Forest Ecology and Management 258 (2009) 1643–1649

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Selective logging and fire as drivers of alien grass invasion in a Bolivian tropical dry forest

J.W. Veldman [a,b,*], B. Mostacedo [a], M. Peña-Claros [a,c], F.E. Putz [b]

[a] Instituto Boliviano de Investigación Forestal, Santa Cruz de la Sierra, Bolivia
[b] Department of Biology, University of Florida, Gainesville, FL 32611-8525, USA
[c] Forest Ecology and Forest Management Group, Centre for Ecosystem Studies, Wageningen University, P.O. Box 47, 6700 AA Wageningen, The Netherlands

ARTICLE INFO

Article history:
Received 19 May 2009
Received in revised form 6 July 2009
Accepted 8 July 2009

Keywords:
Chiquitania
Cynodon nlemfuensis
Disturbance
Invasive exotics
Megathyrsus maximus
Panicum maximum
Poaceae
Savanna
Sorghum halepense
Urochloa brizantha

ABSTRACT

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, we 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 we 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, we 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 fourfold from 400 m^2 (pre-fire) to 1660 m^2; over the same period in a logged but unburned (control) area, *U. maxima* cover decreased from 398 m^2 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.

1. 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 and 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 and 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

* Corresponding author at: Department of Biology, University of Florida, Gainesville, FL 32611-8525, USA. Tel.: +1 269 491 1195.
E-mail address: veldman@ufl.edu (J.W. Veldman).

0378-1127/$ – see front matter © 2009 Elsevier B.V. All rights reserved.
doi:10.1016/j.foreco.2009.07.024

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 and 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 and 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 and D'Antonio, 2003).

In this study we 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). Our 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, we present data on the identities and distributions of native and alien grasses in a tropical dry forest 1–5 yr after selective logging. In light of the grass-fire cycle, we hypothesized that the rate of alien grass invasion is amplified by forest fires. To test this hypothesis we 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.

2. Methods

2.1. 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 and 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 7 months each receiving <100 mm (April through October) and 4 months (June through September) during which potential evapotranspiration exceeds rainfall (M. Peña-Claros, *unpublished data*). Between 2002 and 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 wild-fires occurred on the property for the last 20 yr (1987–2007, M. Peña-Claros, *pers. obs.*).

2.2. Grass species distributions

To determine the effect of forest disturbance by logging on grass colonization, we studied the identities and distributions of grasses within a 2600 ha area of INPA that was selectively harvested between 2002 and 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, we randomly selected 16 log landings to sample during the mid rainy season (February and March, 2007). From these landings we 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; $N = 80$ (16×5 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 we randomly located a single 10 m × 3 m plot to sample grass cover, grass species presence/absence, and forest canopy openness. We 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, we classified 33 evenly spaced sample points in a 3 × 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.

We 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. We classified each species' photosynthetic pathway as either C_3 or C_4 based on Killeen and Hinz (1992b) and Guissani et al. (2001). Nomenclature departs from Killeen (1990) for *U. maxima* and *U. brizantha* (formerly *P. maximum* and *Brachiaria brizantha*, respectively). Molecular data show both species should be together in *Urochloa* (Guissani et al., 2001; but see Simon and Jacobs (2003) who classify *U. maxima* as *M. maximus*). Note that after first mention, species are referred to by their generic names except where ambiguous.

2.3. Alien grass responses to fire

We 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 we 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, we

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 and 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). We 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, we 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, we 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, we 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, we returned annually to measure both the burned and unburned (control) populations of *U. maxima* during the first 3 yr 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.

2.4. Data analysis

We 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. We 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 ($n = 8$); we 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. We used analysis of covariance (ANCOVA) to test the main effects of time since logging (co-variate) and microhabitat (fixed factor) on total grass cover. We 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, we 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, IL USA).

Due to the low logging intensity (4 trees 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, we calculated grass cover percentages for harvested forest as a whole weighted by the proportional area of each microhabitat.

We did not perform statistical analysis on the fire effects data because the treatments were not replicated in this BACI designed experiment. Instead, we 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.

3. Results

3.1. Grass species distributions

We encountered 20 grass species 1–5 yr after logging in this tropical dry forest (Table 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 our samples. None of the native species are characteristic of the region's diverse savannas and savanna woodlands (Killeen and Hinz, 1992a) but instead are either common roadside weeds (i.e., native ruderals) or forest grasses (Killeen, 1990; Table 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 (Fig. 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; Fig. 1B and C). Both grass cover and species richness positively correlated with tree canopy openness across all sites (Fig. 2A and 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 1). Disturbance affinities ranged from −6.3 for *Pharus lappulaceus*, a forest grass that did not occur in highly disturbed

Table 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 m^2 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).

Species	C_3/C_4	DA	Unlogged forests			Felling gaps			Skid trails			Log landings			Roads		
			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	–	–	–	–	–	–

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 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 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, Fig. 1C); 18 of the 20 grass species recorded were present on at least one road (Table 1). In addition to the exotic *U. maxima*, common grasses on roads were the native ruderals: *Leptochloa*, *Panicum millegrana*, and *Axonopus compressus*.

We encountered only four grass species and sparse grass cover (2.4%) in unlogged forest. Of the forest grasses, three are Bambusoideae: *Pharus* 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.

3.2. Alien grass responses to fire

During 3 yr 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; Fig. 3A). Over this same time period, the control population in unburned forest decreased from 398 m^2 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 3 yr after the fire (4 yr post-logging). Canopy openness measured in the burned and unburned forest corresponded with changes in *U. maxima* cover (Fig. 3). Canopy openness in the burn treatment remained at its pre-fire post-logging level of roughly 60% during all 3 yr 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 (Fig. 3A). After increasing threefold 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).

4. Discussion

4.1. 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*, we expect that photosynthetic pathway (i.e., C_3 versus 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

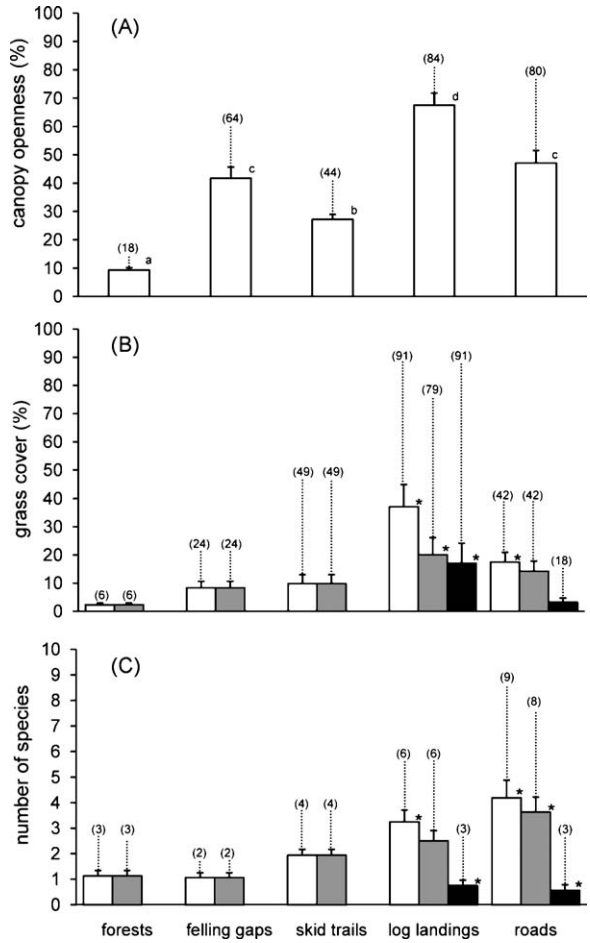

Fig. 1. Canopy openness, grass cover density and species richness in five microhabitats arranged in order of increasing disturbance by selective logging, 1–5 yr after harvest. (A) Canopy openness; habitats labeled with different letters differ at $P < 0.05$ (ANOVA, *post hoc* Tukey, $n = 16$). (B) Grass 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 + 1 SE for sixteen 30 m^2 plots per microhabitat type; values in parentheses denote maximum values.

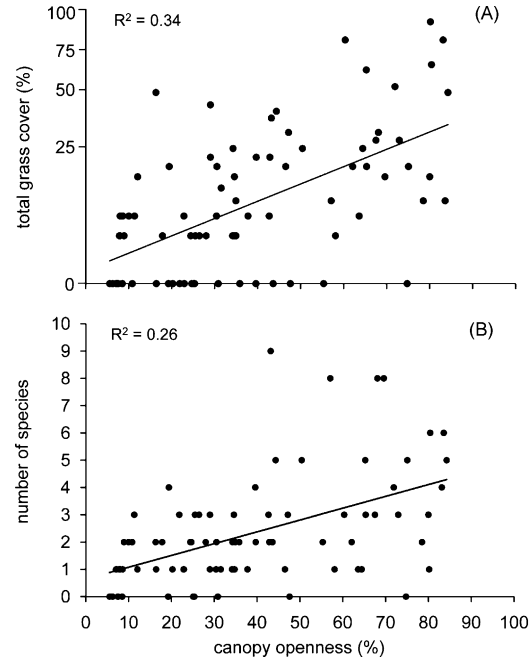

Fig. 2. Grass cover and species richness in relation to tree canopy openness 1–5 yr after selective logging for all habitats combined ($N = 80$). (A) Grass cover: [total grass cover]$^{-2}$ = 0.0631 [canopy openness] + 0.476, $P < 0.001$; note that the grass cover data were square root transformed before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

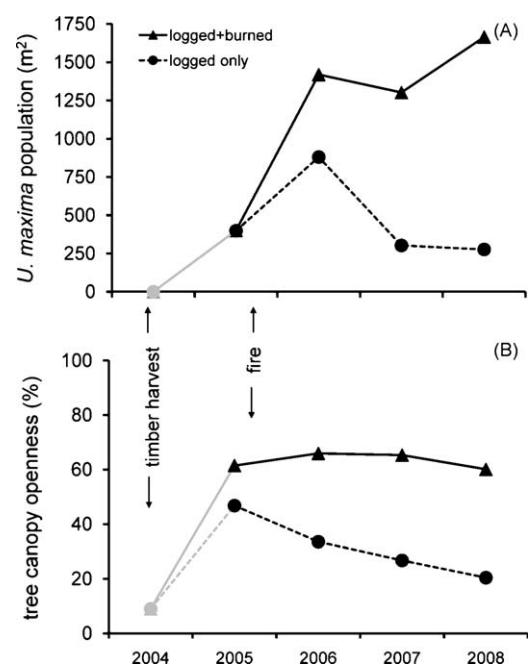

Fig. 3. Responses of alien grass populations and tree canopy cover to an experimental fire in a selectively logged Bolivian tropical dry forest. Black triangles and circles denote measurements during the 3-yr study; in gray, pre-logging (2004) values are inferred from data measured in unlogged areas 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.

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 and 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 we 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 and 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 and 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 and Ashton, 2003, 2006). In contrast to *U. maxima* which can produce 1300 seeds m^{-2} annually (J. Veldman, *unpublished data*), 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 twofold) 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 our 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.

4.2. 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; 3 yr 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 and Schulze, 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-fire) we 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 3 yr 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. Our 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. We can, nonetheless, use the unburned forest data (4 yr post-logging, Fig. 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 5 yr and quite possibly 6–10 yr after logging even without fire or re-entry by loggers.

5. 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. We 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*, a well-known native bamboo that was relatively rare in our 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 and 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.

Acknowledgments

We thank INPA Parket Ltd. for the use of their forest and for providing logistical support. Thanks to C. Pinto for planning and

management of the controlled burn. J. Alvarez, J.C. Alvarez, M. Hoyle, and the late J. Pesoa assisted with field sampling. L. Poorter provided guidance on experimental design and analysis, and we received helpful suggestions from two anonymous reviewers. This work was funded by a National Science Foundation Doctoral Dissertation Improvement Grant and a grant from the Garden Club of America.

References

Ashton, P.M.S., 1992. Some measurements of the microclimate within a Sri-Lankan tropical rain-forest. Agric. For. Meteorol. 59, 217–235.
Betts, R.A., Cox, P.M., Collins, M., Harris, P.P., Huntingford, C., Jones, C.D., 2004. The role of ecosystem–atmosphere interactions in simulated Amazonian precipitation decrease and forest dieback under global climate warming. Theor. Appl. Climatol. 78, 157–175.
Balch, J.K., Nepstad, D.C., Brando, P.M., Curran, L.M., Portela, O., de Carvalho, O., Lefebvre, P., 2008. Negative fire feedback in a transitional forest of southeastern Amazonia. Glob. Change Biol. 14, 2276–2287.
Blate, G.M., 2005. Modest trade-offs between timber management and fire susceptibility of a Bolivian semi-deciduous forest. Ecol. Appl. 15, 1649–1663.
Bond, W.J., 2008. What limits trees in C_4 grasslands and savannas? Annu. Rev. Ecol. Syst. 39, 641–659.
Chapman, G.P., 1996. The Biology of Grasses. CAB International, Wallingford, UK.
Cochrane, M.A., 2003. Fire science for rainforests. Nature 421, 913–918.
Cochrane, M.A., Schulze, M.D., 1998. Forest fires in the Brazilian Amazon. Conserv. Biol. 12, 948–950.
Cochrane, M.A., Schulze, M.D., 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.
Cochrane, M.A., Alencar, A., Schulze, M.D., Souza, C.M., Nepstad, D.C., Lefebvre, P., Davidson, E.A., 1999. Positive feedbacks in the fire dynamic of closed canopy tropical forests. Science 284, 1832–1835.
Cox, P.M., Betts, R.A., Collins, M., Harris, P.P., Huntingford, C., Jones, C.D., 2004. Amazonian forest dieback under climate-carbon cycle projections for the 21st century. Theor. Appl. Climatol. 78, 137–156.
D'Antonio, C.M., Vitousek, P.M., 1992. Biological invasions by exotic grasses, the grass fire cycle, and global change. Annu. Rev. Ecol. Syst. 23, 63–87.
Daubenmire, R., 1972. Ecology of *Hyparrehnia rufa* (Nees) in derived savanna in north-western Costa Rica. J. Appl. Ecol. 9, 11–23.
Gagnon, P.R., Platt, W.J., 2008. Multiple disturbances accelerate clonal growth in a potentially monodominant bamboo. Ecology 89, 612–618.
Gerhardt, K., 1996. Effects of root competition and canopy openness on survival and growth of tree seedlings in a tropical seasonal dry forest. For. Ecol. Manage. 82, 33–48.
Golding, N., Betts, R., 2008. Fire risk in Amazonia due to climate change in the HadCM3 climate model: potential interactions with deforestation. Glob. Biogeochem. Cycl. 22, GB4007.
Griscom, B.W., Ashton, P.M.S., 2003. Bamboo control of forest succession: *Guadua sarcocarpa* in Southeastern Peru. For. Ecol. Manage. 175, 445–454.
Griscom, B.W., Ashton, P.M.S., 2006. A self-perpetuating bamboo disturbance cycle in a neotropical forest. J. Trop. Ecol. 22, 587–597.
Guissani, L.M., Cota-Sánchez, J.H., Zuloaga, F.O., Kellogg, E.A., 2001. A molecular phylogeny of the grass subfamily Panicoideae (Poaceae) shows multiple origins of C_4 photosynthesis. Am. J. Bot. 88, 1993–2012.
Hierro, J.L., Villarreal, D., Eren, O., Graham, J.M., Callaway, R.M., 2006. Disturbance facilitates invasion: the effects are stronger abroad than at home. Am. Nat. 168, 144–156.
Holling, C.S., 1973. Resilience and stability of ecological systems. Annu. Rev. Ecol. Syst. 4, 1–23.
Hutyra, L.R., Munger, J.W., Nobre, C.A., Saleska, S.R., Vieira, S.A., 2005. Climatic variability and vegetation vulnerability in Amazonia. Geophys. Res. Lett. 32, L24712.
Jardim, A., Killeen, T.J., Fuentes, A., 2003. Guía de los arboles y arbustos del bosque seco Chiquitano, Bolivia. FAN, Santa Cruz, Bolivia.
Killeen, T.J., 1990. The grasses of Chiquitania, Santa-Cruz, Bolivia. Ann. Mo. Bot. Gard. 77, 125–201.
Killeen, T.J., Chavez, E., Peña-Claros, M., Toledo, M., Arroyo, L., Caballero, J., Correa, L., Guillén, R., Quevedo, R., Saldias, M., Soria, L., Uslar, Y., Vargas, I., Steininger, M., 2005. The chiquitano dry forest, the transition between humid and dry forest in eastern lowland Bolivia. In: En, T., Pennington, (Eds.), Neotropical Savannas and Seasonally Dry Forests: Plant Diversity, Biogeography and Conservation. CRC Press, England, pp. 206–224.
Killeen, T.J., Hinz, P.N., 1992a. Grasses of the Precambrian shield region in eastern lowland Bolivia. I. Habitat preferences. J. Trop. Ecol. 8, 389–407.
Killeen, T.J., Hinz, P.N., 1992b. Grasses of the Precambrian shield region in eastern lowland Bolivia. II. Life-form and C_3–C_4 photosynthetic types. J. Trop. Ecol. 8, 409–433.
Killeen, T.J., Louman, B.T., Grimwood, T., 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.
Khurana, E., Singh, J.S., 2001. Ecology of seed and seedling growth for conservation and restoration of tropical dry forest: a review. Environ. Conserv. 28, 39–52.
Laurance, W.F., 2003. Slow burn: the insidious effects of surface fires on tropical forests. Trends Ecol. Evol. 18, 209–212.
Lemmon, P.E., 1956. A spherical densiometer for estimating overstory density. For. Sci. 2, 314–320.
Mack, M.C., D'Antonio, C.M., 1998. Impacts of biological invasions on disturbance regimes. Trends Ecol. Evol. 13, 195–198.
Mack, M.C., D'Antonio, C.M., 2003. The effects of exotic grasses on litter decomposition in a Hawaiian woodland: the importance of indirect effects. Ecosystems 6, 723–738.
Mayle, F.E., Burbridge, R., Killeen, T.J., 2000. Millennial-scale dynamics of southern Amazonian rain forests. Science 290, 2291–2294.
Nepstad, D., Lefebvre, P., Da Silva, U.L., Tomasella, J., Schlesinger, P., Solorzano, L., Moutinho, P., Ray, D., Benito, J.G., 2004. Amazon drought and its implications for forest flammability and tree growth: a basin-wide analysis. Glob. Change Biol. 10, 704–717.
Nepstad, D.C., Moriera, A.G., Alencar, A.A., 1999. Flames in the rain forest: origins, impacts and alternatives to Amazonian fire. Pilot Program to Conserve the Brazilian Rain Forest. Brasilia, Brazil.
Parsons, J.J., 1972. Spread of African pasture grasses to the American tropics. J. Range Manage. 25, 12–17.
Pinard, M.A., Huffman, J., 1997. Fire resistance and bark properties of trees in a seasonally dry forest in eastern Bolivia. J. Trop. Ecol. 13, 727–740.
Shukla, J., Nobre, C., Sellers, P., 1990. Amazon deforestation and climate change. Science 247, 1322–1325.
Simon, B.K., Jacobs, S.W., 2003. *Megathyrsus*, a new generic name for *Panicum* subgenus *Megathyrsus*. Austrobaileya 6, 571–574.
Smith, E.P., 2002. BACI design. In: El-Shaarawi, A.H., Piegorsch, W.W. (Eds.), Encyclopedia of Environmetrics. John Wiley & Sons, Ltd., Chichester, UK, pp. 141–148.
Steininger, M.K., Tucker, C.J., Ersts, P., Killeen, T.J., Villegas, Z., Hecht, S.B., 2001. Clearance and fragmentation of tropical deciduous forest in the Tierras Bajas, Santa Cruz, Bolivia. Conserv. Biol. 15, 856–866.
Uhl, C., Buschbacher, R., 1985. A disturbing synergism between cattle ranch burning practices and selective tree harvesting in the Eastern Amazon. Biotropica 17, 265–268.
Uhl, C., Buschbacher, R., Serrão, E.A.S., 1988. Abandoned pastures in eastern Amazonia. I. Patterns of plant succession. J. Ecol. 76, 663–681.
Veldman, J.W., 2008. *Guadua paniculata* (Bambusoideae) en la Chiquitania boliviana: ecología del fuego y la oportunidad para un forraje nativo. Rev. Bol. Ecol. Cons. Amb. 24, 65–74.
Von der Lippe, M., Kowarik, I., 2007. Long-distance dispersal of plants by vehicles as a driver of plant invasions. Conserv. Biol. 21, 986–996.