# 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. micro-chaete* (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 m³/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 m³/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 m³/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 $\chi^2$ 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 m², $N = 16$); logging roads ($N = 16$); log landings (500–700 m²,
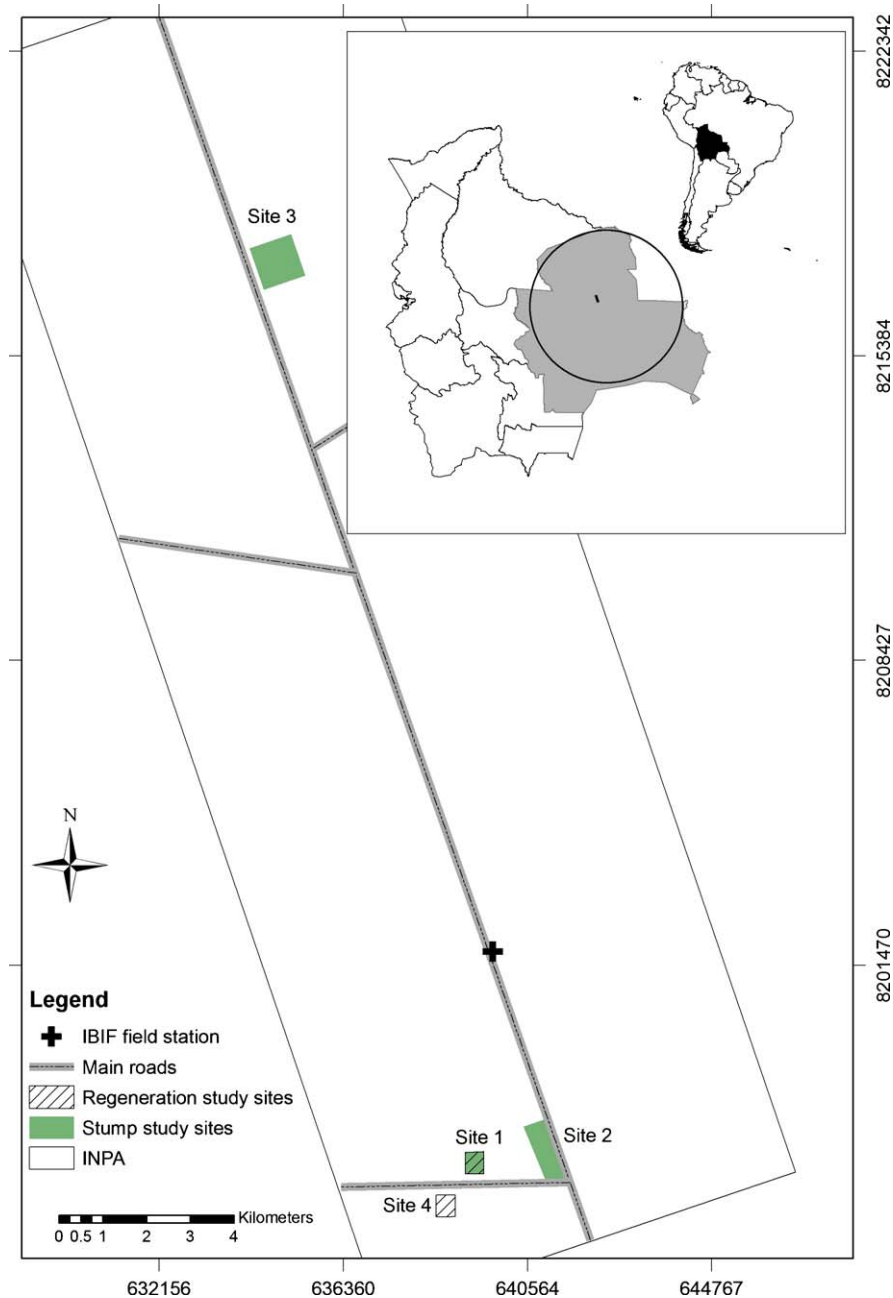
**Fig. 1.** Locations of the study areas in Bolivia. Sites 1, 2, and 3 were used for the stump sprout study, while the modes of regeneration study was conducted in sites 1 and 4. The map is georeferenced using a Universal Transverse Mecator (UTM) System, Zone 20.

$N = 8$); primary skid trails (50–200 m, $N = 16$); and, secondary skid trails (20–100 m, $N = 16$). Secondary skid trails were those used to extract only a single log. In each microsite, we established a 10 m × 4 m plot, and evaluated all plants <2 m tall of 16 canopy tree species (Table 1). Plants were classified as having developed directly from a germinated seed or sprouted from a root or stem. The determination of plant origin often involved excavation but was generally unambiguous. Stem sprouts refer to sprouts emerging from broken or otherwise damaged stems, not those from cut stumps.

ANOVAs followed by Tukey's post hoc comparisons were used to compare densities of true seedlings and root or stem sprouts among logged microsites. For each species and ecological guild, ANOVAs and then Tukey's post hoc comparisons were used to compare mean growth among origin types (i.e., stump sprout, root

sprout, or true seedling). All analyses were carried out with SPSS 12.0 for Windows.

## 3. Results

### 3.1. Sprout characterization

Stump sprouting was common after logging in the dry forest studied; 27 of the 31 species monitored at least occasionally resprouted from stumps and 19 did so frequently (Table 1). *Centrolobium*, *Zeyheria*, and *Tabebuia* were the most frequent stump sprouters (Fig. 2A). Among the six commercial tree species monitored, the proportion of stumps with living sprouts decreased with time after logging (Fig. 2A). Overall, for stumps censused 1, 2, and 5 years after logging the proportion of stumps with live sprouts

**Table 1**
Frequency of root and stem sprouting and shade tolerance of commercial and non-commercial canopy tree species in a tropical dry forest in Bolivia. Shade tolerance classes based on Pinard et al. (1999) and Mostacedo and Fredericksen (1999): SLP, short-lived pioneer; LLP, long-lived pioneer; PST, partially shade tolerant; TST, totally shade tolerant.

| Species | Abbreviation | Family | Resprout type/frequency | | Shade tolerance |
| --- | --- | --- | --- | --- | --- |
| | | | Root | Stem | |
| Commercial timber species | | | | | |
| *Amburana cearensis* (Allemão) A.C. Sm. | AMCE | Caesalpinaceae | No | Yes/low | LLP |
| *Anadenanthera macrocarpa* (Benth.) Brenan | ANMA | Mimosaceae | No | Yes/low | LLP |
| *Aspidosperma rigidum* Rusby | ASRI | Apocynaceae | Yes/low | Yes/high | PST |
| *Astronium urundeuva (Allemão)* Engl. | ASUR | Anacardiaceae | No | No | LLP |
| *Caesalpinia pluviosa* DC. | CAPL | Caesalpiniaceae | Yes/low | Yes/high | PST |
| *Cariniana ianeirensis* R. Knuth | CAIA | Lecythidaceae | Yes/low | Yes/high | LLP |
| *Cedrela fissilis* Vell. | CEFI | Meliaceae | Yes/low | Yes/low | LLP |
| *Centrolobium microchaete* (Mart. ex Benth.) Lima ex G. P. Lewis | CEMI | Fabaceae | Yes/high | Yes/high | LLP |
| *Copaifera chodatiana* Hassl. | COCH | Caesalpiniaceae | Yes/low | Yes/high | PST |
| *Cordia alliodora* (Ruiz and Pav.) Oken | COAL | Boraginaceae | Yes/low | Yes/low | SLP |
| *Hymenaea courbaril* L. | HYCO | Caesalpiniaceae | Yes/low | Yes/low | PST |
| *Machaerium scleroxylon* Tul. | MASC | Fabaceae | Yes/low | Yes/high | PST |
| *Phyllostylon rhamnoides* (J. Poiss.) Taub. | PHRH | Rhamnaceae | No | Yes/high | TST |
| *Platymiscium ulei* Harms | PLUL | Fabaceae | No | Yes/high | LLP |
| *Schinopsis brasiliensis* Engl. | SCBR | Anacardiaceae | No | No | LLP |
| *Sweetia fruticosa* Spreng. | SWFR | Fabaceae | No | Yes/low | PST |
| *Tabebuia impetiginosa* (Mart. ex DC.) Standl. | TAIM | Bignoniaceae | Yes/low | Yes/high | LLP |
| *Tabebuia serratifolia* (Vahl) G. Nicholson | TASE | Bignoniaceae | Yes/high | Yes/low | LLP |
| *Zeyheria tuberculosa* (Vell.) Bureau | ZETU | Bignoniaceae | No | Yes/high | LLP |
| Non-commercial species | | | | | |
| *Acacia bonariensis* Gillies ex Hook. and Arn. | ACBO | Mimosaceae | No | No | LLP |
| *Acosmium cardenasii* H.S. Irwin and Arroyo | ACCA | Fabaceae | Yes/high | Yes/high | TST |
| *Aspidosperma cylindrocarpon* Müll. Arg. | ASCY | Apocynaceae | Yes/high | Yes/high | PST |
| *Capparis prisca* J.F. Macbr. | CAPR | Capparaceae | No | Yes/high | TST |
| *Casearia gossypiosperma* Briq. | CAGO | Flacourtiaceae | Yes/high | Yes/high | LLP |
| *Ceiba samauma* (Mart.) K. Schum. | CESA | Bombacaceae | No | Yes/low | LLP |
| *Chorisia speciosa* A. St.-Hil. | CHSP | Bombacaceae | Yes/high | Yes/high | LLP |
| *Eriotheca roseorum* (Cuatrec.) A. Robyns | ERRO | Bombacaceae | No | Yes/low | LLP |
| *Gallesia integrifolia* (Spreng.) Harms | GAIN | Phytolacaceae | No | Yes/high | PST |
| *Machaerium acutifolium* Vogel | MAAC | Fabaceae | Yes/high | Yes/low | PST |
| *Piptadenia viridiflora* (Kunth) Benth. | PIVI | Mimosaceae | No | No | LLP |
| *Spondias mombin* L. | SPMO | Anacardiaceae | No | Yes/low | LLP |

was 55%, 43%, and 38%, respectively, but the rate of stump sprout mortality varied by species. In particular, 80% of the *Caesalpinia* stumps and 73% of the *Centrolobium* stumps had live sprouts 5 years after the trees were felled. In contrast, whereas some *Anadenanthera* and *Copaifera* stumps initially sprouted (23% and 13%, respectively), neither species had living stump sprouts in the plot logged 5 years prior to this study.

Root sprouting was also common after logging in the tropical dry forest of Inpa. Of the 31 tree species monitored (Table 1), 16 sprouted from lateral roots, 7 of which did so at high frequencies. *A. cardenasii*, *Centrolobium*, and *Casearia gossypiosperma* were the most frequent root sprouters.

Most of the 27 species that frequently sprouted from roots or stumps were shade tolerant (9 species) or at least partially shade tolerant (8 species). Among pioneer species there was no clear pattern in sprouting behavior; this includes some very frequent sprouters (*Centrolobium*) and many that infrequently if at all (e.g., *Astronium*, *Piptadenia viridifolia*, *Acacia bonariensis*, and *Schinopsis brasiliensis*) (Table 1).

*Caesalpinia pluviosa* had the largest ($20.0 \pm 4.40$; mean $\pm$ S.E.) number of sprouts per stump, followed by *Centrolobium* ($15.4 \pm 1.47$; mean $\pm$ S.E.) and *Zeyheria* ($14.2 \pm 1.50$; mean $\pm$ S.E.). The other four of the seven species monitored had <5 sprouts/stump, with the lowest numbers observed in *Copaifera* and *Anadenanthera* (Fig. 2B).

The probability of stump sprouting in relation to stump diameter varied among species (Fig. 3). In *Copaifera*, *Anadenanthera*, *Tabebuia*, and *Centrolobium*, the percentages of sprouted stumps were 17%, 24%, 57%, and 97%, respectively, and did not vary with stump diameter. In *Zeyheria*, sprouting reached 98% of the

stumps 38–40 cm diameter but decreased to only 40% among stumps 90 cm in diameter (Fig. 3). Observed and predicted proportions of sprouted stumps based on the overall average did not differ among the five species (*Copaifera*: $\chi^2 = 11.8$, $P = 0.16$; *Anadenanthera*: $\chi^2 = 3.4$, $P = 0.84$; *Tabebuia*: $\chi^2 = 3.17$, $P = 0.93$; *Centrolobium*: $\chi^2 = 8.43$, $P = 0.39$; *Zeyheria*: $\chi^2 = 4.48$, $P = 0.8$). The probability of sprouting in relation to stump height varied among species. The proportions of sprouted stumps of *Copaifera*, *Anadenanthera*, and *Centrolodbium* did not vary with stump height. In contrast, a *Tabebuia* stump 10 cm tall was almost certain to sprout (0.98) whereas this probability declined to 0.13 for a 72 cm tall stump. In *Zeyheria*, the probability of sprouting was high (0.91) and did not vary with stump height.

### 3.2. Effects of logging on modes of tree regeneration

In the plots censused 1.5 years after logging, 45% of juveniles <2 m tall of canopy tree species were root and stem sprouts, not true seedlings (ANOVA; $F_{2,181} = 14.4$, $P < 0.0001$; Fig. 4). At the species level there was great variation in the proportions of true seedlings. All 15 species evaluated sprouted at least occasionally from roots whereas only 9 species were represented by stem sprouts. Three species sprouted predominantly from roots whereas stem sprouting was the predominant mode of regeneration in only one species. Short-lived pioneer species tended to regenerate more from seeds and root sprouts than from stem sprouts (ANOVA; $F_{2,793} = 12.10$, $P = < 0.0001$), whereas partially shade tolerant and shade tolerant species regenerated more from seeds (ANOVA; $F_{2,420} = 4.46$, $P = 0.01$; $F_{2,359} = 8.01$, $P = 0.0004$, respectively).
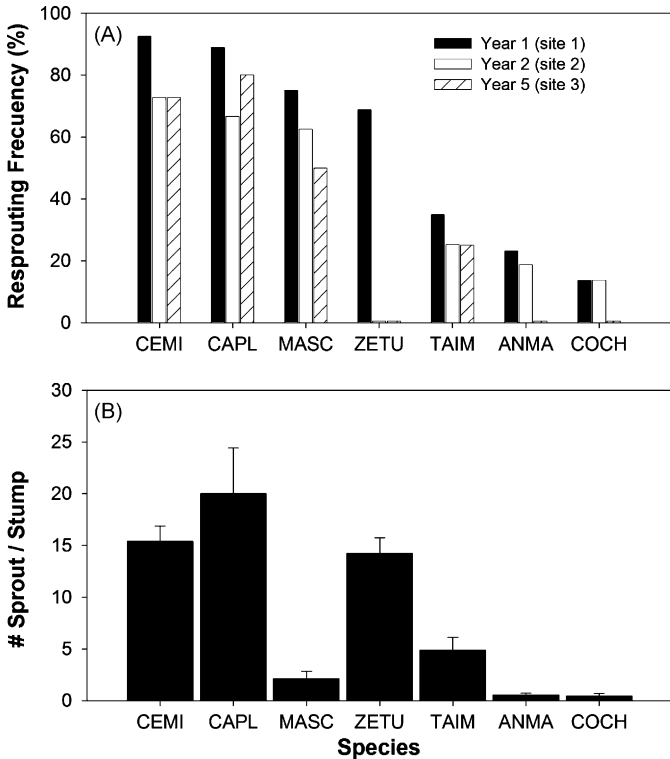
Fig. 4. Mean (±1S.E.) densities of juveniles <2 m tall of commercial tree species that were true seedlings, stem sprouts, and root sprouts. Different letters indicate significant differences between origin types determined with Tukey's post hoc comparisons with 95% confidence.

Fig. 2. The proportions of stumps with live sprouts over time since logging (A) and mean (±1S.E.) numbers of sprouts/stump for the most frequent sprouting species (B). CEMI, *Centrolobium microchaete*; CAPL, *Caesalpinia pluviosa*; MASC, *Machaerium scleroxylon*; TAIM, *Tabebuia impetiginosa*; ANMA, *Anadenanthera macrocarpa*; COCH, *Copaifera chodatiana*; ZETU, *Zeyheria tuberculosa*.

Densities of plants <2 m tall of canopy tree species did not vary among the different logging microsite types (ANOVA; $F_{4,181}$ = 2.08, $P$ = 0.09), but microsites differed in the relative contributions of true seedlings and sprouts (Table 2). True seedlings were twice as abundant as root and stem sprouts combined in logging gaps (ANOVA; $F_{2,45}$ = 9.91, $P$ = 0.0001). In contrast, there was no difference in plant density by mode of regeneration on logging roads (ANOVA; $F_{2,32}$ = 0.38, $P$ = 0.68). Densities of plants of sprout-origin and true seedlings were similar in log landings (ANOVA; $F_{2,14}$ = 1.95, $P$ = 0.18). On primary skid trails most plants <2 m tall were true seedlings, with some root sprouts and almost no stem sprouts (ANOVA; $F_{2,45}$ = 13.57, $P$ < 0.0001). On secondary skid trails, true seedlings were much more common than plants of either sprout type (ANOVA; $F_{2,45}$ = 4.6, $P$ = 0.01).

### 3.3. Growth of sprouts

Based on measures of the tallest sprout per stump, the growth rates of stump sprouts varied among species by more than an order of magnitude (Fig. 5A). *Anadenanthera* (mean = 204 cm/year), *Centrolobium* (mean = 203 cm/year) and *Zeyheria* (mean = 192 cm/year) had the highest growth rates, while *Aspidosperma* (mean = 4 cm/year) and *Copaifera* (mean = 27 cm/year) had the lowest (ANOVA, $F_{15,1443}$ = 79.7, $P$ < 0.0001). Stump sprouts of long-lived pioneer species grew faster than those of partial shade tolerant species (ANOVA; $F_{3,81}$ = 5.85; $P$ = 0.001), but there was a great deal of within species variation, especially in the growth rates of the latter. Stump sprouts of long-lived pioneer species grew at about the same rates as stump sprouts of shade tolerant species.

Among the stem and root sprouts <2 m tall of canopy tree species, both root and stem sprouts grew faster than seedlings and, in 5 of 12 species monitored, root sprouts grew faster than stem sprouts (Table 3). *Centrolobium* and *Chorisia speciosa* had the tallest root sprouts. We found no *Anadenanthera*, *Aspidosperma*, *Casearia*
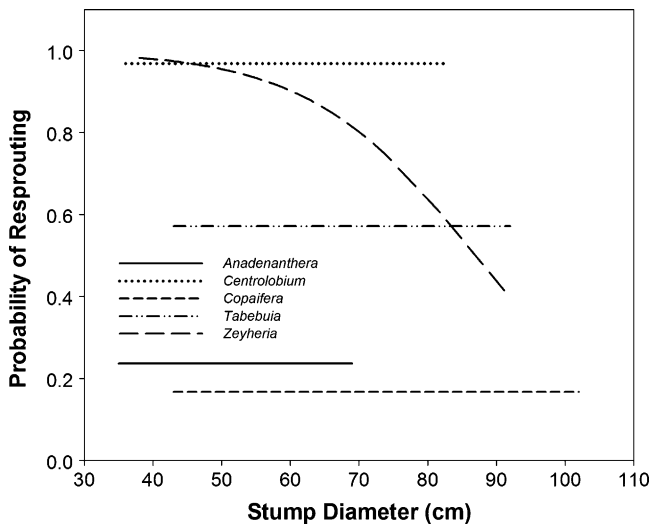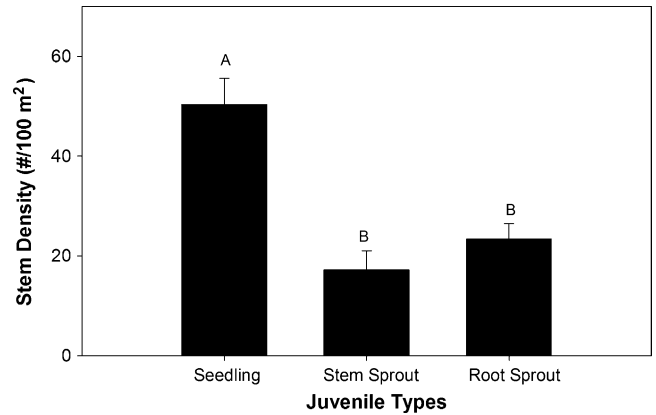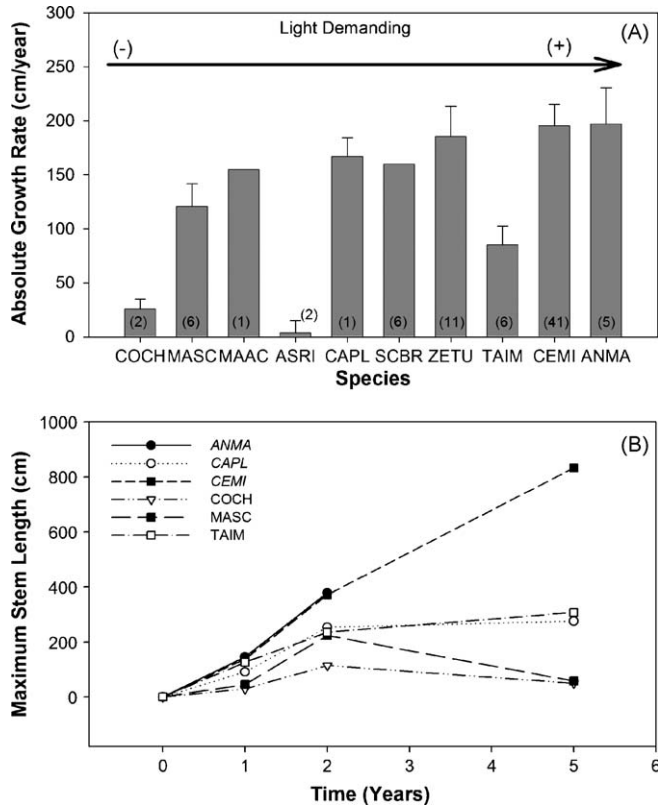


Fig. 3. Probabilities of stump sprouting as a function of stump diameter for the most frequently sprouting commercial tree species (curves fit by logistic regression).

**Table 2**

Mean (±1S.E.) densities (#/40 m²) of true seedlings, stem sprouts, and root sprouts in 10 m × 4 m plots in microsites created during selective logging. $N$ = 8 for the log landings, and $n$ = 16 for the other microsites. Different letters indicate differences between microsites in the densities of plants of different origins using Tukey's post hoc comparisons with 95% of confidence.

| Microsites | Seedling | Stem sprout | Root sprout | Mean of square | $F$ | $P$ |
|---|---|---|---|---|---|---|
| Logging gaps | 78.7 (10.5)[a] | 21.9 (5.2)[b] | 23.4 (8.8)[b] | 11341 | 9.91 | 0.0001 |
| Logging roads | 28.4 (11.4)[a] | 8.3 (3.3)[a] | 26.1 (6.8)[a] | 513 | 0.38 | 0.68 |
| Landings | 34.6 (15.8)[a] | 0.6 (0.6)[a] | 24.6 (7.8)[a] | 1411 | 1.95 | 0.18 |
| Primary skid trail | 50.1 (9.5)[a] | 4.2 (1.9)[c] | 24.1 (4.9)[b] | 8493 | 13.57 | 0.0001 |
| Secondary skid trail | 59.8 (11.5)[a] | 31.4 (10.6)[b] | 19.5 (5.2)[b] | 6866 | 4.64 | 0.01 |

**Fig. 5.** (A) Mean of relative growth rates (±1S.E.) of stump sprouts measured over the first 2 years after logging for commercial tree species arranged by light requirements, and (B) mean growth rates of stump sprouts through time for the main commercial tree species as based on measurements of the tallest sprouts on different stumps 1, 2, and 5 years after creation. Species abbreviations are given in Table 1.

*arborea*, *Machaerium scleroxylon*, *Phyllostylon rhamnoides*, or *Piptadenia* stem sprouts (Table 3). Among the root sprouters and true seedlings, long-lived pioneer species grew faster than partially shade tolerant and shade tolerant species. Among the stem sprouters, growth was similar among ecological guilds (Table 4).

Stump sprout heights varied over time and among the six species censused 1, 2, and 5 years after logging (Fig. 5B). Height growth rates increased through the second year and then decreased in all species except for *Centrolobium*, which continued to grow at a rapid rate through the fifth year. *Anadenanthera* sprouts grew rapidly through the second year, but we found no live stumps in the plot logged 5 year prior to our census.

## 4. Discussion

Of the 31 canopy tree species studied in a dry tropical forest in Bolivia, 27 (87%) displayed some capacity to sprout from either roots or stumps. Sprouting is apparently characteristic of many tropical dry forest tree species and helps them persist in an environment where stress is severe and disturbances are frequent (Bellingham, 2000; Bond and Midgley, 2001). The high proportion of species that sprouted from broken and cut stems in Inpa may be related to the high frequency with which stems lose their terminal buds due to herbivore browsing during the dry season when other browse is scarce as well as to the direct effects of drought stress (Bossard and Rejmanek, 1994; Del Tredici, 2001; Grol, 2005). As observed in the USA (Jones and Raynal, 1988), Mexico (Dickinson et al., 2000), and Uganda (Mwavu and Witkowski, 2008) root sprouting was also promoted by logging damage to roots.

### 4.1. Natural regeneration and shade tolerance: true seedlings vs. sprouts

Scarcity of natural regeneration from seeds is common for most tree species in tropical dry forest in Bolivia (Fredericksen

**Table 3**
Means (±1S.E.) of stem heights by species that sprouted from stems or roots compared to the heights of true seedlings. Different letters indicate significant differences in plant origins within species using Tukey's post hoc comparisons at the 95% confidence level.

| Species | Seedlings | Stem resprouts | Root sprouts | Mean square | F | P |
|---|---|---|---|---|---|---|
| *Acosmium cardenasii* | 18.3 (2.3)[b] | 42.4 (4.0)[a] | 46.2 (3.6)[a] | 28623 | 27.35 | 0.0001 |
| *Anadenanthera macrocarpa* | 25.1 (1.5)[b] | – | 72.6 (10.6)[a] | 11042 | 19.6 | 0.0001 |
| *Aspidosperma rigidum* | 30.0 | – | 55.0 (5.68) | 568 | 1.76 | 0.22 |
| *Caesalpinia pluviosa* | 54.7 (16.5) | 100.5 (29.8) | 112.5 (29.8) | 6770 | 1.90 | 0.18 |
| *Casearia arborea* | 125.0 (52.0) | – | 105.0 (90.1) | 300 | 0.037 | 0.86 |
| *Casearia gossypiosperma* | 102.7 (10.9) | 100.0 (19.5) | 78.8 (13.8) | 1844 | 0.97 | 0.39 |
| *Centrolobium microchaete* | 67.8 (26.6)[b] | 138.7 (39.9)[a] | 154.2 (4.8)[a] | 32850 | 5.15 | 0.006 |
| *Chorisia speciosa* | 141.2 (15.7) | – | 125.0 (22.2) | 352 | 0.20 | 0.67 |
| *Copaifera chodatiana* | 31.7 (16.6) | 61.4 (12.9) | 33.0 (28.8) | 961 | 1.15 | 0.37 |
| *Cordia alliodora* | 135.0 (39.1) | 155.0 (67.6) | 55.0 (67.6) | 3040 | 0.66 | 0.60 |
| *Machaerium acutifolium* | 33.6 (2.5)[b] | 59.2 (5.3)[a] | 60.7 (4.1)[a] | 23291 | 21.09 | 0.0001 |
| *Machaerium scleroxylon* | – | – | 70.0 (5.0) | – | – | – |
| *Phyllostylon rhamnoides* | 14.0 (2.27) | – | 15.0 | 0.8 | 0.03 | 0.86 |
| *Piptadenia viridifolia* | 69.0 (6.2)[b] | – | 140.0 (19.1)[a] | 54643 | 12.51 | 0.001 |
| *Sweetia fruticosa* | 58.0 (17.2) | 110.0 | 120.0 | 2552 | 1.23 | 0.36 |
| *Tabebuia impetiginosa* | 44.5 (36.8) | 90.0 (52.0) | 116.9 (11.4) | 10001 | 1.85 | 0.17 |

**Table 4**
Mean (±1S.E.) heights of trees ≤2 m tall that were root sprouts, stem sprouts, or seedlings grouped by ecological guild. Different letters indicate significant differences between ecological guilds using Tukey's post hoc comparisons at the 95% confidence level. Number of species was used as replicate unit for each ecological guild.

| Origin types | Long-lived pioneer (LLP) | Partially shade tolerant (PST) | Total shade tolerant (TST) | N (LLP, PST, TST) | Mean square | F | P |
|---|---|---|---|---|---|---|---|
| Root sprout | 104.4 (14.0)[b] | 81.2 (13.2)[ab] | 30.6 (15.6)[a] | 7, 7, 2 | 4320 | 3.49 | 0.06 |
| Stem sprout | 98.1 (34.8)[a] | 84.2 (10.3)[a] | 42.4 (0.0)[a] | 4, 5, 1 | 1265 | 0.53 | 0.61 |
| Seedling | 95.1 (16.2)[b] | 42.1 (5.0)[ab] | 16.2 (2.2)[a] | 7, 6, 2 | 7114 | 7.26 | 0.008 |

and Mostacedo, 2000; Mostacedo, 2007). The main reasons for this scarcity appear to be high seed predation, low seed viability, and high seedling mortality during the dry season (Fredericksen et al., 2000; Grol, 2005). Sprouting from broken and cut stems, along with root sprouting, appear to be important regeneration mechanisms in the tropical dry forest we studied in Bolivia where 45% of the regeneration of canopy trees originated from root or stem sprouts. Sprouting is reportedly also important in oak forest in the USA (Clark and Hallgren, 2003; Nyland et al., 2006), boreal forest in Russia (Homma et al., 2003), montane forest in Jamaica (Bellingham et al., 1994), African miombo (savanna) woodlands (Luoga et al., 2004), southern African savannas (Neke et al., 2006), and semi-deciduous tropical forest in Brazil (Castellani and Stubblebine, 1993), Venezuela, and Paraguay (Kammesheidt, 1999). Overall, sprouting seems to represent the predominant mode of regeneration in forests frequently subjected to logging, wind damage, and fire (Bond and Midgley, 2001).

Natural regeneration by sprouting from lateral roots is common in some commercial species in this study. In particular, *Centrolobium*, *Tabebuia*, *Aspidosperma*, and *M. scleroxylon* regenerated mostly from root sprouts. *Centrolobium* was previously reported as a root sprouting species (Fredericksen et al., 2000), but the importance of this mode of regeneration in the other species has apparently been overlooked. It remains to be seen whether root sprouts mature into sound trees, and there are reasons to suspect that they will not. First of all, given that most new stems emerge from damaged stems or roots, sprouts of all sorts could be prone to butt and root rots. Second, we observed that several *Centrolobium* root sprouts that were 5–8 cm DBH 5 years after sprouting still had not developed their own root systems and consequently were mechanically unstable when pushed perpendicular to the orientation of the source root. Given the general importance of root sprouting after fires, logging, and other severe disturbances, such as also observed in tropical dry forest in Paraguay and moist semi-deciduous forest in Venezuela (Kammesheidt, 1999), root sprout longevity is an issue that deserves more attention from researchers.

Partially shade tolerant and shade tolerant species were more likely to sprout than light-demanding species. Most of the partially shade tolerant species in Inpa sprouted from either roots or stems; similar findings were reported for a moist but seasonal tropical forest in Panama (Paciorek et al., 2000). In contrast, after slash-and-burn agriculture in a moist tropical forest in eastern Paraguay, light-demanding species contributed more sprouts than shade tolerant species (Kammesheidt, 1998). Although some light-demanding species in Inpa did not sprout (13%), others stump sprouted frequently, such as species in the Bombacaceae and Flacourtiaceae. Furthermore, the long-lived pioneer species that did sprout grew faster than sprouts from other ecological groups.

### 4.2. Stump sprouting and stump size

The probability of sprouting varied substantially among species but we observed no effect of stump diameter on the probability of sprouting in four of the five species studied. For example, *Centrolobium* had the highest probability of stump sprouting (97%), while *Copaifera* had the lowest (17%). In contrast, *Zeyheria* stumps showed a decreasing probability of sprouting with increasing diameter, a pattern also observed for other species in a wetter but still seasonal tropical lowland forest in Panama (Putz and Brokaw, 1989) and in an oak forest in southern Indiana (Weigel and Peng, 2002). The probability of stump sprouting did not vary with stump height except in *Tabebuia*, in which the probability decreased with stump height. These results suggest that harvesting trees of any tree size promotes the same probability of sprouting,

except for *Zeyheria* in which it is better to cut smaller trees and in *Tabebuia* in which low stumps are preferred if sprouting is to be encouraged.

### 4.3. Growth of stem and root sprouts compared with true seedlings

One advantage of natural regeneration via sprouting that was confirmed in this study is that sprouts typically grow more rapidly than true seedlings, at least initially (Gould et al., 2002; Kennard et al., 2002). We also observed that small plants of sprout-origin typically appeared less affected by drought than true seedlings (personal observation). Nevertheless, in our study forest as well as in Australia (Enright and Goldblum, 1999) and South Africa (Kruger et al., 1997), true seedlings of some species grew just as fast as sprouts. In several species we studied, especially light-demanding pioneers (e.g., *Cordia alliodora*, *Casearia gossypiosperma*), height growth rates were similar between true seedlings, root sprouts, and stem sprouts.

## 5. Conclusions

Due to the high costs and frequent failures of artificial regeneration, natural regeneration is critical for the sustainable management of tropical dry forest tree species in Bolivia. Given that so many tree species sprout prolifically from stumps of all sizes or from lateral roots, especially after mechanical damage, sprouts need to be considered as a source of regeneration. The abundance of sprouts and their typically rapid growth rates compared with true seedlings adds to the potential value of sprouts for forest management. Our data suggest that in forests designated for timber stand management, sprouts deserve at least as much attention from researchers as seeds and true seedlings. That said future studies should consider the long-term fates of sprouts. The observation in this study that the stump sprouts of most species essentially stopped growing after 2 years needs to be verified and otherwise explored, as do the factors that cause high rates of mortality of the stump sprout of some species. In the case of root sprouts, which were also abundant in our study area, long-term monitoring is needed to determine whether they ever grow up to be sound canopy trees. Studies should also include consideration of the reduced genetic variability and potentially the reduced reproductive success of species with high sprouting capacity.

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