disturbance increased grass emergence in closed canopy forest, but in felling gaps (i.e., open canopy, high light conditions) there was no effect of soil scarification on survival of sown grass seeds. *Urochloa maxima* seeds probably contain sufficient energy reserves to grow through leaf litter but can only then survive where there is sufficient light. The growth and survival of plants grown in shade houses under 10% full sun nonetheless demonstrates that this C_4 pasture grass is more shade tolerant than might be expected, and suggests that areas of logged forest with even intermediate levels of canopy and soil disturbance (i.e., skid trails) are suitable recruitment sites.

In the months following disturbance by selective logging, the forest contains more potential than realized recruitment sites for alien grasses. The seed addition experiment showed that felling gaps are suitable sites for *U. maxima* establishment. Given that alien grasses were not found in felling gaps (~10% of the area of selectively logged forest) but were common in the 1% of logged forest occupied by roads and log landings (Veldman et al. 2009), I conclude that few seeds ever arrive in felling gaps. It is also unlikely that seeds are regularly dispersed into unlogged stands, but even if they were, low light availability and lack of disturbed soil would preclude their establishment. This contention is consistent with the assertion by Fine (2002) that undisturbed tropical forests are perceived as resistant to invasion because many introduced species, like the grass in this study, are light demanding.

Seed transport by trucks appears to be the primary method of grass seed dispersal into this selectively logged forest. In the early dry season, during the peak of grass seed production and the commencement of timber extraction activities, log trucks dispersed large quantities of

alien grass seeds long-distances into what was old-growth tropical forest. Sixty-nine percent of log landings in this forest contain alien grasses (Veldman et al. 2009); I provide at least circumstantial evidence that these populations were largely established from seeds dispersed by trucks. I also found grass seeds on the tires and in the wheel wells of passengers vehicles, a well documented phenomenon (Clifford 1959), but did not estimate the number of seeds they actually deposited on log landings. The seeds collected from logging vehicles almost certainly originated from roadsides between the sawmill and the log landings; given ~8000 seeds/ m produced along an estimated 4 km of exotic grass-invaded roadside, some 30 million alien grass seeds were available to vehicles traveling into the forest. In general, motor-vehicle dispersal helps explain why alien grasses are limited to roads and log landings when many other appropriate establishment sites are opened by selective logging.

The mechanism of seed attachment to motor vehicles for the grasses encountered in this study appears to be different than is commonly proposed for other vehicle-dispersed roadside floras. Other studies have emphasized the importance of precipitation and mud for attaching seeds to passing motor vehicles (Zwaenepoel et al. 2006), but in this forest seeds were transported and dispersed in the absence of precipitation and were primarily carried on or in vehicles as opposed to being stuck in attached mud. Fertile culms of *U. maxima*, *U. brizantha*, *S. halepense*, and *R. cochinchinensis* grow 1-3 m tall with inflorescences that hang over roadways. When vehicles pass with the windows open, seeds fall into the passenger compartments; when people exit automobiles they presumably carry some of these seeds with them (Wichmann et al. 2009). The flatbed trailers of trucks are ~1.5 m tall, an ideal height to collect grass seeds that get lodged amongst bark fragments from logs from previous trips. Indeed, the vast majority of seeds delivered to log landings in this study were swept from the beds of log trucks.

Alien grass invasions in forests are worrisome for various reasons including their effects on forest flammability (D'Antonio & Vitousek 1992) and because their vigorous growth during the rainy season (when logging operations cease) makes transit of primary logging roads difficult. Clearing the roads using bulldozers has become both a nuisance and cost for forest managers (D. Velasquez, *pers. comm.*). Fortunately, simple measures could be taken during periods of grass seed production (late rainy and early dry season) to substantially reduce seed dispersal by logging activities in this forest. Truck beds should be swept off at the saw mill after delivery of timber from the forest and once again before entering the property to remove accumulated seeds. Seed transport by automobiles could be minimized if both the interior and exterior of vehicles were regularly cleaned to remove accumulated seeds. Although not included in this study, I expect that heavy equipment (i.e., bulldozers and graders) also move invasive plant propagules. Forest managers should time road maintenance activities so that grass-invaded areas are avoided during periods of seed production. When this is not feasible, clearing of roadways using machetes or mowers such that grass seeds fall to the ground at the site of seed production would limit the number of seeds that could fall onto truck beds or accumulate in the passenger compartments of automobiles.

This study links vehicle dispersal of invasive species to an active invasion process in a remote area of tropical forest. The sampling design used guaranteed that collected seeds traveled at least 500 m, but given that new roads that extend up to 5 km into previously unlogged forest support populations of alien grasses and that alien grasses occur at the farthest points of the property (30 km from the entrance), it is clear that grass seeds are commonly transported much farther from parent populations. In light of my results, and the previously demonstrated potential of motor vehicles to drive biological invasions (von der Lippe and Kowarik 2007), biologists and

ecosystem managers should be aware that human movements can unintentionally disperse seeds even in areas intended for native ecosystem conservation through natural forest management.

Table 3-1. Alien grass seeds collected from motor vehicles arriving at log landings during selective logging of a seasonally dry Bolivian forest (mean ± 1 SD).

				Alien grass seed rain	
Vehicle class	Source	*n*	Seeds/Sample	Seeds/Log deck	Seeds/m^2
log trucks	log loading	8	5 ± 6	50	0.1
	flatbed cleaning	5	350 ± 140	1750	2.4
automobiles	tires/wheel wells	3	50 ± 80	-	-
	interior floor mats	3	90 ± 50	-	-
			Total	1800	2.5

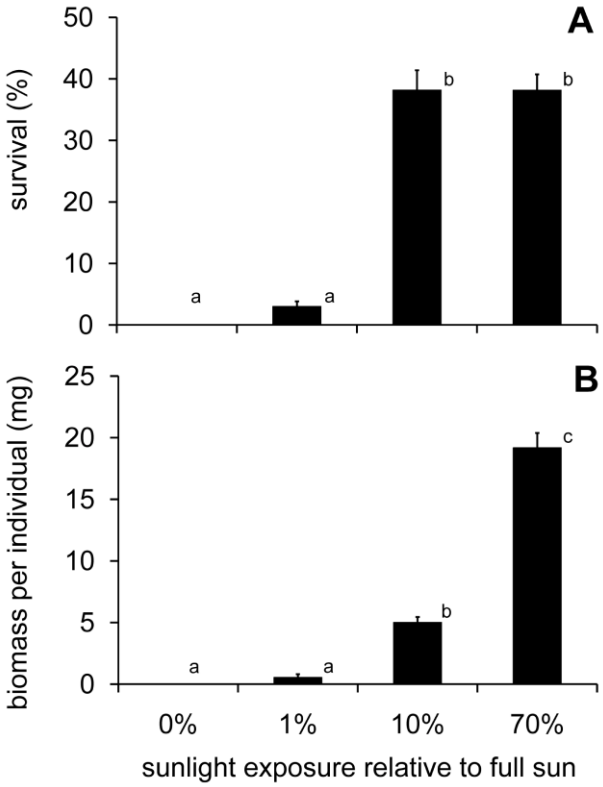

Figure 3-1. Survival and total biomass at 1 mo of *Urochloa maxima* seedlings emerging from 50 seeds sown and grown under 0, 1, 10 or 70% sunlight for 1 mo. (mean+1SE; letters indicate differences between light treatments at $p < 0.05$, ANOVA, post hoc Tukey, $n = 12$). (A) Number of seedlings surviving 1 mo as a proportion of the number of seeds planted. (B) Average biomass per seedling for live plants at the end of 1 mo.

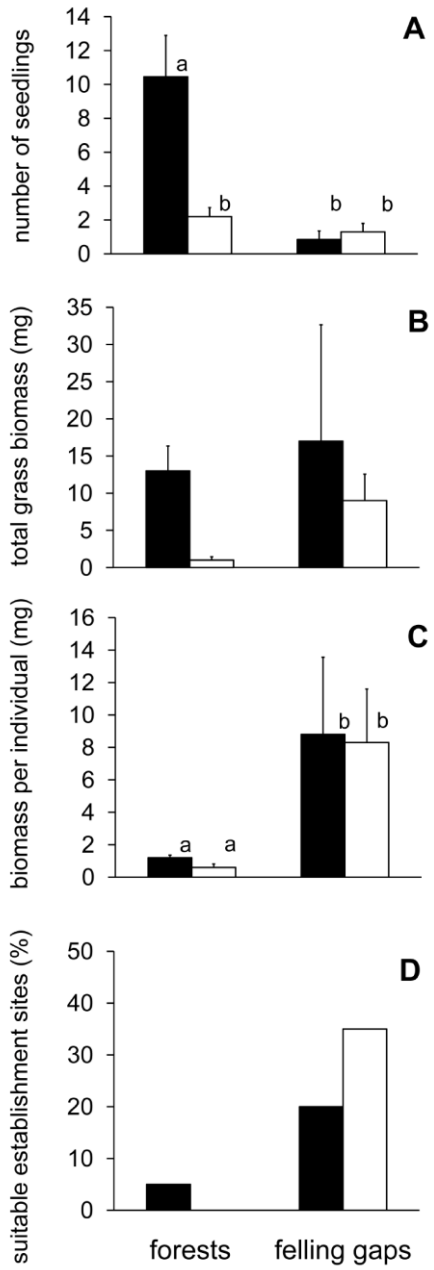

Figure 3-2. Emergence of *Urochloa maxima* seedlings (mean+1SE) 1 mo after planting 200 seeds in 0.2 m^2 plots in a 2 x 2 factorial design combining two habitat treatments (unlogged forests and felling gaps) and two soil treatments (scarified soil and untreated soil; bar colors: black = scarified soil; white = untreated soil). (A) Number of seedlings per 0.2 m^2 plot; there were significant effects of soil treatment, habitat type and an interaction between factors; letters indicate differences between treatments at $p < 0.05$ (two-way ANOVA, *post hoc* Tukey, $n = 20$ treatment blocks). (B) Total grass biomass per 0.2 m^2 plot; no differences. (C) Biomass per individual for plots with live plants; effect of habitat type only ($n = 17, 15, 6, 9$; plots with no plants were excluded). (D) Proportion of plots suitable for *U. maxima* establishment defined as plots with a biomass per individual ≥ 3 mg ($X^2 = 10.0$, $df = 3$, $p < 0.02$).

CHAPTER 4
GUADUA PANICULATA (BAMBUSOIDEAE) IN THE BOLIVIAN CHIQUITANIA: FIRE ECOLOGY AND A POTENTIAL NATIVE FORAGE GRASS[3]

Guadua paniculata Munro is a fire-adapted bamboo that dominates large areas of the Chiquitano dry forest in eastern lowland Bolivia. In this study I present data from eight sites (bamboo stands with 35-100% *Guadua* cover) located across the Chiquitania region to 1) investigate the interaction between *Guadua*, fire, and trees; 2) describe the vegetation associated with *Guadua*; and, 3) estimate *Guadua* forage production and analyze its nutrient contents. *Guadua* stands supported both low densities of trees and low tree basal area (240 trees/ha, ≥ 5 cm DBH; 5.8 m^2/ha) presumably due to frequent intense fires that result from fuel loads produced by the bamboo. *Guadua* is able to produce up to 16 Mg/ha of fine and small biomass (< 25 mm; 8 ±4 Mg/ha, mean±1SD) that increases flammability and fire intensity. *Guadua* appears able to convert forests to bamboo stands by contributing to fire-induced tree mortality. As such, it will be important to include *Guadua* in studies of the conservation and management in this fire-susceptible region. On the positive side, *Guadua* leaves serve as cattle forage and bamboo stands produce up to 4.7 Mg/ha of high quality forage (10.5% protein content). Although more research is needed to determine how to make the forage produced available for animal production, *Guadua* could be utilized as a native forage species in a region that is experiencing high deforestation rates due to the cultivation of exotic pasture grasses.

[3] Reprinted with permission from: Veldman, J. W. 2008. *Guadua paniculata* (Bambusoideae) en la Chiquitania Boliviana: Ecología de fuego y la oportunidad para un forraje nativo. Revista Boliviana de Ecología y Conservación Ambiental **24**:65-74.

Introduction

Disturbance regimes in the Chiquitania of Bolivia are changing due to human activities that increase the frequency of forest fires, disturb forests during timber extraction, and replace forests with crops or planted forage grasses (Steininger et al. 2001). Forest fires kill trees, cause nutrient losses, and increase the risk of future fires (Laurance 2003). Timber extraction increases forest susceptibility to fires in large part due to the construction of logging roads that open the canopy and provide ignition sources (Nepstad et al. 1999). The expansion of cattle ranching does not simply represent deforestation but the substitution of a diversity of forest species by one or two exotic forage grasses; additionally, planted pastures are frequent sources of fires that spread into adjacent forests (Uhl & Buschbacher 1985; Martinez M. et al. 2003). Given the current increases in fire frequency, large areas of forest affected by logging, and high rates of deforestation for cattle production, it is important to know more about the plant species favored by these conditions and thus likely to increase in abundance in Chiquitania.

A native lowland Bolivian species that is well-adapted to disturbances, including fire, is the bamboo *Guadua paniculata* Munro, locally known as "guapa." In Chiquitania, *Guadua* has a widespread distribution and is estimated to dominate "thousands" of ha (Killeen 1990). *Guadua* can form large (up to 1000 ha) bamboo-dominated patches locally known as "guapasales" or small colonies (10-100 m^2) in forests. Although *Guadua* is a dominant species in many parts of the region (Jardim et al. 2003; Killeen et al. 1990), it has received little attention in previous studies of Chiquitano dry forest. Normally *Guadua* is described as being characteristic of woodlands or scrub (i.e., "cerradão" or mattoral; Killeen et al. 1990; Killeen & Hinz 1992a, respectively). The Bolivian vegetation map by Navarro and Ferrreira (2007) includes *Guadua* stands within "chaparral" and "secondary forest" classifications. The fact that *Guadua* is simply considered a component of these vegetation types, however they are labeled, ignores the

dynamic potential of bamboo to promote ecosystem flammability and fire intensity (e.g., Keeley & Bond 1999) that can contribute to forest tree mortality. Killeen et al. (1990) and Jardim et al. (2003) recognized that *Guadua* occurs in "forest-savanna transitions" (a more dynamic name) and Killeen et al. (1990) noted that *Guadua* stands frequently burn.

Guadua, like many bamboo species, resprouts readily after fires and can produce large quantities of highly flammable fine fuel (e.g., Gagnon & Platt 2008). The grass-fire cycle proposes that the interaction of grasses and fire represents a positive feedback that can transform an ecosystem originally dominated by trees to one dominated by grasses and characterized by frequent fires. Given its characteristics, *Guadua* seems likely to fit within this grass-fire framework. The broad objective of this study was to determine if the interaction of *Guadua* and fire deserves greater attention in our understanding of the ecology and conservation of Chiquitano dry forest.

Because of its traditional uses in house construction, *Guadua* is recognized as a non-timber forest product (Sandoval 2001), but is less well known as a forage for livestock. The palatability of *Guadua* to cattle was recognized by Killeen (1990) but cattle ranchers generally view *Guadua* as a weed (B. Colombara, pers. com.). Although some ranches and communities graze cattle in bamboo stands, clearing of *Guadua* to sow cultivars of *Urochloa* spp. (formerly *Brachiaria* spp. and *Panicum maximum*) is very common (J. Veldman, pers. obs.). Given that deforestation and the expansion of planted pasture grasses threaten Chiquitano dry forest, the second objective of this study was to provide basic information about the potential of *Guadua* as a native forage. Understanding the potential uses of this species is relevant given that its abundance in the region could increase due to anthropogenic forest disturbance and increased incidences of forest fires.

Methods

The ecosystems of Chiquitania, Boliva located on the southern border of the Amazon Basin, are as dynamic as they are diverse. For example, as recently as 3000 years ago areas that are currently forests were savannas (Mayle et al. 2000). The native savannas of the region "cerrados" cover much of Chiquitania and typically burn annually (Killeen and Hinz 1992a). Although the present mosaic of forests and savannas largely corresponds with soil characteristics, topography, and hydrology (Killeen et al. 1990), climate change in the long term (Hutyra et al. 2005) and changing disturbance regimes in the short term (i.e., fire, logging) are expected to alter vegetation distributions regionally (e.g., Nepstad et al. 2001; Nepstad et al. 2004).

To better understand the vegetation associated with a species that is well-adapted to fire and understudied in Chiquitania, I analyzed data from eight *Guadua* stands (minimum 25% bamboo cover) in the Provinces of Nũflo de Chaves and Velasco in the Department of Santa Cruz Bolivia (Table 4-1). The *Guadua* stands are part of a more extensive project studying the conversion of forest to savanna and that includes 29 sites across the Chiquitania (Chapter 1). These sites were selected at random from a satellite image analysis that identified areas that changed from forest to savanna (including *Guadua* stands) between 1986 and 2005. Six of the eight bamboo stands included in this study are recently derived (i.e., areas that were forest in 1986) and the other two were already established in 1986.

Field sampling took place during the late rainy season and early dry season (February – May 2008). Studies on the potential *Guadua* forage production and quality were conducted on the Estancia Cacarachi, a privately owned cattle ranch (694285 8185262; UTM WGS 84 Zone 20 S) located 22 km west of the town of San Ignacio de Velasco. *Guadua* stands at Estancia

Cacarachi were sampled during the first week of June 2008 following 9 months of leaf production after a fire in 2007.

Biophysical Characteristics of Bamboo Stands

To describe the vegetation associated with *Guadua* and investigate the relationship between *Guadua*, fire, and trees, I randomly positioned two to five 20 m transects in each bamboo stand (n = 8). Along each transect I measured: 1) percent cover by *Guadua* by noting its presence or absence at 41 points spaced every 0.5 m; 2) the height of *Guadua* where present; 3) *Guadua* biomass < 25 mm diameter in three clip plots of 1m^2 (3 m^2/transect; all culms rooted in the plot were harvested); 4) biomass of *Guadua* litter in three subplots of 50 x 50 cm (0.75 m^2/transect), separating *Guadua* litter from litter from other sources. Samples were weighed in the field and subsamples were collected and dried for 48 hr at 65°C to correct for moisture content. Within 4 m of the same transects (20 x 8 m), I identified all trees >5 cm, and measured their diameter at breast height (DBH) and height. At the center and endpoints of each transect I measured tree canopy density using a spherical densitometer held at 1.3 m (Lemmon 1956). Canopy density measurements do not include *Guadua*. As an indication of the intensity of past fires, I measured the maximum char height on the trunk of each tree (Fry 2008). To estimate grazing pressure, I counted the number of cattle trails that crossed extensions of each transect (number of trails per 40 m; Lange 1969; Pringle & Landsberg 2004).

Forage Production and Nutrient Content

Total aboveground biomass of *Guadua* cannot be converted directly into an estimate of forage production because cattle only consume the leaf blades, leaf-sheaths, and the smallest branches enclosed by the sheaths. In a *Guadua* stand in Estancia Cacarachi, I randomly located four 20 m transects following the methods described above to estimate the total standing biomass of *Guadua*. I then separated and weighed all of the material suitable as forage. I dried

subsamples to correct for moisture content and then related total standing biomass (< 25 mm diameter) to potential forage production using linear regression. Forage samples were analyzed for protein, phosphorous, and calcium content at the laboratory of CIAT (Centro de Investigación Agrícola Tropical) in Santa Cruz. Protein and phosphorous content of laminas collected in eight other *Guadua* stands (Table 4-1) were also analyzed.

Data and Analysis

Measurements from each transect were averaged to obtain a single value for each of the eight sites; the values I report are the mean ± 1 SD for $n = 8$ bamboo stands. Regression analyses to relate tree, *Guadua*, fire data, and forage production were performed in SPSS 12.0 (SPSS Inc. Chicago, Illinois). Data not normally distributed were log transformed prior to analysis.

Results and Discussion

***Guadua* and Fire**

Guadua stands in Chiquitania are characterized by frequent fires, low tree density, and open tree canopies (Table 4-2). The sites in this study had 35-100% cover of *Guadua*, which formed a canopy 2.6 m tall (mean) with maximum bamboo canopy heights of 3-7 m (Table 4-2). All bamboo stands had burned within the previous two years and supported large bamboo fuel loads (8±4 Mg/ha; Table 4-2). The low tree densities associated with *Guadua* are probably due to a combination of high tree mortality and limited tree regeneration caused by frequent fires.

Guadua is light-demanding and its abundance (i.e., % cover) appears to depend on tree canopy openness. *Guadua* abundance decreased as tree canopy cover increased (Figure 4-1). Based solely on these observational data, *Guadua* may simply grow in sites that cannot support tall forest trees and lack closed tree canopies (e.g., Killeen et. al 1990). Likewise, one could conclude that *Guadua* is a species typical of secondary forests, growing where humans have

disturbed the forest canopy (e.g., Navarro and Ferriera 2007). Although soil fertility and canopy openess certainly influence the abundance and distributions of *Guadua*, a notion of *Guadua* as merely growing were there are few trees, ignores the possibility that *Guadua* is an active modifier of the ecosystems were it occurs.

In the Chiquitania, *Guadua* can increase its own access to light by increasing forest flammability and the intensity of fires that kill competing trees. Bamboo fuel loads measured in *Guadua* stands were negatively correlated to both tree density and tree basal area (Figure 4-2ab). In these same sites char heights on tree trunks were also negatively correlated with tree density (Figure 4-2c), suggesting that the intensity of past fires influenced the number of trees present. *Guadua* stands had lower tree density (240±180 trees/ha) and lower basal area (5.8±4.0 m^2/ha) compared to forests in the region where *Guadua* is absent [e.g., 914 trees/ha with basal area of 27.6 m^2/ha in Lomerio (Killeen et al. 1998); and 427 trees/ha with basal area of 21 m^2/ha in INPA near Concepción (Villegas et al. 2009)].

The trees that co-occurred with *Guadua* included both species typical of forests as well and species typical of savannas. In total I recorded 43 species of which seven accounted for 50% of the stems measured. These common species include trees typical of savanna environments: *Magonia pubescens* A. St.-Hil. (Sapindaceae; 15%), *Luehea paniculata* Mart. (Malvaceae, Tilioidae; 10%), *Phyllostylon rhamnoides* (J. Pois.) Taub. (Ulmaceae; 6%); as well as typical forest species: *Combretum leprosum* Mart. (Combretaceae; 6%), *Anadenanthera culubrina* (Vell.) Brenan (Fabaceae; 5%), *Aspidosperma rigidum* Rusby (Apocynaceae; 4%), and *Eriotheca roseorum* (Cuatrec.) A. Robyns (Malvaceae, Bombacoidae; 4%). Of these common trees, *Anadenanthera* and *Phyllostylon* are the only timber species. Other timber species (and their relative abundances) were the savanna species *Tabebuia roseo-alba* (Ridl.) Sandwith

(Bignoniaceae; 2.1%), and forest species *Caesalpinia pluviosa* DC (Fabaceae; 1.9%), *Astronium urundeuva* (Allemão) Engl. (Anacardiaceae; 1.6%), *Aspidosperma tomentosum* Mart. (Apocynaceae; 1.4%), *Aspidosperma cylindrocarpon* Müll. Arg. (Apocynaceae; 0.9%) y *Tabebuia serratifolia* (Vahl) G. Nicholson (Bignoniaceae; 0.5%). Disproportionate to their relative abundance, forest species *Anadenanthera* and *Astronium*, accounted for 15% and 13% of dead standing trunks, respectively. A possible explanation is that frequent fires are favoring savanna species better adapted to tolerate fires (e.g., *Magonia*) while contributing to the low densities of forest species (Hoffmann et al. 2009; Pinard & Huffman 1997). In the two old *Guadua* stands only 20% of trees were forest species (80% were savanna species), whereas trees in the six newly formed bamboo stands 53% of trees were forest species (47% savanna species).

The coincidence of *Guadua* and fire argues that more attention be given to this species by efforts to conserve and manage the Chiquitano dry forest. Underscoring the potential implications of *Guadua* proliferation for forests of the region, I found a clear relationship between signs of high fire intensity and large bamboo fuel loads in areas with low tree densities. Additionally, six of the eight *Guadua* stands were forests 22 years prior to this study, indicating that the interaction between *Guadua* and fire has almost certainly favored the expansion of bamboo at the expense of forest tree species.

To advance a dynamic notion of the interactions between *Guadua*, fires, and trees I propose two diagrams (Figure 4-3a,b) to conceptualize the interaction between *Guadua* and fire, and to elucidate factors that determine the abundance of *Guadua* and trees in the Chiquitania. *Guadua* is not the only bamboo that benefits from a self-catalyzed disturbance cycle to form bamboo-dominate stands within tropical forests. In Peru, for example, *Guadua weberaueri* and

Guadua sarcocarpa climb and pull down trees and proliferate in the high light environments of the tree fall gaps it helps create (Griscom & Ashton 2006).

Studies of the Chiquitano dry forest have primarily focused on areas containing high densities of timber species and very little *Guadua* (Fredericksen et al. 2000; Killeen et al. 2005; Killeen et al. 1998). As a consequence, the implications of *Guadua* for sustainable forest management has yet to be explored (but see Rockwell et al. 2007 for studies on *G. weberaueri* and *G. sarcocarpa*). *Guadua* is often abundant along roadsides and in forest gaps created by logging activities (Veldman et al. 2008), but without studies that include pre- and post-logging data, or that are conducted in forests with larger *Guadua* populations, it is difficult to know the degree to which logging increases bamboo abundance. In a scenario in which *Guadua* proliferates following logging and then further expands due to subsequent bamboo-fueled fires (Figure 4-3a), the consequences for sustainable timber management could be catastrophic. I argue that more areas that contain *Guadua* should be studied in Chiquitania and that *Guadua* be included in forest monitoring projects.

Guadua as a Native Forage

Although *Guadua* is associated with fire and forest degradation, it has a high potential to serve as cattle forage in Chiquitania given its productivity and nutrient contents (Table 4-3; Table 4-4). The production of bamboo forage measured in this study is comparable to exotic forage grasses in the genus *Urochloa* (formerly *Brachiaria brizantha*, *B. decumbens*, and *Panicum maximum*), and can even exceed production by *U. brizantha*, the most commonly planted forage grass in Chiquitania (Table 4-3). Impressively, the *Guadua* harvested in the Estancia Cacarachi yielded 4.7±3.3 Mg/ha of forage (Table 4-3). Based on the equation that relates total *Guadua* biomass to available forage (Figure 4-4), I calculated that the other eight

Guadua stands in this study (Table 4-1) produced less than Cacarachi but were nonetheless very productive (1.5±1.3 Mg/ha, range 0.3-4.1 Mg/ha; Table 4-2; Table 4-3).

In addition to productivity, nutrient content (i.e., protein and minerals) is an important aspect of forage value for livestock. The material harvested at Estancia Cacarachi had protein contents sufficient to meet cattle nutritional requirements (Table 4-4). The 10.5% protein measured in the *Guadua* forage is much higher than the values of 6.0 to 7.5% reported for *U. brizantha* and *U. decumbens* in other parts of the Department of Santa Cruz (Joaquin & Herrero 2003). Considering leaf laminas alone, protein content was even higher (13.2%; Table 4-4). The *Guadua* forage collected also contained high concentrations of phosphorous and calcium, minerals critical for animal nutrition (Table 4-4).

The objective of presenting data on the production and nutritive quality of *Guadua* is to suggest the possibility that this native grass be integrated with other forages for cattle production. That said there are some limitations of *Guadua* that need to be overcome. To promote *Guadua* without any sort of management would result in bamboo stands with canopies exceeding 2 m tall and the majority of leaves out of reach of animals. Additionally, high culm densities can limit access to grazing cattle and make it difficult for humans to enter *Guadua* stands. Another important consideration is that some populations produce spines on the culms.

If *Guadua* were to grow in a manner that made all of its leaves accessible to cattle, this grass would likely be the preferred forage species in Chiquitania. However promising, the potential of *Guadua* as a native forage will remain unrealized until we determine how to manage its growth. Some possible management methods include: 1) planting and harvest of *Guadua* as a cut (not grazed) forage; 2) opening trails into bamboo stands to facilitate cattle access; 3) pruning of *Guadua* culms in order to maintain them at a height accessible to cattle.

Unfortunately, base on this study alone, we cannot know if the high forage production estimated for *Guadua* can be maintained under management. More research is clearly needed to determine how to manage and utilize this species that will likely become more and more abundant in Chiquitania if the frequency of forest fires remains high. Given its nutritive qualities and high productivity it seems an obvious focus for further study. As evidence that *Guadua* really is palatable to livestock, one night during field sampling I found a horse with its head in the bed of my pick-up truck; it had eaten 2 kg of *Guadua* collected the previous day.

Table 4-1. Locations and number of transects for eight sites used to study *Guadua* in Chiquitania, Bolivia (organized west to east). The coordinates and elevations are average values obtained with a GPS at the center of each transect. Based on a satellite image change analysis (1986-2005, Chapter 1), New indicates newly formed *Guadua* stands in areas that were forest in 1986, and Old are those bamboo stands that were already established in 1986. Coordinates are UTM WGS 84 Zone 20 S.

Age	Zone or nearest town	Province	Coordinates		Elevation (m)	Number of Transects
New	San Ramón	Nũflo de Chaves	553792	8183011	375	3
New	Lomerio	Nũflo de Chaves	622004	8158285	417	3
New	Concepción	Nũflo de Chaves	631775	8244874	412	4
New	San Ignacio	Velasco	687416	8187409	452	5
Old	San Ignacio	Velasco	696168	8184592	449	5
New	Carmen de Ruiz	Velasco	715546	8249468	281	2
New	San Ignacio	Velasco	716102	8209649	410	2
Old	Paragua	Velasco	725938	8264433	222	2

Table 4-2. Biophysical variables measured in *Guadua* stands in Chiquitania (*n* = 8).

	Mean ±1SD	Range (min-max)
Guadua		
cover (%)	67 ± 21	35 – 100
mean height (m)	2.6 ± 0.7	1.3 – 3.5
máximum height (m)	5.0 ± 1.5	3.0 – 7.0
standing biomass (Mg/ha)	6.5 ± 3.7	1.8 – 14
bamboo litter (Mg/ha)	1.5 ± 1.0	0.2 – 2.6
potencial forrage (Mg/ha)	1.5 ± 1.3	0.3 – 4.1
fine fuel (Mg/ha)	8.0 ± 4.1	2.0 – 16
Trees		
canopy cover (%)	30 ± 22	9 – 63
mean canopy height (m)	4.2 ± 3.6	0 – 11
máximum canopy height (m)	14 ± 8	0 – 25
density(trees/ha)	240 ± 180	25 – 530
basal area (m2/ha)	5.8 ± 4.0	0 – 12
Fire		
char height (m)	2.2 ± 1.8	0.6 – 5.2
time since fire (años)	1.2 ± 0.4	1 – 2
Grazing		
cattle crossings (trails/40 m)	0.8 ± 1.0	0 – 2.6

Table 4-3. Comparison of forage (leaf) production and total biomass of *Guadua paniculata* and cultivated forage grasses in the genus *Urochloa* (including the former *Brachiaria brizantha, B. decumbens,* and *Panicum maxima)*.

Species	Forage (Mg/ha)	Total biomass (Mg/ha)	Measurement	Management	Site(s)	Source
Guadua	4,7	17,1	available	no grazing, 9 mo since fire	Estancia Cacarachi	This study
Guadua	1,5[a]	6,5	available	various	Chiquitania Table 4-1	This study
U. brizantha	1,3[b]	5,4	available	no grazing, 3 yr since fire	San Ignacio de Velasco	J. Veldman, unpublished data
U. decumbens	1,1	6,6	Production 12 mo	cattle grazing	Area Integrada de Santa Cruz	Joaquin y Herrero (2003)
U. maxima	5,2[b]	15,0	Production 12 mo	cattle grazing + fertilizer	Ribeirão Preto, Brazil	Silveira et al. (2005)

[a] calculated with equation in Figure 4-4
[b] calculated from data in Rivero (1999; cited by Joaquin & Herrero 2003) to relate total dry weight to the weight of leaves.

Table 4-4. Concentration of protein, phosporous (P), and calcium (Ca) in forage of *Guadua paniculata* harvested at Estancia Cacarachi, 23 km east of San Ignacio de Velasco, Santa Cruz Bolivia (column 1). As a reference, minimum values (critical levels) and recomended levels for cattle are also included.

	Forage (lamina + sheath)	Lamina only[a]	Critical level[b]	Recommended level[c]	*Guadua* quality
Protein (%)	10,5	13,2	< 7%	11,2	good
P (%)	0,15	0,15	< 17 ppm	0,22	good
Ca (%)	0,2	-	< 72 ppm	0,22 - 0,35	good

[a] mean for leaves collected in eight *Guadua* stands (Table 4-1)
[b] McDowell & Conrad (1977) cited by Velásquez-Pereira et al. (1997)
[c] Minson *et al*. (1976)

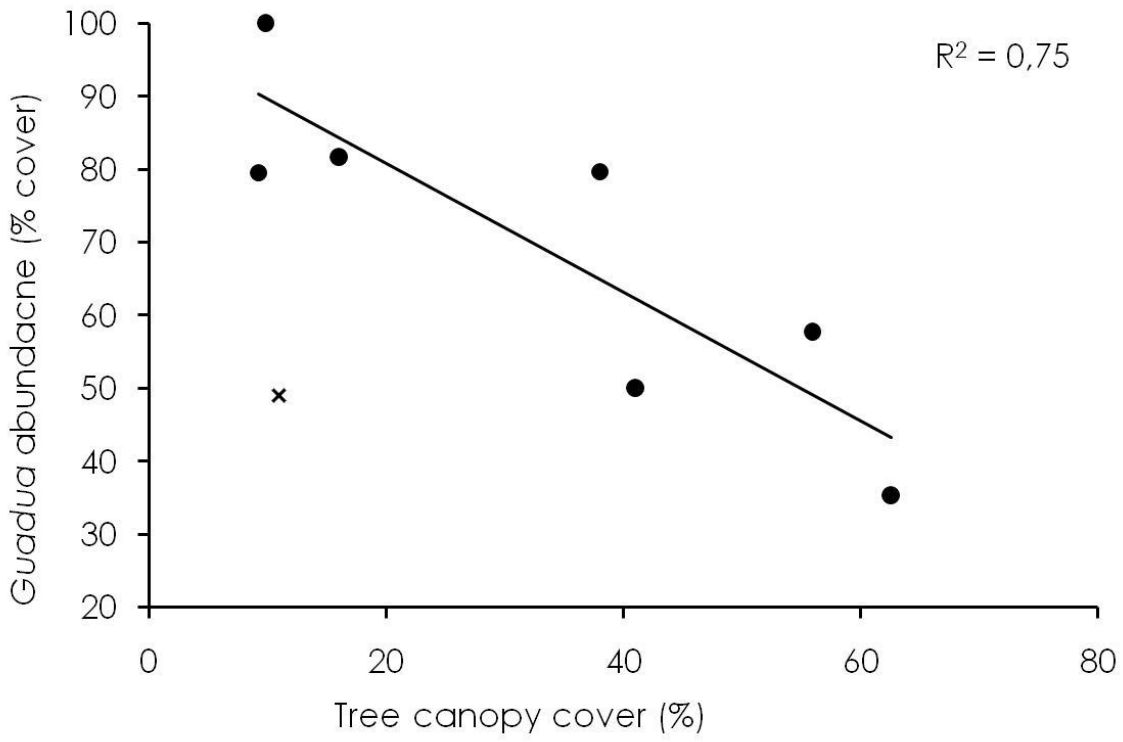

Figure 4-1. Relationship between *Guadua* abundance and tree canopy cover; *Guadua* cover (%) = -0.88 [tree canopy cover] + 98.4; p = 0.011. The site marked by × was excluded from the analysis because it was more heavily grazed than the other sites (2.6 cattle trails/40 m). If this outlier is included, the analysis still has a negative relationship (R^2 = 0,44; p = 0.071).

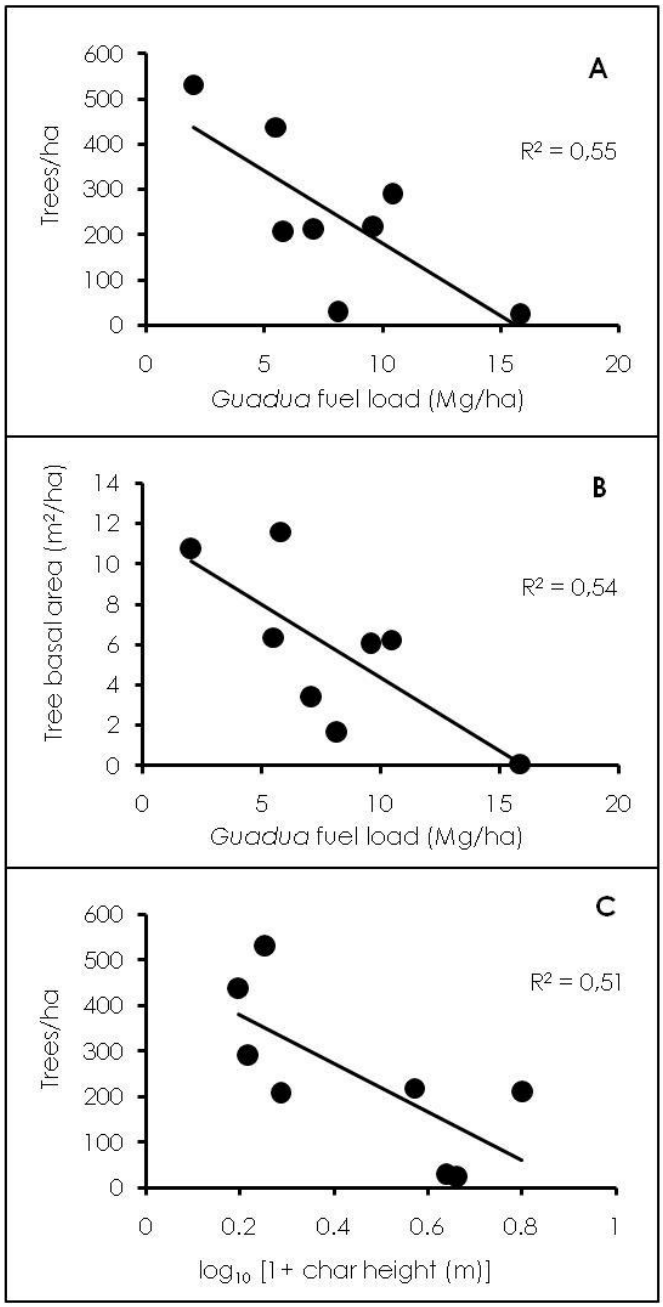

Figure 4-2. Relationships between trees, bamboo fuel loads, and fire intensities, that suggest the combination of *Guadua* and fire influences tree abundance in the Chiquitano dry forest. A) Relationship between *Guadua* fuel loads (dry mass < 25 mm diameter) and tree density (>5 cm DBH; trees = -32[biomass *Guada*] +502; p = 0.035). B) Relationship between *Guadua* fuel loads and tree basal area (basal area = -0.727 [biomass *Guadua*] +11.6; p = 0.037). C) Relationship between average char heights on tree trunks and tree density (trees/ha = -528 log10[1+char height] +484; p = 0.046).

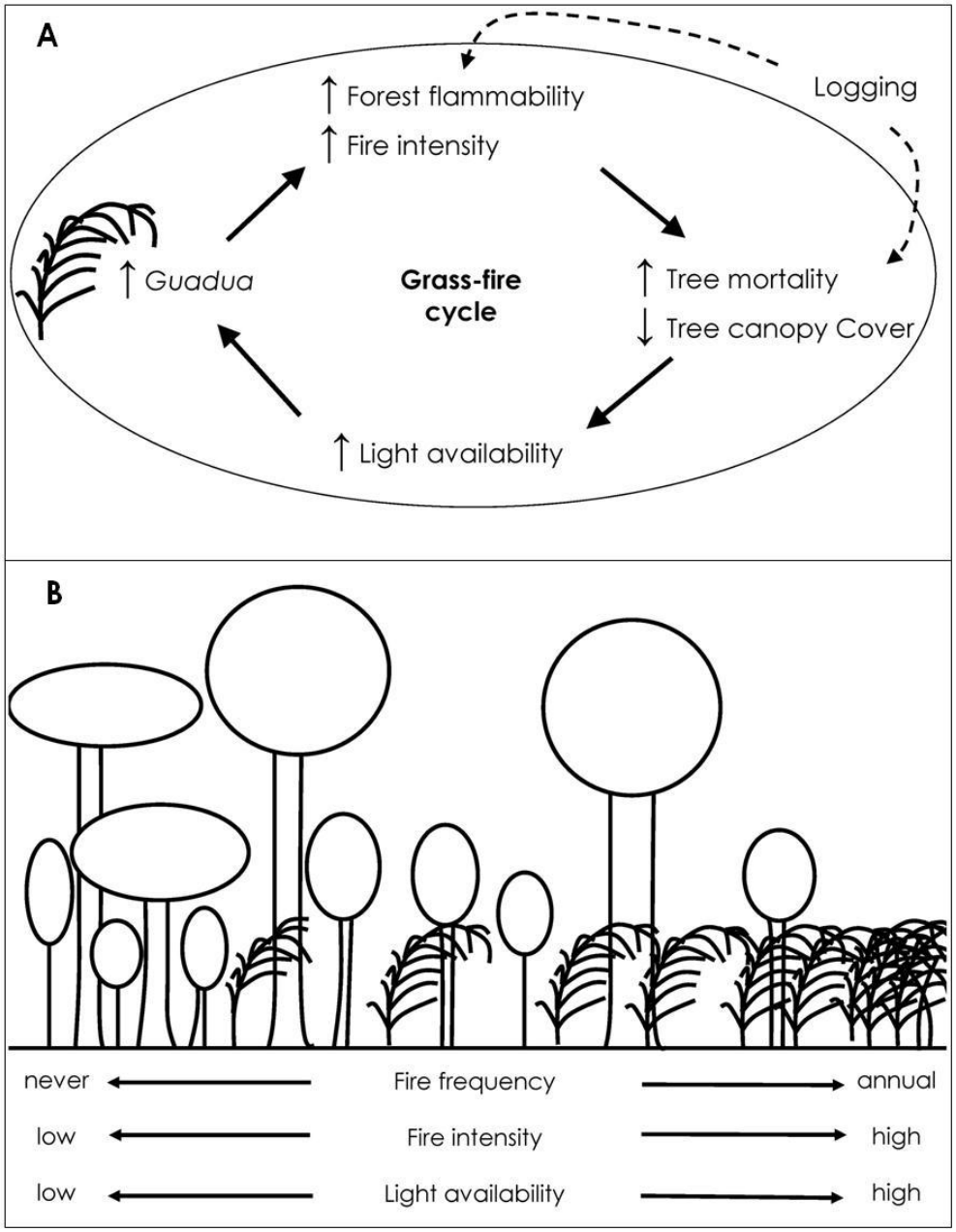

Figure 4-3. Diagrams that incorporate fire to explain abundances of *Guadua* and trees in the Chiquitano dry forest. A) Model of the grass-fire cycle in which a grass such as *Guadua* is part of a self-catalyzing cycle that increases flammability and replaces forest with grass-dominated ecosystems characterized by frequent fires (based on D'Antonio & Vitousek 1992, Keeley & Bond 1999). Logging and other disturbances (e.g., wind, Gagnon & Platt 2008) can interact with the cycle and contribute to the proliferation of *Guadua*. B) Diagram of trees and *Guadua* along a gradient of fire and tree canopy openness.

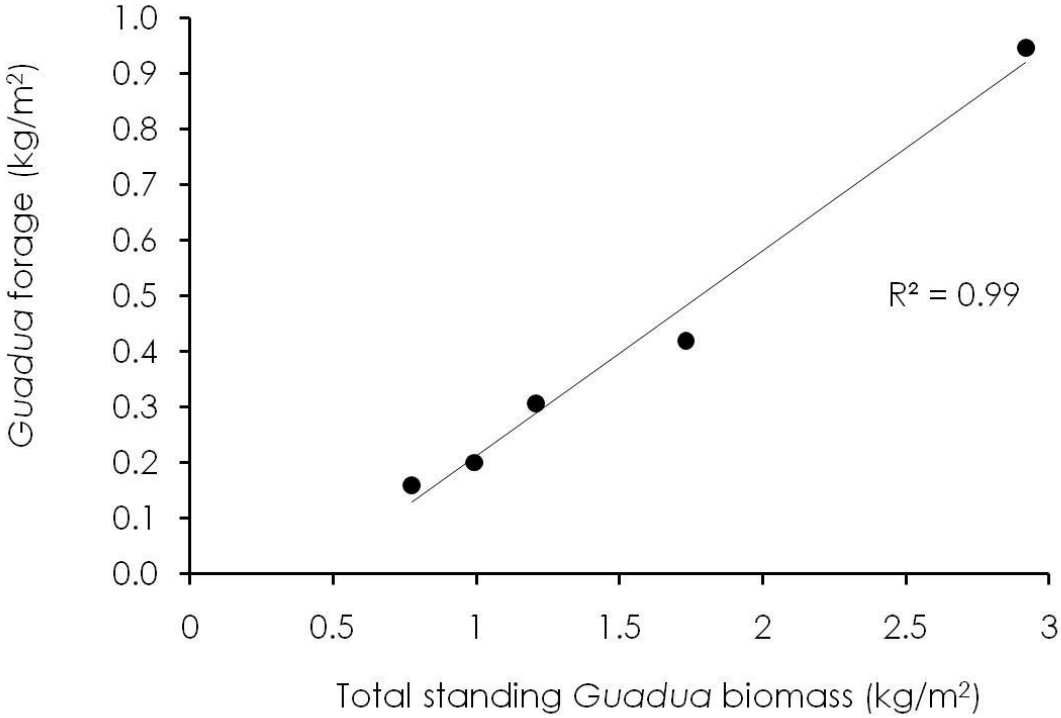

Figure 4-4. Relationship between the total standing biomass of *Guadua* and the mass of leaves suitable as cattle forage. Each point represents a transect where harvested and measured the total biomass of *Guadua* in three 1 m^2 clip plots as well as the weight of the leaves and leaf sheaths. Dry forage = 0.369 [total *Guadua* biomass] – 0.157.

APPENDIX A
GRASS SPECIES IN NATIVE AND DERIVED SAVANNAS

Table A-1. Frequency, mean cover and maximum cover for grass species in native (n = 12) and derived (n = 17) savannas. Species are listed in increasing value on DCA-1. Exotic species are indicated with an asterisk.

	Native			Derived				
Species[a]	frequency (%)	mean cover (%)	maximum cover (%)	frequency (%)	mean cover (%)	maximum cover (%)	DCA-1	DCA-2
Aristida riparia	17	0.19	1.9	-	-	-	-4.11	0.07
Leptocoryphium lanatum	17	1.26	9.8	-	-	-	-3.93	0.11
Sorghastrum minarum	25	0.24	2.0	-	-	-	-3.81	0.12
Thrasya petrosa	67	2.21	13.7	-	-	-	-3.76	0.14
Schizachyrium sanguineum	42	1.33	6.1	-	-	-	-3.74	0.02
Aristida sp.	17	0.06	0.5	-	-	-	-3.65	0.11
Axonopus fissifolius	17	0.07	0.7	-	-	-	-3.47	0.07
Axonopus marginatus	17	2.20	13.7	-	-	-	-3.46	0.39
Schizachyrium scabriflorum	25	0.20	1.0	-	-	-	-3.33	0.17
Loudetia flammida	25	0.75	7.8	-	-	-	-3.29	0.22
Eragrostis articulata	-	-	-	6	0.03	0.5	-3.27	-0.14
Trachypogon	67	4.67	20.7	-	-	-	-3.24	0.13
Gymnopogon spicatus	33	0.29	2.2	-	-	-	-3.18	-0.08
Panicum quadriglume	25	0.13	0.9	-	-	-	-2.99	0.40
Axonopus chrysoblepharis	42	0.42	2.6	6	0.01	0.2	-2.82	0.13
Elionurus muticus	75	11.48	26.3	-	-	-	-2.74	0.25
Axonopus barbigerus	67	1.24	5.9	6	0.06	1.0	-2.55	0.25
Schizachyrium microstachyum	50	0.62	2.4	6	0.01	0.2	-2.35	0.27
Paspalum erianthum	58	0.96	3.9	-	-	-	-2.28	0.26
Paspalum stellatum	58	1.82	9.8	6	0.09	1.5	-2.04	-0.06
Andropogon leucostachyus	25	0.24	2.0	-	-	-	-1.90	-0.02
Ichnathus procurrens	50	0.53	1.7	-	-	-	-1.68	0.05
**Hyparrhenia rufa*	67	2.04	11.7	18	0.60	8.5	-1.47	0.23
Andropogon selloanus	42	0.29	1.2	6	0.06	1.0	-1.29	0.45
Tripsacum australe	8	0.04	0.5	6	0.17	2.9	-1.19	0.65
Paspalum plicatulum	75	0.68	3.4	18	0.27	3.4	-1.18	0.17

Table A-1. Continued

Species[a]	Native frequency (%)	Native mean cover (%)	Native maximum cover (%)	Derived frequency (%)	Derived mean cover (%)	Derived maximum cover (%)	DCA-1	DCA-2
Digitaria dioica	42	0.52	3.4	-	-	-	-1.17	0.63
Setaria parviflora	33	0.16	1.0	12	0.06	0.5	-0.80	0.39
Olyra spp.	-	-	-	18	0.33	3.8	-0.62	0.20
Paspalum malacophyllum	25	0.07	0.5	24	0.21	2.0	-0.34	0.04
Guadua paniculata	42	8.58	79.5	53	18.13	72.2	0.07	-0.81
Setaria scandens	17	0.06	0.5	35	0.54	5.9	0.10	-0.87
Setaria vulpisetia	-	-	-	18	0.65	10.2	0.30	-1.27
Lasiacis sorghoidea	8	0.02	0.2	18	0.17	1.5	0.38	-1.48
Imperata brasiliense	50	0.41	2.4	35	3.14	25.9	0.40	3.29
Axonopus compressus	8	0.06	0.7	18	0.28	4.1	0.65	-1.82
**Rottboellia cochinchinensis*	-	-	-	12	0.14	1.5	1.09	2.54
Panicum trichoides	-	-	-	35	0.38	4.1	1.15	-1.78
Leptochloa virgata	-	-	-	35	0.37	2.0	1.31	2.53
**Urochloa decumbens*	-	-	-	12	1.89	28.8	1.39	-1.97
Digitaria insularis	-	-	-	24	4.69	50.2	1.42	1.90
Digitaria ciliaris	-	-	-	24	0.22	2.9	1.68	0.28
Panicum laxum	8	0.02	0.2	6	0.18	3.1	2.21	-0.28
**Cynodon spp.*	-	-	-	12	0.23	2.9	2.50	-0.20
Paspalum conjugatum	-	-	-	12	0.52	8.3	2.87	0.93
**Urochloa brizantha*	8	0.02	0.2	53	13.86	75.1	3.31	-0.09
Oplismenus hirtellus	-	-	-	6	0.03	0.5	3.39	-0.30
Panicum millegrana	-	-	-	6	0.03	0.5	3.48	0.91
Panicum trichanthum	-	-	-	12	0.32	3.9	4.19	0.03
**Urochloa maxima*	-	-	-	18	1.65	22.9	4.54	0.21

[a] Grasses present in just one site and therefore not included were: *Acroceras zizanioides, Andropogon lateralis, Aristida capillacea, Axonopus canescens, Chloris elata, Eragrostis maypurensis, E. amabilis, E. ciliaris, Eriochloa distachya, Guadua chacoensis, Hackelochloa granularis, Ichnathus inconstans, I. pallens, Mesosetum cayennensis, Oplismenus burmannii, Panicum peladoense, P. stenodes, P. stoloniferum, Paspalum gardnerianum, P. pictum, Schizachyrium maclaudii, Sporobolus cubensis, S. indicus, S. pyramidalis, Zea mays*.

APPENDIX B
TREE SPECIES IN NATIVE AND DERIVED SAVANNAS

Table B-1. Frequency, mean stem density, and mean basal area for tree species in native (n = 12) and derived (n =17) savannas. Species are listed in increasing value on DCA-1. Species typical of savanna are indicated by an asterisk.

	Native			Derived				
Species [a]	frequency (%)	density (ind./ha)	basal area (m^2/ha)	frequency (%)	density (ind./ha)	basal area (m^2/ha)	DCA-1	DCA-2
**Caryocar brasiliense*	33	94	1.87	-	-	-	-2.37	-0.17
**Myrica pubescens*	50	57	0.58	6	4	0.03	-2.16	-0.36
**Qualea grandifolia*	100	339	3.93	6	4	0.03	-2.08	-0.06
**Callisthene fasciculate*	42	57	0.59	6	4	0.07	-2.04	-0.62
**Pseudobombax heteromorphum*	33	42	0.50	6	4	0.02	-2.00	-0.85
**Brosimum gaudichaudii*	42	36	0.18	-	-	-	-1.81	-0.07
Simira rubescens	-	-	0.67	6	4	0.07	-1.80	-0.41
**Vochysia rufa*	33	36	0.18	-	-	-	-1.66	0.08
**Curatella americana*	92	297	4.59	-	-	-	-1.47	0.19
**Diptychandra aurantiaca*	42	104	2.58	6	22	0.52	-1.33	-0.46
**Guettarda viburnoides*	33	47	0.23	6	15	0.08	-1.28	-0.46
**Tabebuia aurea*	50	42	0.61	-	-	-	-1.11	0.06
**Dilodendron bipinnatum*	33	36	0.78	12	33	0.57	-0.99	-0.81
**Phyllostylon rhamnoides*	67	94	0.55	35	26	0.63	-0.97	1.93
Eriotheca roseorum	8	57	0.34	12	22	0.54	-0.97	-1.03
**Dipteryx alata*	33	21	0.30	6	15	0.31	-0.88	-0.61
**Qualea spp.*	33	57	1.59	-	-	-	-0.82	0.46
Hexachlamys boliviana	25	16	0.17	12	18	0.10	-0.62	-0.80
**Terminalia argentea*	33	68	0.91	6	11	0.15	-0.60	-0.18
**Astronium fraxinifolium*	17	10	0.10	6	15	0.22	-0.55	-0.73
**Myrsine umbellate*	-	-	-	6	15	0.08	-0.51	-1.35
Piper sp.	-	-	-	6	4	0.02	-0.51	-1.35
Protium heptaphyllum	-	-	-	6	4	0.01	-0.51	-1.35
**Ximenia Americana*	8	5	0.01	6	7	0.06	-0.46	-0.74

Table B-1. Continued

Species [a]	Native frequency (%)	Native density (ind./ha)	Native basal area (m^2/ha)	Derived frequency (%)	Derived density (ind./ha)	Derived basal area (m^2/ha)	DCA-1	DCA-2
Tabebuia serratifolia	8	5	0.02	6	4	0.13	-0.37	-0.77
**Simarouba amara*	42	63	-	12	7	0.02	-0.36	-0.82
Erythroxylumsp.	8	5	0.02	12	29	0.24	-0.33	0.25
Alibertia verrucosa	8	5	0.04	6	7	0.04	-0.15	-0.38
**Cybistax antisyphilitica*	-	-	-	18	59	0.48	-0.13	-1.95
Astronium urundeuva	25	21	0.74	41	51	2.32	-0.10	0.80
Physocalymma scaberrimun	8	10	0.20	24	26	0.62	0.13	-0.45
Attalea speciosa	8	5	0.57	12	11	1.05	0.21	0.81
Combretum leprosum	-	-	-	12	7	0.02	0.24	-1.37
**Rhamnidium elaeocarpum*	17	10	0.05	29	63	0.54	0.34	2.68
Apeiba tibourbou	8	5	0.15	29	37	0.43	0.35	-0.49
**Luehea paniculata*	33	31	0.30	41	37	0.34	0.54	-1.46
**Plathymenia reticulate*	8	5	0.06	6	4	0.21	0.62	3.22
Tabebuia impetiginosa	-	-	-	6	4	0.27	0.83	-3.01
**Tabebuia roseo-alba*	8	5	0.03	29	22	0.35	0.85	2.14
**Acrocomia aculeate*	42	36	0.77	18	15	0.31	0.86	-0.07
Spondias mombin	-	-	-	12	7	0.61	0.86	-2.92
Aspidosperma tomentosum	8	5	0.03	18	15	0.35	0.93	2.62
Neea steimbachii	8	5	0.04	6	4	0.01	1.01	3.39
Casearia gossypiosperma	-	-	-	6	15	0.06	1.09	-0.69
Rollinia herzogii	-	-	-	6	4	0.02	1.09	-0.69
Neea sp.	-	-	-	6	4	0.03	1.10	0.58
Anadenanthera culubrina	8	10	0.03	35	114	2.23	1.17	-2.34
Caesalpinia pluviosa	8	16	0.30	12	18	0.62	1.29	-0.45
Aspidosperma cylindrocarpon	-	-	-	12	11	0.55	1.74	3.29
Sapium glandulosum	-	-	-	12	18	0.09	2.17	0.06
Guazuma ulmifolia	-	-	-	47	59	0.68	2.56	0.54
Cedrela fissilis	-	-	-	12	11	0.74	2.65	-0.74

Table B-1. Continued

Species [a]	Native frequency (%)	Native density (ind./ha)	Native basal area (m^2/ha)	Derived frequency (%)	Derived density (ind./ha)	Derived basal area (m^2/ha)	DCA-1	DCA-2
Piptadenia viridiflora	-	-	-	12	7	0.04	2.71	1.02
Cordia alliodora	8	5	0.10	18	11	0.12	2.81	-0.06
Cecropia concolor	-	-	-	24	44	0.48	2.88	-0.06
Maclura tinctoria	-	-	-	18	11	0.06	2.91	0.06
Machaerium villosum	8	10	0.05	18	11	0.12	2.93	1.34
Pouteria macrophylla	-	-	-	12	7	0.08	2.96	1.96
Albizia niopoides	-	-	-	12	15	0.39	3.00	-0.76
Ficus sp.	8	5	0.16	6	4	0.53	3.80	0.02
Attalea phalerata	-	-	-	18	11	1.79	4.21	0.08
Hymenaea courbaril	-	-	-	12	7	0.37	5.98	-0.19

[a] Species present in just one site and therefore not included were: *Aspidosperma rigidum*, *Bauhinia rufa, Calycophyllum spruceanum, Cariniana ianeirensis, Ceiba samauma, Gallesia integrifolia, Heliocarpus americanus, *Luehea candicans, Syagrus sancona, Urera baccifera, Vataireopsis speciosa,* and *Zanthoxylum coco.*

LIST OF REFERENCES

Aliscioni, S.S., L.M. Giussani, F. O. Zuloaga, E. A. Kellogg. 2003. A molecular phylogeny of Panicum (Poaceae : Paniceae): Tests of monophyly and phylogenetic placement within the Panicoideae. American Journal of Botany **90**:796-821.

Angelsen, A., and D. Kaimowitz. 1999. Rethinking the causes of deforestation: Lessons from economic models. World Bank Research Observer **14**:73-98.

Ashton, P. M. S. 1992. Some measurements of the microclimate within a Sri-Lankan tropical rain-forest. Agricultural and Forest Meteorology **59**:217-235.

Balch, J. K., D. C. Nepstad, P. M. Brando, L. M. Curran, O. Portela, O. de Carvalho, and P. Lefebvre. 2008. Negative fire feedback in a transitional forest of southeastern Amazonia. Global Change Biology **14**:2276-2287.

Barlow J., and C. A. Peres. 2008. Fire-mediated dieback and compositional cascade in an Amazonian forest. Philosophical Transactions of the Royal Society B-Biological Sciences **363**:1787-1794.

Betts, R. A., P. M. Cox, M. Collins, P. P. Harris, C. Huntingford, and C. D. Jones. 2004. The role of ecosystem-atmosphere interactions in simulated Amazonian precipitation decrease and forest dieback under global climate warming. Theoretical and Applied Climatology **78**:157-175.

Blate, G. M. 2005. Modest trade-offs between timber management and fire susceptibility of a Bolivian semi-deciduous forest. Ecological Applications **15**: 1649-1663.

Bond, W. J. 2008. What limits trees in C4 grasslands and savannas? Annual Review of Ecology and Systematics **S.39**: 641–659.

Borhidi, A. 1988. Vegetation dynamics of the savannization process on Cuba. Vegetatio **77**: 177-183.

Cavelier J., T.M. Aide, C. Santos, A.M. Eusse, J.M. Dupuy. 1998. The savannization of moist forests in the Sierra Nevada de Santa Marta, Colombia. Journal of Biogeography **25**:901-912.

Chapman, G. P. 1996. The Biology of Grasses. CAB International, Wallingford, UK.

Christen, D., and G. Matlack. 2006. The role of roadsides in plant invasions: a demographic approach. Conservation Biology **20**: 385-391.

Clifford, H. T. 1959. Seed dispersal by motor vehicles. Journal of Ecology **47**: 311-315.

Cochrane, M. A. 2003. Fire science for rainforests. Nature **421**: 913-918.

Cochrane, M. A., A. Alencar, M. D. Schulze, C. M. Souza, D. C. Nepstad, P. Lefebvre, and E. A. Davidson. 1999. Positive feedbacks in the fire dynamic of closed canopy tropical forests. Science **284**:1832-1835.

Cochrane, M. A., and M. D. Schulze. 1998. Forest fires in the Brazilian Amazon. Conservation Biology **12**:948-950.

Cochrane, M. A., and M. D. Schulze. 1999. Fire as a recurrent event in tropical forests of the eastern Amazon: effects on forest structure, biomass and species composition. Biotropica **31**: 2-16.

Corlett, R. T. 2009. Seed dispersal distances and plant migration potential in tropical East Asia. Biotropica **41**: 592-598.

Cox, P. M., R. A. Betts, M. Collins, P. P. Harris, C. Huntingford, and C. D. Jones. 2004. Amazonian forest dieback under climate-carbon cycle projections for the 21st century. Theoretical and Applied Climatology **78**:137-156.

D'Antonio, C. M., and P. M. Vitousek. 1992. Biological invasions by exotic grasses, the grass fire cycle, and global change. Annual Review of Ecology and Systematics **23**: 63-87.

Daubenmire, R. 1972. Ecology of *Hyparrehnia rufa* (Nees) in derived savanna in north-western Costa Rica. Journal of Applied Ecology **9**: 11-23.

Fine, P.V.A. 2002. The invasibility of tropical forests by exotic plants. Journal of Tropical Ecology18: 687-705.

Foster, J.R., P.A. Townsend, C.E. Zganjar. 2008. Spatial and temporal patterns of gap dominance by low-canopy lianas detected using EO-1 Hyperion and Landsat Thematic Mapper. Remote Sensing of Environment **112**:2104-2117.

Fredericksen, T. S., M. J. Justiniano, B. Mostacedo, D. Kennard, and L. McDonald. 2000. Comparative regeneration ecology of three leguminous timber species in a Bolivian tropical dry forest. New Forests **20**:45-64.

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

Gelbard, J. L., and J. Belnap. 2003. Roads as conduits for exotic plant invasions in a semiarid landscape. Conservation Biology **17**: 420-432.

Gerhardt, K. 1996. Effects of root competition and canopy openness on survival and growth of tree seedlings in a tropical seasonal dry forest. Forest Ecology and Management **82**: 33-48.

Golding, N. and R. Betts. 2008. Fire risk in Amazonia due to climate change in the HadCM3 climate model: Potential interactions with deforestation. Global Biogeochemical Cycles **22**:GB4007.

Grime, J. P., K. Thompson, R. Hunt, J. G. Hodgson, J. H. C. Cornelissen, I. H. Rorison, G. A. F. Hendry, T. W. Ashenden, A. P. Askew, S. R. Band, R. E. Booth, C. C. Bossard, B. D. Campbell, J. E. L. Cooper, A. W. Davison, P. L. Gupta, W. Hall, D. W. Hand, M. A. Hannah, S. H. Hillier, D. J. Hodkinson, A. Jalili, Z. Liu, J. M. L. Mackey, N. Matthews, M. A. Mowforth, A. M. Neal, R. J. Reader, K. Reiling, W. RossFraser, R. E. Spencer, F. Sutton, D. E. Tasker, P. C. Thorpe, and J. Whitehouse. 1997. Integrated screening validates primary axes of specialisation in plants. Oikos **79**:259-281.

Griscom, B.W. and P.M.S. Ashton. 2006. A self-perpetuating bamboo disturbance cycle in a neotropical forest. Journal of Tropical Ecology **22**:587-597.

Griscom, B.W. and P.M.S. Ashton. 2003. Bamboo control of forest succession: *Guadua sarcocarpa* in Southeastern Peru. Forest Ecology and Management **175**: 445-454.

Guissani L. M., J. H. Cota-Sánchez, F. O. Zuloaga, E. A. Kellogg 2001. A molecular phylogeny of the grass subfamily Panicoideae (Poaceae) shows multiple origins of C4 photosynthesis. American Journal of Botany **88**:1993-2012.

Hierro, J. L., D. Villarreal, O. Eren, J. M. Graham, and R. M. Callaway. 2006. Disturbance facilitates invasion: the effects are stronger abroad than at home. American Naturalist **168**:144-156.

Higgins, S. I., and D. M. Richardson. 1999. Predicting plant migration rates in a changing world: The role of long-distance dispersal. American Naturalist **153**: 464-475.

Hobbs, R. J., S. Arico, J. Aronson, J. S. Baron, P. Bridgewater, V. A. Cramer, P. R. Epstein, J. J. Ewel, C. A. Klink, A. E. Lugo, D. Norton, D. Ojima, D. M. Richardson, E. W. Sanderson, F. Valladares, M. Vila, R. Zamora, and M. Zobel. 2006. Novel ecosystems: theoretical and management aspects of the new ecological world order. Global Ecology and Biogeography **15**:1-7.

Hodkinson, D. J., and K. Thompson. 1997. Plant dispersal: the role of man. Journal of Applied Ecology **34**: 1484-1496.

Hoffmann, W. A., R. Adasme, M. Haridasan, M. T. d. Carvalho, E. L. Geiger, M. A. B. Pereira, S. G. Gotsch, and A. C. Franco. 2009. Tree topkill, not mortality, governs the dynamics of savanna-forest boundaries under frequent fire in central Brazil. Ecology **90**:1326-1337.

Hoffmann, W.A., and R.B. Jackson. 2000. Vegetation-climate feedbacks in the conversion of tropical savanna to grassland, Journal of Climate **13**:1593-1602.

Hoffmann, W. A., V. Lucatelli, F. J. Silva, I. N. C. Azeuedo, M. D. Marinho, A. M. S. Albuquerque, A. D. Lopes, and S. P. Moreira. 2004. Impact of the invasive alien grass Melinis minutiflora at the savanna-forest ecotone in the Brazilian Cerrado. Diversity and Distributions **10**:99-103.

Holling, C.S. 1973. Resilience and stability of ecological systems. Annual Review of Ecology and Systematics **4**:1-23.

Hutyra, L. R., J. W. Munger, C. A. Nobre, S. R. Saleska, and S. A. Vieira. 2005. Climatic variability and vegetation vulnerability in Amazonia. Geophysical Research Letters **32**:L24712.

Jardim, A., T. J. Killeen, and A. Fuentes 2003. Guía de los arboles y arbustos del bosque seco Chiquitano, Bolivia. FAN, Santa Cruz, Bolivia, 324 pp.

Joaquin, N., and M. Herrero. 2003. Referencias para el manejo de pasturas de género Brachiaria. Documento técnico. Centro de Investigación Tropical. Santa Cruz, Bolvia.

Keeley J. E., and W. J. Bond. 1999. Mast flowering and semelparity in bamboos: the bamboo fire cycle hypothesis. The American Naturalist **153:**383-391.

Khurana, E. and J. S. Singh. 2001. Ecology of seed and seedling growth for conservation and restoration of tropical dry forest: a review. Environmental Conservation **28**:39-52.

Killeen, T. J. 1990. The grasses of Chiquitania, Santa-Cruz, Bolivia. Annals of the Missouri Botanical Garden **77:**125-201.

Killeen T. J., E. E. Garcia, S. G. Beck. 1993. Guía de árboles de Bolivia. Herbario Nacional de Bolivia and Missouri Botanical Garden, 958 pp.

Killeen, T.J., B. T. Louman, T. Grimwood. 1990. La ecología paisajística de la región de Concepción y Lomerio en la provincia de Ñuflo de Chavez, Santa Cruz, Bolivia. Ecología en Bolivia **16**:1-45.

Killeen, T. J., and P. N. Hinz. 1992a. Grasses of the Precambrian shield region in eastern lowland Bolivia I: habitat preferences. Journal of Tropical Ecology **8**:389-407.

Killeen, T. J., and P. N. Hinz. 1992b. Grasses of the Precambrian shield region in eastern lowland Bolivia II: life-form and C3-C4 photosynthetic types. Journal of Tropical Ecology **8**:409-433.

Killeen, T. J., E. Chavez, M. Peña-Claros, M. Toledo, L. Arroyo, J. Caballero, L. Correa, R. Guillén, R. Quevedo, M. Saldias, L. Soria, Y. Uslar, I. Vargas, M. Steininger. 2005. The Chiquitano dry forest, the transition between humid and dry forest in eastern lowland Bolivia. In T. Pennington (Ed.). Neotropical savannas and seasonally dry forests: plant diversity, biogeography and conservation. CRC Press, England. pp. 206-224

Lange, R. T. 1969. Piosphere - Sheep Track and Dung Patterns. Journal of Range Management **22**:396-400

Laurance, W. F. 2003. Slow burn: the insidious effects of surface fires on tropical forests. Trends in Ecology & Evolution. **18**: 209-212.

Lemmon, P. E. 1956. A spherical densiometer for estimating overstory density. Forest Science **2**: 314-320.

Lippincott, C.L. 2000. Effects of *Imperata cylindrica* (L.) Beauv. (cogongrass) invasion on fire regime in Florida sandhill (USA). Natural Areas Journal **20**:140-149.

Lugo, A. E. 2009. The emerging era of novel tropical forests. Biotropica **41**: 589-591.

MacDonald, G.E. 2004. Cogongrass (*Imperata cylindrica*) - Biology, ecology, and management. Critical Reviews in Plant Sciences **23**:367-380.

Mack, M. C., and C. M. D'Antonio. 1998. Impacts of biological invasions on disturbance regimes. Trends in Ecology & Evolution **13**: 195-198.

Mack, M. C., and C. M. D'Antonio. 2003. The effects of exotic grasses on litter decomposition in a Hawaiian woodland: the importance of indirect effects. Ecosystems **6**:723-738.

Malhi, Y., L. Aragao, D. Galbraith, C. Huntingford, R. Fisher, P. Zelazowski, S. Sitch, C. McSweeney, and P. Meir. 2009. Exploring the likelihood and mechanism of a climate-change-induced dieback of the Amazon rainforest. Proceedings of the National Academy of Sciences of the United States of America **106**:20610-20615.

Martinez M., J.A., V. G. Morales, G. Z. Villegas, A. M. Malla. 2003. Fuego en el pantanal: Incendios forestales y pérdida de recursos de biodiversidad en San Matías - Santa Cruz. Fundación PIEB, La Paz - Bolivia, 188 pp.

Mayle, F.E., D. J. Beerling, W. D. Gosling, M. B. Bush. 2004. Responses of Amazonian ecosystems to climatic and atmospheric carbon dioxide changes since the last glacial maximum. Philosophical Transactions of the Royal Society B-Biological Sciences **359**:499-514.

Mayle, F. E., R. Burbridge, and T. J. Killeen. 2000. Millennial-scale dynamics of southern Amazonian rain forests. Science **290**:2291-2294.

McDowell, L. R., and J. H. Conrad. 1977. Trace mineral nutrition in Latin America. World Animal Review. **24**:24-33. (cited by Velásquez-Pereira et al. 1997).

Minson, D. J., T. H. Stobbs, M. P. Hegarty, and M. J. Playne. 1976. Measuring the nutritive value of pasture plants. *In* N. H. Shaw and W. W. Bryan (Eds.). Tropical pasture research principles and methods. Commonwealth Agricultural Bureaux, Farnham Royal, Bucks, England. pp. 308-337.

Mokat, D.N., V.W. Bendale, S.S. Deokule, B.B. Jadhav, J. L. Mehta. 2005. Allelopathic effect of *Hyptis suaveolens* on rice. Journal of Ecobiology **17**:479-483.

Murthy, E.N., V.S. Raju, C.S. Reddy. 2007. Occurrence of exotic *Hyptis suaveolens*. Current Science **93**:1203-1203.

Navarro, G., and W. Ferreira. 2007. *Mapa de Vegetación de Bolivia a escala 1:250.000*. The Nature Conservancy (TNC). Ed. digital. Santa Cruz de la Sierra. ISBN 978-99954-0-168-9

Nepstad, D., G. Carvalho, A. C. Barros, A. Alencar, J. P. Capobianco, J. Bishop, P. Moutinho, P. Lefebvre, U. L. Silva, and E. Prins. 2001. Road paving, fire regime feedbacks, and the future of Amazon forests. Forest Ecology and Management **154**:395-407.

Nepstad, D., P. Lefebvre, U. L. Da Silva, J. Tomasella, P. Schlesinger, L. Solorzano, P. Moutinho, D. Ray, and J. G. Benito. 2004. Amazon drought and its implications for forest flammability and tree growth: a basin-wide analysis. Global Change Biology **10**:704-717.

Nepstad, D. C., A. G. Moriera, and A. A. Alencar. 1999. Flames in the rain forest: origins, impacts and alternatives to Amazonian fire. Pilot Program to Conserve the Brazilian Rain Forest. Brazilia, Brazil, 190 pp.

Nepstad, D.C., C. M. Stickler, B. Soares, F. Merry. 2008. Interactions among Amazon land use, forests and climate: prospects for a near-term forest tipping point. Philosophical Transactions of the Royal Society B-Biological Sciences **363**:1737-1746.

Nepstad, D. C., A. Verissimo, A. Alencar, C. Nobre, E. Lima, P. Lefebvre, P. Schlesinger, C. Potter, P. Moutinho, E. Mendoza, M. Cochrane, and V. Brooks. 1999. Large-scale impoverishment of Amazonian forests by logging and fire. Nature **398**:505-508.

Oliviera, P. S., and R. J. Marquis 2002. The Cerrados of Brazil: Ecology and Natural History of a Neotropical Savanna. Columbia University Press, New York, 398 pp.

Parendes, L. A., and J. A. Jones. 2000. Role of light availability and dispersal in exotic plant invasion along roads and streams in the H. J. Andrews Experimental Forest, Oregon. Conservation Biology **14**: 64-75.

Parsons, J. J. 1972. Spread of African pasture grasses to the American tropics. Journal of Range Management **25**:12-17.

Pinard, M. A., and J. Huffman. 1997. Fire resistance and bark properties of trees in a seasonally dry forest in eastern Bolivia, Journal of Tropical Ecology **13**:727-740.

Pinard, M.A., F. E. Putz, J. C. Licona. 1999. Tree mortality and vine proliferation following a wildfire in a subhumid tropical forest in eastern Bolivia. Forest Ecology and Management **116**:247-252.

Platt, W. J., and R. M. Gottschalk. 2001. Effects of exotic grasses on potential fine fuel loads in the groundcover of south Florida slash pine savannas. International Journal of Wildland Fire **10**:155-159.

Poorter, L., and L. Markesteijn. 2008. Seedling traits determine drought tolerance of tropical tree species. Biotropica **40**: 321-331.

Pringle, H. J. R., and J. Landsberg. 2004. Predicting the distribution of livestock grazing pressure in rangelands. Austral Ecology **29**:31-39.

Putz F.E., and K. H. Redford. 2010. The importance of defining 'forest': tropical forest degradation, deforestation, long-term phase shifts, and further transitions. Biotropica **42**: 10-20.

Quesada, C. A., J. Lloyd, M. Schwarz, S. Patiño, T. R. Baker, C. Czimczik,N. M. Fyllas, L. Martinelli, G. B. Nardoto, J. Schmerler,A. J. B. Santos, M. G. Hodnett, R. Herrera, F. J. Luizão, A. Arneth, G. Lloyd, N. Dezzeo, I. Hilke, I. Kuhlmann, M. Raessler, W. A. Brand, H. Geilmann, J. O. Moraes Filho, F. P. Carvalho, R. N. Araujo Filho, J. E. Chaves, O. F. Cruz Junior, T. P. Pimentel, and R. Paiva. 2009. Chemical and physical properties of Amazon forest soils in relation to their genesis. Biogeosciences Discussion **6**: 3923–3992.

Renvoize, S. A. 1998. Gramíneas de Bolivia. The Royal Botanical Gardens, Kew, 644 pp.

Rockwell, C. A., K. A. Kainer, C. L. Staudhammer, and C. Baraloto. 2007. Future crop tree damage in a certified community forest in southwestern Amazonia. Forest Ecology and Management **242**:108-118.

Sandoval M, L. M. 2001. Uso y manejo del bambú en dos zonas agroecológicas de Santa Cruz. Graduate Thesis. Universidad Mayor de San Simon, Cochabamba

Setterfield, S. A., M. M. Douglas, L. B. Hutley, and M. A. Welch. 2005. Effects of canopy cover and ground disturbance on establishment of an invasive grass in an Australia savanna. Biotropica **37**: 25-31.

Shukla, J., C. Nobre, and P. Sellers. 1990. Amazon Deforestation and Climate Change. Science **247**:1322-1325.

Simon, B.K. and Jacobs, S.W. 2003. *Megathyrsus*, a new generic name for *Panicum* subgenus *Megathyrsus*. Austrobaileya **6**:571 574.

Smith, E. P. 2002. BACI design. Pages 141-148 in A. H. El-Shaarawi, and W. W. Piegorsch, editors. Encyclopedia of Environmetrics. John Wiley & Sons, Ltd., Chichester, UK.

Steininger, M. K., C. J. Tucker, P. Ersts, T. J. Killeen, Z. Villegas, and S. B. Hecht. 2001. Clearance and fragmentation of tropical deciduous forest in the Tierras Bajas, Santa Cruz, Bolivia. Conservation Biology **15**:856-866.

Suding, K. N., K. L. Gross, G. R. Houseman. 2004. Alternative states and positive feedbacks in restoration ecology. Trends in Ecology and Evolution **19**:46-53.

Totey N.G., D. K. Shadangi, P. K. Khatri. 1994. Allelopathic effects of van-tulsi (*Hyptis suaveolens*) on germination and growth of teak (*Tectona grandis*) seedlings. Indian Journal of Forestry **17**:137-141.

Uhl, C., and R. Buschbacher. 1985. A disturbing synergism between cattle ranch burning practices and selective tree harvesting in the Eastern Amazon. Biotropica **17**:265-268.

Uhl, C., R. Buschbacher, and E. A. S. Serrão. 1988. Abandoned pastures in eastern Amazonia I. Patterns of plant succession. Journal of Ecology **76**:663-681.

Uhl, C., A. Verissimo, M. M. Mattos, Z. Brandino, and I. C. G. Vieira. 1991. Social, economic, and ecological consequences of selective logging in an Amazon frontier - the case of Tailandia. Forest Ecology and Management **46**:243-273.

Usberti, R., and L. Martins. 2007. Sulphuric acid scarification effects on Brachiaria brizantha, B. humidicola and Panicum maximum seed dormancy release. Revista Brasileira de Sementes **29**:143-147.

Van Deusen, P.C. 1996. Unbiased estimates of class proportions from thematic maps. Photogrammetric Engineering and Remote Sensing **62**:409-412.

Velásquez-Pereira J., L. McDowell, J. Conrad, N. Wilkinson and F. Martin. 1997. Nivel mineral existente en suelos, forrajes y ganado bovino en Nicaragua. II. Macrominerales y composición orgánica de forrajes. Revista de la Facultad de Agronomía de La Universidad del Zulia. **14**: 91-110.

Veldman, J. W. 2008. *Guadua paniculata* (Bambusoideae) en la Chiquitania Boliviana: Ecología de fuego y la oportunidad para un forraje nativo. Revista Boliviana de Ecología y Conservación Ambiental **24**:65-74.

Veldman, J. W., B. Mostacedo, M. Peña-Claros, and F. E. Putz. 2009. Selective logging and fire as drivers of alien grass invasion in a Bolivian tropical dry forest. Forest Ecology and Management **258**: 1643-1649.

Veldman J.W., and F. E. Putz. 2010. Long-distance dispersal of invasive grasses by logging vehicles in a tropical dry forest. Biotropica (*in press*).

Villegas, Z., M. Pena-Claros, B. Mostacedo, A. Alarcon, J. C. Licona, C. Leano, W. Pariona, and U. Choque. 2009. Silvicultural treatments enhance growth rates of future crop trees in a tropical dry forest. Forest Ecology and Management **258**:971-977.

von der Lippe, M. and I. Kowarik 2007. Long-distance dispersal of plants by vehicles as a driver of plant invasions. Conservation Biology **21**:986-996.

Wichmann, M. C., M. J. Alexander, M. B. Soons, S. Galsworthy, L. Dunne, R. Gould, C. Fairfax, M. Niggemann, R. S. Hails, and J. M. Bullock. 2009. Human-mediated dispersal of seeds over long distances. Philosophical Transactions of the Royal Society B-Biological Sciences **276**:523-532.

Zwaenepoel, A., P. Roovers, and M. Hermy. 2006. Motor vehicles as vectors of plant species from road verges in a suburban environment. Basic and Applied Ecology **7**:83-93.

BIOGRAPHICAL SKETCH

Joseph W. Veldman spent his formative years in the dunes, forests, and beaches on the shores of Lake Michigan. He attended Hope College, in Holland Michigan, were he studied biology and chemistry and ran cross country and track. It was during his time in college that he developed an interest in ecological research. Encouraged by Professor K. Greg Murray, he studied seed chemical defense and attended a tropical ecology field course in Costa Rica. After college, a brief stint in the private sector and an attempt to run semi-professionally convinced Joseph to apply to graduate school. In the fall of 2003 he arrived at the University of Florida to study with Francis E. "Jack" Putz in what was then the Department of Botany and to begin a career of conservation research and teaching at the college level. Joseph's officemate, Bonifacio Mostacedo, encouraged him to develop a project in Bolivia. In 2005 he began working with the Bolivian Institute of Forestry Research (IBIF) on grass invasions and fire in selectively logged tropical dry forests. Later, with funding from the Garden Club of America and a NSF Doctoral Disseratation Improvement Grant, he expanded his studies to cover a large region of eastern lowland Bolivia. Much of his time in Bolivia was spent living in tents, cooking on fires, bathing in rivers, and benefiting from the hospitality of ranchers and rural villagers. After two years of fieldwork, Joseph left his life and friends in Bolivia to return to the United States to complete his dissertation. Readjustment to the "comforts" of life in our material-rich society left him longing for a life that feels more real. He struggles with the guilt of his privileged position in the world but is nonetheless grateful for the opportunities he has had. Joseph hopes that even if his dissertation research does not change much in the world, that the personal relationships and experiences over the last six years have had positive, if intangible, impacts.