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Contributions of root and stump sprouts to natural regeneration of a logged tropical dry forest in Bolivia

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ABSTRACT

A major impediment to the sustainable management of tropical dry forests in Bolivia is the scarcity of natural regeneration of commercial timber tree species. Where regeneration is present, true seedlings of many species are outnumbered by vegetative sprouts from roots, broken stems, and the stumps of felled trees. This study evaluates the importance of resprouts promoted by logging operations for the regeneration of commercially important canopy tree species. The objectives of the study were: (1) to characterize stump and root sprouting behaviors of canopy tree species harvested for timber; (2) to quantify the effect of logging on relative abundances and growth rates of stump sprouts, root sprouts, and true seedlings; (3) to relate the species-specific probabilities of stump sprouting to stump diameter and stump height; and (4) to explore how sprouting varies with the ecological requirements of canopy tree species. The study was carried out 1–5 years after logging of a privately owned land in a Bolivian tropical dry forest. Twenty-seven of the 31 species monitored resprouted at least occasionally, among which *Centrolobium microchaete* (Leguminosae-Fabaceae) and *Zeyheria tuberculosa* (Bignoniaceae) were the most frequent stump sprouters, and *Acosmium cardenasii* (Leguminosae-Fabaceae) and *C. microchaete* were the most frequent root sprouters. In all species the number of sprouts declined with increasing stump diameter and stump height. The probability of stump resprouting differed among species but did not vary consistently with stump diameter, except in *Z. tuberculosa* in which it declined. Approximately 45% of juveniles <2 m tall of canopy tree species originated from root or stem sprouts. Light-demanding species tended to regenerate more from seeds and root sprouts than from stumps. Seedling densities were higher in microsites opened by logging, while root and stem sprouts were equally common across microsites. Given their abundance and the fact that root and stem sprouts at least initially grew faster than true seedlings, we conclude that vegetative regeneration in this tropical dry forest is an important mode of post-logging regeneration especially for species that regenerate poorly from seed. Resprout management should be considered as a potentially effective strategy for the procurement of regeneration following logging, especially for species that do not readily recruit from seed.
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1. Introduction

Securing sufficient natural regeneration of commercial tree species after logging is critical for sustainable forest management. Most studies of tropical forest regeneration focus on tree recruitment from seed and, consequently, regeneration is often viewed as depending on seed production, seed dispersal, and seed viability, as well as on satisfying the environmental requirements for seed germination and seedling establishment (Holl, 1999; Dalling and Hubbell, 2002; De Steven and Wright, 2002). In tropical dry forests, many tree species produce abundant and well-dispersed seeds with high viability, but due to seed predation, water stress, and a multitude of other factors, successful recruitment from seed is often rare (Mostacedo and Fredericksen, 1999). Furthermore, in forests in general and in tropical dry forests in particular, tree seedlings that become established often grow more slowly than sprouts (Miller and Kauffman, 1998; Khurana and Singh, 2001). Successful regeneration after disturbance in dry forest (such as logging, severe windstorms, or fire) may therefore depend greatly on resprouts from stumps and roots (Mwavu and Witkowski, 2008).

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The general capacity of dry forest tree species to sprout may represent an adaptive response to an evolutionary history of fire (e.g., Bond and Midgley, 2001) and other large-scale disturbances. Whatever its evolutionary history, sprouting is of interest to forest managers and ecologists because sprouts often grow faster than true seedlings (Daniel et al., 1979; Clark and Hallgren, 2003). In a variety of seasonal tropical forests, logging reportedly stimulates abundant stump sprouting of felled and broken trees as well as sprouting from superficial roots damaged by heavy equipment (Kauffman, 1991; Kammesheidt, 1998; Miller and Kauffman, 1998; Kammesheidt, 1999; Bell, 2001). In the Chiquitano dry forest in Bolivia, although sprouting has been reported following logging (Fredericksen et al., 2000) and fires (Gould et al., 2002; Kennard and Putz, 2005), little is known about the overall contributions of sprout-origin plants to forest recovery. Whereas interspecific comparisons of sprouting ability are numerous for Mediterranean ecosystems (Bellingham, 2000; Pausas, 2001), such comparisons are relatively rare for seasonally dry tropical systems, and it is even less clear how resprouting ability varies with light requirements and other ecological attributes (but see Paciorek et al., 2000). The purpose of this study was to examine the contribution of sprouts to the natural regeneration of a tropical dry forest following logging. More specifically, we characterized the patterns of stump and root sprouting of several commercial canopy tree species. We also then measured the effects of logging on the relative abundances and growth rates of stump sprouts, root sprouts, and true seedlings. Focusing on felled trees, we related the species-specific probabilities of stump sprouting to stump diameter and stump height. Finally, we explored how sprouting ability varies with the light requirements of canopy tree species.

2. Methods

2.1. Study area

This study was conducted on the property of Inpa Parket (hereafter Inpa), a 30,000-ha tract of privately owned seasonally dry deciduous tropical forest 30 km NE of the town of Concepción (16°6′45″S, 61°42′47″), 250 km northeast of the city of Santa Cruz de la Sierra, Bolivia. The study area is flat to gently sloping, at an altitude of approximately 380 m, with a mean annual temperature of 24.3 °C, and mean annual precipitation of 1160 mm. During the 5-month dry season (May–October), most trees are deciduous; many tree species flower and fruit following rain events in the mid- to late-dry season. The forest canopy in Inpa is 20–25 m tall with common species including *A. cardenasii*, *Tabebuia impetiginosa*, *Anadenanthera macrocarpa*, *Astronium urundeuva*, and *C. microchaete* (Mostacedo et al., 2006); after first mention, species are referred to by their generic names except where ambiguous. Currently, 21 tree species, including all those mentioned above, are harvested for timber that is mostly processed into parquet flooring.

During the rainy season, canopy openness, as measured 1 m above the ground with a spherical densiometer, was 8% and 14% in control and logged areas, respectively, but during the dry season canopy openness triples (Mostacedo, 2007). The understory is dense, partially due to the abundance of lianas, and typically 30–40% of the ground is covered by the bromeliad, *Pseudananas sagenarius*.

2.2. Sampling design, data collection and analysis

2.2.1. Stump sprouts

We measured all stump sprouts from harvested trees in three areas that varied in time since logging. The first study site (Fig. 1, 50 ha) was selectively logged (10–12 species harvested; ≈4 trees/ha and 4 m^3/ha) by Inpa in 2002, 1 year prior to commencement of this study. Stumps and stump sprouts of the five most commonly harvested tree species (*Anadenanthera*, *Centrolobium*, *Copaifera chodatiana*, *Tabebuia*, and *Z. tuberculosa*) were mapped marked, and their diameters and heights were measured. Stump sprout survival and height growth were monitored for 1 year. The second study site (Fig. 1, 20 ha) covers one of the permanent plots maintained by the Instituto Boliviano de Investigación Forestal (IBIF) for monitoring forest dynamics following low intensity selective logging. Two years prior to our study, 4–8 trees/ha (5.3–6.4 m^3/ha, 14 species) were logged from these plots. We monitored sprouting of the same species as described above. The third study site (Fig. 1, 60 ha) was logged (2–3 trees/ha, ≈3 m^3/ha, and 5–7 species harvested) 5 years before our study. In this third site we measured sprout heights of the same species with a 7 m telescoping measuring rod but did not include *Zeyheria* because at the time of logging, this species was not harvested by Inpa.

In 2003 we checked for sprouts on the stumps of trees harvested in 2002 (site 1, 6 species), 2001(site 2, 10 species), and 1998 (site 3, 6 species). The 498 stumps evaluated in the three sites were from trees ≥40 cm DBH (stem diameter at 1.4 m or above buttresses) that were felled with chainsaws 10–90 cm above the ground. Each species was classified into one of the following four ecological guilds based on field observations and the literature (Mostacedo and Fredericksen, 1999; Poorter and Kitajima, 2007): short-lived pioneers with high light requirements for regeneration; long-lived pioneers with high light requirements; partial shade tolerant species that establish in shade but mature only under moderate to high light intensities; and, total shade tolerant species that can establish and survive under a closed canopy. Species considered in our study included five long-lived pioneers and five partial shade tolerant species. We counted all sprouts and measured the heights of the two tallest on each stump (from the point of origin) as well as the height and diameter of each stump dating from the 2001 and 2002 harvests.

We used logistic regression to determine the probability of sprouting in relation to stump diameter and height for each the five species that sprouted frequently (*Anadenanthera*, *Centrolobium*, *Copaifera*, *Tabebuia*, and *Zeyheria*). Nagelkerke *R*-square values were used to determine the percentage of variance explained by each regression and a Hosmer and Lemeshow χ^2 goodness-of-fit test was used to determine the significance of each relationship (Field, 2000). To test whether stump diameter and height (independent variables) influence the number and maximum heights of sprouts (response variables), we used regression analyses with linear, quadratic, cubic, and inverse models. For each species, the simplest (i.e., fewest parameters) model with a high R^2 value was selected in which each parameter had a reasonable biological explanation. Absolute annual height growth rates of stump sprouts were calculated for 10 species based on their height 2 years after logging (site 2) and for the 6 tree species studied in the 3 logged plots (sites 1–3). We assumed that the sprouts started growing immediately after the trees were felled. Stump sprout heights were compared among ecological guilds (long-lived pioneers: $n = 7$; partial shade tolerant: $n = 7$; total shade tolerant: $n = 2$) using analyses of variance (ANOVAs) and Tukey's post hoc tests.

2.2.2. Modes of regeneration in relation to microsites created by logging

In two of IBIF's 20-ha experiment plots (sites 1 and 4, Fig. 1) (Mostacedo et al., 2006), we compared the densities and sizes of seedlings and sprouts <2 m tall in the following microsites created during selective logging 1.5 years previously: logging gaps (280–330 m^2, $N = 16$); logging roads ($N = 16$); log landings (500–700 m^2,

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