STUMP SPROUTING OF FELLED TREES OF 33 SPECIES IN A SELECTIVELY LOGGED AND SILVICULTURALLY TREATED FOREST IN SURINAME

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To evaluate the contributions of sprouted stumps to stand conditions after selective logging and liberation thinning around future crop trees, we censused the stumps of 120 trees belonging to 33 species in a lowland forest in Suriname. Nearly half of the stumps supported live sprouts 13–18 months after felling. The likelihood of sprouting varied among the 33 species sampled and was lower among stumps of large diameter and thick bark. Sprouting was not related to stump height, topographic location, or canopy cover. To avoid competition from stump sprouts, we recommend that arboricides be used for liberation treatments.

Keywords: Stump sprouts, liberation thinning, coppicing

INTRODUCTION

Sprouting from cut, burned and broken stems is a form of vegetative recovery of aboveground tissues of which many tree species are capable. The capacity to sprout is of particular importance in ecosystems subjected to frequent large-scale natural disturbances such as hurricanes and fire (Byer & Weaver 1977, Ewel 1977, Stocker 1981, Uhl et al. 1981). Stump sprouting also occurs after logging (Bellingham & Sparrow 2000, Del Tredici 2001, Fuashi et al. 2020, Ramdial et al. 2020) and slash-and-burn agriculture (De Rouw 1993, Peltier et al. 2014) even in ecosystems where top-killing disturbances are uncommon and not considered important in the evolutionary history of the species. One explanation for the retention of the capacity to sprout is that, even in forests where cataclysmic events are infrequent, many woody plants suffer stem damage from smaller-scale disturbances such as branch and tree fall (e.g. Clark & Clark 1991, Paciorek et al. 2000) as well as breakage by large animals (Ickes et al. 2003). Everham and Brokaw (1996)

suggested that sprouting is more common among tropical than temperate tree species, but the latter are much better studied. This argument is supported by a study of sprouting post-logging in a semi-deciduous forest in Uganda by Mwavu and Witkowski (2008) who reported that 814 of 835 stumps sprouted, which comprised 119 species of 31 families.

Despite the prevalence of stump sprouting, some species and phylogenetic lineages of trees lack this capacity or lose it when they become large. Examples of the phylogenetic effect are that few pines (*Pinus* spp.) or dipterocarps (Dipterocarpaceae spp.) sprout whereas sprouting is common among oaks (*Quercus* spp.) and eucalypts (*Eucalyptus* spp.). Within plant communities, whether or not a stump sprouts is likely determined by its characteristics as well as by environmental conditions (Clarke et al. 2013). Many studies reported that the sprouting ability of trees typically decreases as they become older and larger (Lust & Mohammady 1973).

In contrast, coppiced stumps of several metres diameter have been in production for centuries in Europe (Rackham 1980). The number of sprouts per stump often increases with stump diameter until bark thickness, which increases with tree diameter, hinders bud emergence. Several authors reported that sprout survival decreases with stump height (Lust & Mohammady 1973, Keim et al. 2006). How height affects sprouting is not clear but stumps (i.e. stools) managed for coppice are typically cut low to the ground (Evans 1992). A large number of tree stems were snapped after a windstorm in Panama and Putz and Brokaw (1989) observed a high initial proportion of sprouted stems but then diminishing numbers of live sprouts over the first year. Several authors suggested that exposure to light promotes stump sprouting (e.g. Lust & Mohammady 1973), but the mechanism for this purported phenomenon is not clear.

Stump sprouting is the basis for coppice management, a forestry technique employed at least since the Bronze Age (Rackham 1980) and still employed for commercial production of wood fibre, fuel, and small dimension building materials (e.g. Evans 1992). In contrast, stump sprouting is undesirable in stands managed for trees grown directly from seeds that suffer from competition from stump sprouts. Shade cast by stump sprouts might be important, but belowground competition may be of particular importance where soils are nutrient-poor and water availability is at least seasonally limited (Putz & Canham 1992, Coomes & Grubb 2000). Furthermore, long-term retention of live stumps may increase the risks of pathogen and pest spread from stumps to nearby conspecific trees to which they are connected with root grafts (Lev-Yadun 2011).

We studied stump sprouting in a forest managed for timber in Suriname where the trait is undesired but little studied. Our main objective was to determine the likelihood of sprouting for canopy tree species, in relation to stump diameter and height, bark thickness and canopy openness. The presence of stumps that resulted from an experimental silvicultural treatment designed to liberate future crop trees of commercial species from competition from nearby neighbours allowed us to study a wider range of stem diameters than created by selective logging alone. We also inspected the area for sprouted stumps from the previous round of logging some 25 years prior to our study.

MATERIALS AND METHODS

Study site

Characteristics of stump sprouts were measured in mesophytic tropical rainforest (Lindeman & Moolenaar 1959) in the N.V. Takt Timber Concession in the Mapane region of Suriname (5° 11′ N, 54° 50′ W). The well-drained red Ferrasol (Oxisol) in the area is nutrient poor. The mean annual temperature is 27 ºC and the area receives 1700–2500 mm of precipitation annually but often suffers water deficits during the August–March dry season. The general area was selectively logged about 25 years prior to our study, but no information was available about the species harvested and logging intensity. The 35-ha study area on which we focused was selectively logged and silviculturally treated 13–18 months prior to our measurements. Treatment involved felling of trees overtopping designated future crop trees (i.e. liberation thinning).

Field data collection and data analysis

To locate stumps of harvested trees and those of trees felled as part of the liberation treatment, we used harvest plan stem maps and traversed the area thoroughly. When we encountered a stump, we determined whether or not it supported live or dead sprouts, identified it to species, and measured its diameter, height (on the uphill side), and bark thickness at 50 cm above the ground. We also classified the heartwood of each stump as either sound or rotten, and with or without termites. To characterise the stump environment, we estimated percent canopy openness with a canopy densiometer (Lemmon 1956), measured slopes 5 m above and below each stump with a clinometer, and assigned a topographic position (i.e. ridge top, slope or valley bottom) to each stump encountered. We also searched for sprouted stumps from the trees felled about 25 years prior to our study. All analyses were performed using R software version 3.6.1 (R Core Team 2019) with significance set at $\alpha < 0.05$.

RESULTS

Of the 120 stumps of 33 species encountered, 57 sprouted; the sprouts were dead on seven of the
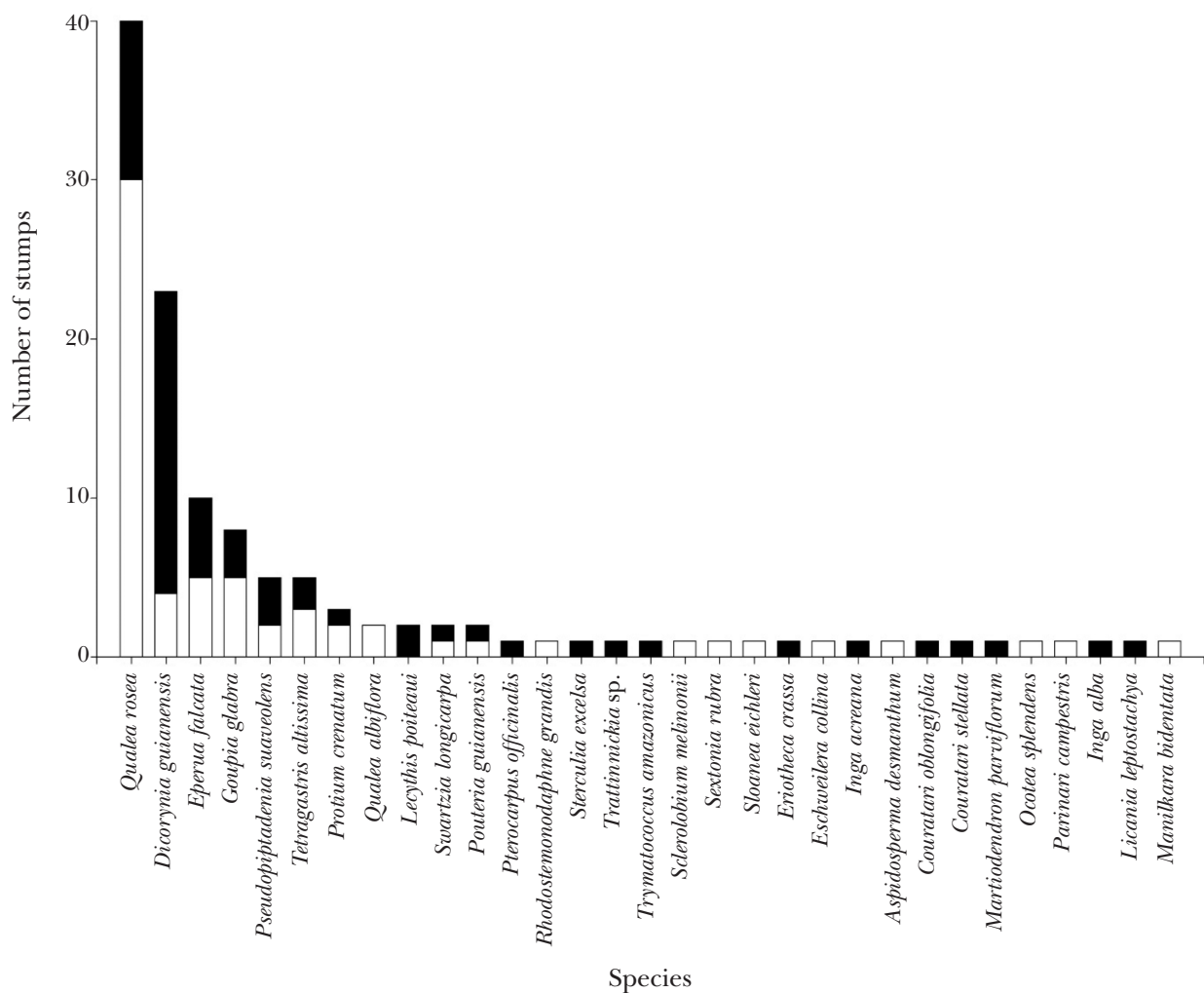
sprouted stumps (Figure 1). Among the species with the most abundant stumps, sprouting was common in *Dicorynia guianensis* (18 of 23; after first mention, species are referred to by their generic names; see Appendix for the complete list of species and the raw data) and *Eperua falcata* (5 of 10). In contrast, sprouting was rare in *Qualea rosea* (6 of 40). The proportions of sprouted stumps differed between the three common species (χ^2 = 24.9, p < 0.005). After sprouting, all sprouts died on one *Dicorynia* stump and four *Qualea* stumps. In *Tetragastris,* 2 of 5 stumps sprouted and in *Pseudopiptadenia* and *Goupia,* 3 of 5 stumps sprouted. In the remaining 23 species represented by only 1 stump, 12 sprouted of which 2 died and 11 did not sprout.

Considering all the stumps we surveyed, those that sprouted were smaller in diameter (mean ± 1 standard deviation; $\overline{x}$ = 54.4 ± 2.68 cm, n = 57) than stumps that did not sprout ($\overline{x}$ = 63.2 ± 2.39 cm, n = 63, t = 2.45, p < 0.02; Figure 2). This community-level pattern was not maintained for the species with more than nine stumps (*Dicorynia, Eperua and Qualea*).

At the community level (i.e. with all stumps considered of all species) there was no difference in stump height for sprouted stumps ($\overline{x}$ = 98.1 ± 3.93 cm, n = 57) and stumps that did not sprout ($\overline{x}$ = 93.5 ± 2.98 cm, t = 0.95, p = 0.34, n = 63; Figure 3). In contrast, in one of the species represented by more than nine stumps (*Qualea*), sprouted stumps ($\overline{x}$ = 115.1 ± 9.49 cm, n = 10) were taller than non-sprouted stumps ($\overline{x}$ = 95.6 ± 4.05 cm, n = 30, t = 2.20, p = 0.03); *Dicorynia* showed a similar tendency while *Eperua* did not.

In regards to bark thickness, when we considered all trees of all species (Figure 4), the bark on stumps that did not sprout ($\overline{x}$ = 11.1 ±

Figure 1   The number of sprouted (black bars) and non-sprouted (white bars) stumps of 33 species of canopy trees cut 13–18 months prior to this survey
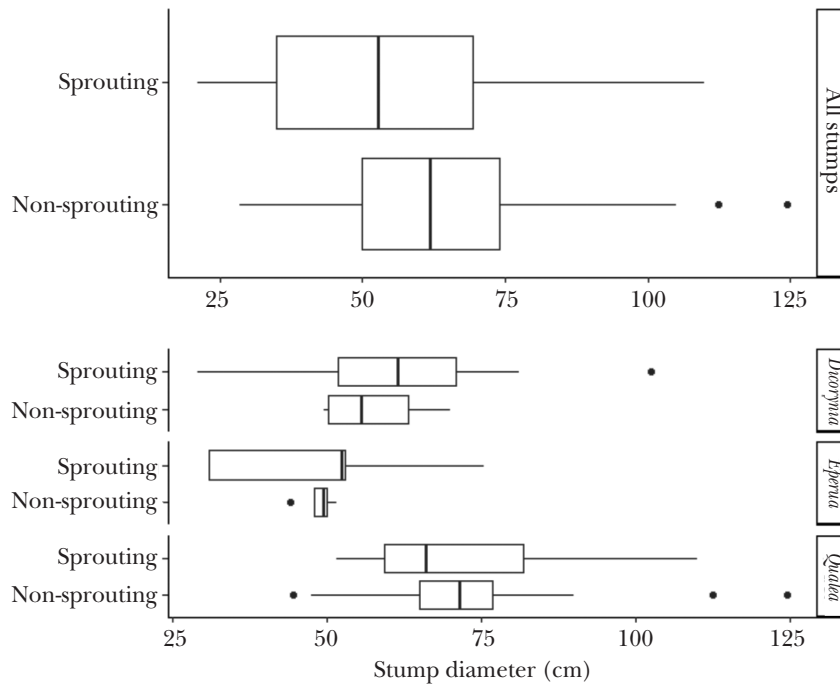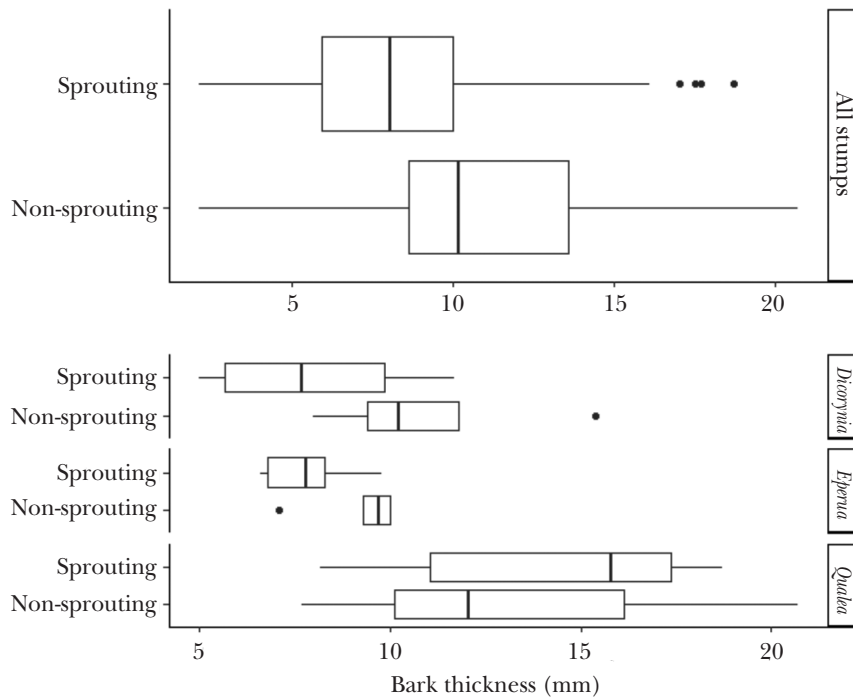
Figure 2   Diameters of sprouted and not-sprouted stumps of all 33 species and the three species with more than nine stumps
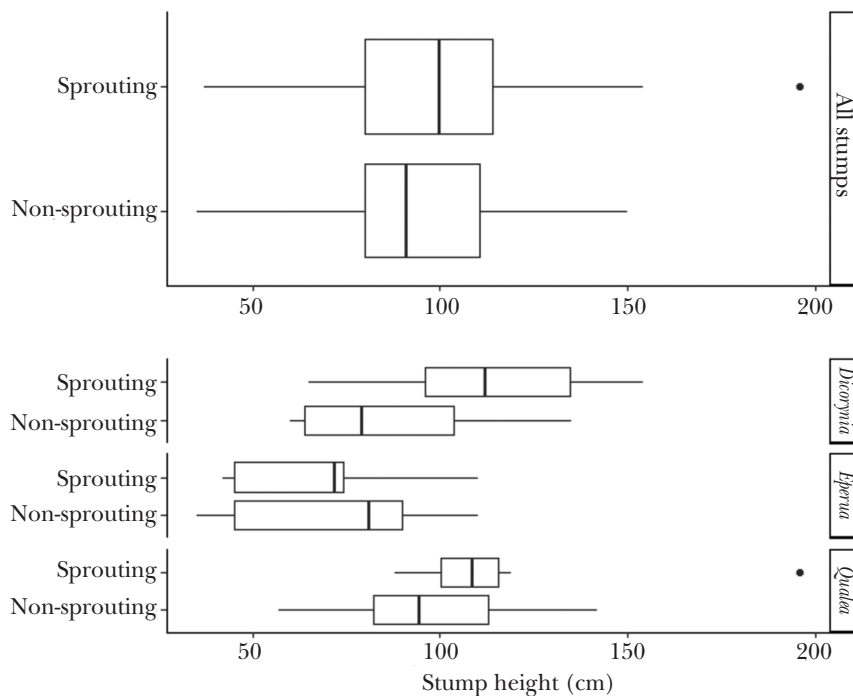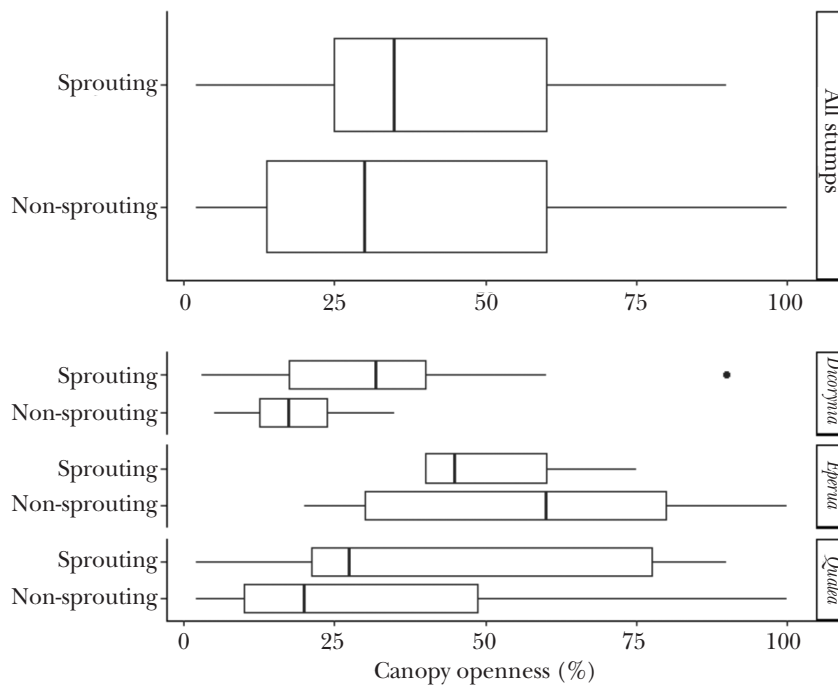

Figure 3   Heights of sprouted and non-sprouted stumps of all 33 species and the three species with more than nine stumps

17.54 mm, n = 63) was thicker than on stumps that did sprout ($\bar{x}$ = 8.7 ± 15.05 mm, n = 57, t = 3.03, p < 0.01). In contrast, comparisons of sprouted and non-sprouted stumps of the species with sample sizes of more than nine stumps showed no differences in bark thickness.

Among the environmental variables potentially associated with stump sprouting (topography, soil drainage, soil type, and canopy openness), only canopy openness showed any trend, but none of the differences were significant (Figure 5).

Figure 4   Bark thickness of sprouted and non-sprouted stumps of all 33 species and the three species with more than nine stumps

Figure 5   Canopy openness (%) over sprouted and non-sprouted stumps of all 33 species and the three species with more than nine stumps

DISCUSSION

In the selectively logged and silviculturally treated lowland tropical forest we studied in Suriname, slightly less than half of the stumps supported live sprouts 13–18 months after felling. This relatively low proportion perhaps reflected the large sizes of the stumps we surveyed, which averaged > 50 cm in diameter with none less than 25 cm. Numerous other studies reported that sprouting decreases with stump diameter (Lust & Mohammady 1973). We observed a weak but

significant trend in our forest, but those other studies focused on much smaller trees. We expected but did not find that the likelihood of sprouting increased with stump height but, as with diameter, the range of stump heights in our study was small (Figure 3). As expected, at least at the community level, the likelihood of sprouting decreased with bark thickness. In contrast, within the three well-sampled species, sprouting did not vary with bark thickness perhaps because many sprouts on one of them (*E. falcata*) emerged from the exposed vascular cambium on the cut surface of the stump and thus avoided the need to penetrate the bark (Ramdial et al. 2020). Also contrary to multiple reports in the literature (Lust & Mohammady 1973, Pelc et al. 2011), we observed no relationship between canopy opening and whether or not stumps sprouted. We note that the range of canopy openness above the stumps we studied was small and most received substantial light. This observation was to be expected given that the stumps were created by the felling of canopy trees, which would assure at least some light reaching down to the stumps. Perhaps the effect of light intensity on stump sprouting was only evident among stumps in deeper shade than observed in our study.

We searched for but did not find the large, multiple-stemmed trees that might indicate stump sprouting after the previous round of selective logging, some 25 years prior to our study. Although all the sprouts were dead on only 7 of the 57 sprouted stumps in our study (of 120), the absence of older stump sprouts suggested that many more will soon die. In contrast, in nearby Guyana, Rijks et al. (1998) reported that 20 years after logging, 55% of the *Chlorocardium rodiei* (greenheart) stumps still supported live sprouts of up to 8.1 cm diameter at breast height. That finding notwithstanding, given their vulnerability to diseases that enter through the stump and their inherent biomechanical instability, stump sprouts rarely grow into large trees with sound boles. Nevertheless, even if sprouts are relatively short-lived, they use resources that might otherwise be available to small trees with better prospects for longevity and good form. For this reason, we recommend that, at least for silvicultural treatments that involve liberation of future crop trees from competition from neighbours, instead of felling the competitors, they be poison-girdled. This treatment eliminates resprouting and reduces the stand damage done when the competitor finally falls.

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Appendix Stumps of 120 trees of 33 species surveyed for sprouts in a 35-ha block of selectively logged and silviculturally treated forest in Suriname

Scientific name	Sprouting	Non-Sprouting	Total
Aspidosperma desmanthium		1	1
Couratari oblongifolia	1		1
Couratari stellata	1		1
Dicorynia guianensis	19	4	23
Eperua falcata	5	5	10
Eriotheca crassa	1		1
Eschweilera collina		1	1
Goupia glabra	3	5	8
Inga acreana	1		1
Inga alba	1		1
Lecythis poiteaui	2		2
Licania leptostachya	1		1
Manilkara bidentata		1	1
Martiodendron parviflorum	1		1
Ocotea splendens		1	1
Parinari campestris		1	1
Pouteria guianensis		1	1
Protium crenatum	1	1	2
Pseudopiptadenia suaveolens	3	2	5
Pterocarpus officinalis	1		1
Qualea albiflora		2	2
Qualea rosea	10	30	40
Rhodostemonodaphne grandis		1	1
Sclerolobium melinonii		1	1
Sextonia rubra		1	1
Sloanea eichleri		1	1
Sterculia excelsa	1		1
Swartzia longicarpa	1	1	2
Tetragastris altissima	2	3	5
Trattinnickia sp.	1		1
Trymatococcus amazonicus	1		1
Grand total	57	63	120

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Stump Sprout Characteristics of Three Commercial Tree Species in Suriname

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Abstract: We compared stump sprouting by three common timber species in Suriname on the basis of sprout origins on stumps, sprout densities, and sprout height:diameter ratios. We then compared some leaf and stem functional traits of 15–18-month-old resprouts and nearby conspecific saplings of the same height (0.5–3.5 m) but unknown age. Stumps of *Dicorynia guianensis* Amsh. (29–103 cm in diameter) produced the most sprouts (x = 9.2/stump), followed by the 50–71 cm diameter stumps of *Eperua falcata* Amsh. (10.6/stump), and the 30–78 cm diameter *Qualea rosea* Amsh. (5.9/stump); sprout density did not vary with stump diameter. Sprouts emerged from the lower, middle, and upper thirds of the stumps of all three species, but not from the vicinity of the exposed vascular cambium in *Qualea*. With increased resprout density, heights of the tallest sprout per stump tended to increase but height:diameter ratios increased only in *Dicorynia*. Compared to conspecific saplings, sprouts displayed higher height-diameter ratios, higher leaf-to-wood mass ratios (LWR), and lower wood densities, but did not differ in leaf mass per unit area (LMA) or leaf water contents. These acquisitive functional traits may reflect increased resprout access to water and nutrients via the extensive root system of the stump. That we did not encounter live stump sprouts from the previous round of selective logging, approximately 25 years before our study, suggests that stump sprouts in our study area grow rapidly but do not live long.

Keywords: allometry; coppicing; sprout biomass; tree height:diameter ratios; tropical forestry

1. Introduction

Stump sprouting is common among trees in ecosystems characterized by frequent top-killing disturbances such as from fire [1] but is also common in the tropics after storms [2] and logging [3–5]. Resprouting is also the basis of silvicultural coppice management systems, such as those used for many centuries in Europe to produce firewood and small-dimension building materials [6]. In the tropics, coppicing is commonly used for the rapid production of small stems for fiber and fuel from species of *Eucalyptus* and *Acacia* [7]. Where stands are managed for the production of large timber trees, it is less clear that stump sprouts are beneficial given the likelihood that they will develop basal rots before

they reach harvestable size. Furthermore, where trees growing from seed are desired, fast-growing resprouts can be serious competitors [8]. In this study we explore stump sprouting by three species of commercial timber trees in Suriname to understand the silvicultural roles of stump sprouts after selective logging. In particular, we investigate the exceedingly rapid growth rates of stump sprouts by comparing several leaf and stem functional traits between resprouts and saplings (i.e., individuals growing directly from seed) of conspecifics of the same height. Comparisons of the three study species, which differ somewhat in life-history traits, are used as a preliminary assessment of the generality of emergent patterns related to stump sprouting and characteristics of the sprouts themselves.

Stump sprouts may grow more rapidly and tolerate drought better than seedlings because they have access to stored below-ground resources and benefit from the extensive root system of the top-killed tree [9–13]. These advantages might also influence the characteristics of the resprouts themselves and vary with where on the stump they emerge. Some species tend to sprout from the lower portions of stumps [14], others from the tops of stumps [15,16], and others from all along the stump [17]. At least one study reported that the tallest (i.e., longest) sprouts emerge from close to the top of stumps [18].

Crowding among resprouts and their increased access to below-ground resources are expected to result in differences between sprout and conspecific saplings of similar size and growing under otherwise similar conditions. In response to the crowding of sprouts on stumps, we expected higher height:diameter (H:D) ratios of sprouts than saplings. Given that sprouts are supplied with water and soil nutrients by the extensive root system of the stump, we expected them to invest relatively more in leaves than in stems and branches and to produce larger leaves with lower dry mass per unit area (LMA) and higher moisture contents. Based on their more rapid growth rates, we predicted lower wood densities in sprouts than conspecific saplings.

2. Materials and Methods

We studied 15–18-month-old stump sprouts in a tropical rain forest in the Mapane region of Suriname (5°11′40″ N, 54°50′0″ S) at 35–55 m above sea level in the Nv. Takt Timber Concession. Annual precipitation in the area ranges 1700–2500 mm and falls mostly during the main rainy season of April–August; mean annual temperature is 27 °C. The soil is a well-drained and nutrient-poor ferralsol on gently rolling terrain with slopes mostly <10%; lateritic concretions were evident on many road cuts.

The 50 ha area was selectively logged and silviculturally treated 15–18 months prior to this study. Logging removed an estimated 10 m^3/ha from 3–5 trees/ha. The experimental silvicultural treatment consisted of felling all trees >25 cm dbh (stem diameter at 1.3 m or above buttresses) that overtopped future crop trees defined as trees of commercial species smaller than the minimum cutting diameter of 50 cm dbh; this treatment resulted in the cutting of an additional 2–3 trees per hectare and increased the range of stump sizes available for our study. We studied the sprouts from stumps of the dominant species harvested: *Dicorynia guianensis* Amsh. ("basralocus," Fabaceae, subfamily Dialioideae), *Eperua falcata* Aubl. ("wallaba," Fabaceae, subfamily Detariodeae), and *Qualea rosea* Aubl. ("berg gronfolo," Vochysiaceae; all species hereafter referred to by their genus names). Based on studies of seed characteristics and seedling distributions in French Guiana [19,20], we surmise that *Dicorynia* is the most light-demanding of the three study species although its seeds (0.35 g per seed) are much larger than those of the other light-demanding non-pioneer *Qualea* (0.096 g/seed) and much smaller than those of the shade-tolerant *Eperua* (3.52 g/seed). None of these species produce root nodules, but *Eperua* benefits substantially from nitrogen fixation by free-living rhizospheric microbes [21]. We lack detailed records about the history of the study site other than that it was subjected to low intensity selective logging 25 years prior to our study; at that time, the same species were harvested.

To locate sprouted stumps of the three species, we searched the study area and consulted maps prepared for the harvest. While we searched for sprouted stumps from the recent harvest, we also sought out stump sprouts from the previous harvest. Although after 25 years sprouts from small

stumps might be difficult to distinguish from trees that grew directly from seed, sprouts from the large stumps of harvested trees remain easy to distinguish by their basal morphologies or multiple stems. When we encountered a sprouted stump we measured its diameter and height and then collected basic information about the sprouts. First of all, we counted sprouts that emerged from the vicinity of the vascular cambium exposed on the cut surface of the stump and then those on the upper, middle, and lower thirds of the stump sides (only one instance of obvious root sprouting was encountered, so this sprout origin was not considered). For stumps with >10 sprouts, we measured the heights and basal diameters (at 10 cm above the point of origin) of two randomly selected sprouts from each origin category; if there were <10 sprouts, we measured them all. We also measured the heights and diameters of the two tallest sprouts on each stump.

To compare conspecific sprouts and saplings, we used the data from the tallest sprout per stump and made similar measurements on conspecific saplings of a similar height in the same area (Figure 1). The sprouts were 15–18 months old at the time of sampling whereas we do not know the ages of the saplings. We harvested the sprouts and saplings and measured their total above-ground fresh mass and the proportion of that mass allocated to leaves (i.e., leaf weight ratio: LWR). Subsamples of leaves and woody material were collected to determine fresh-to-dry weight conversion factors by oven-drying to constant mass at 105 °C. From each sprout and sapling we selected the five largest leaves to determine lamina area with Image J software, moisture contents, and leaf mass per area (LMAs; for *Dicorynia* and *Eperua*, the data collected pertain to individual leaflets).


(**a**)　　　　　　　　　　　　　　　　　　　　　　(**b**)
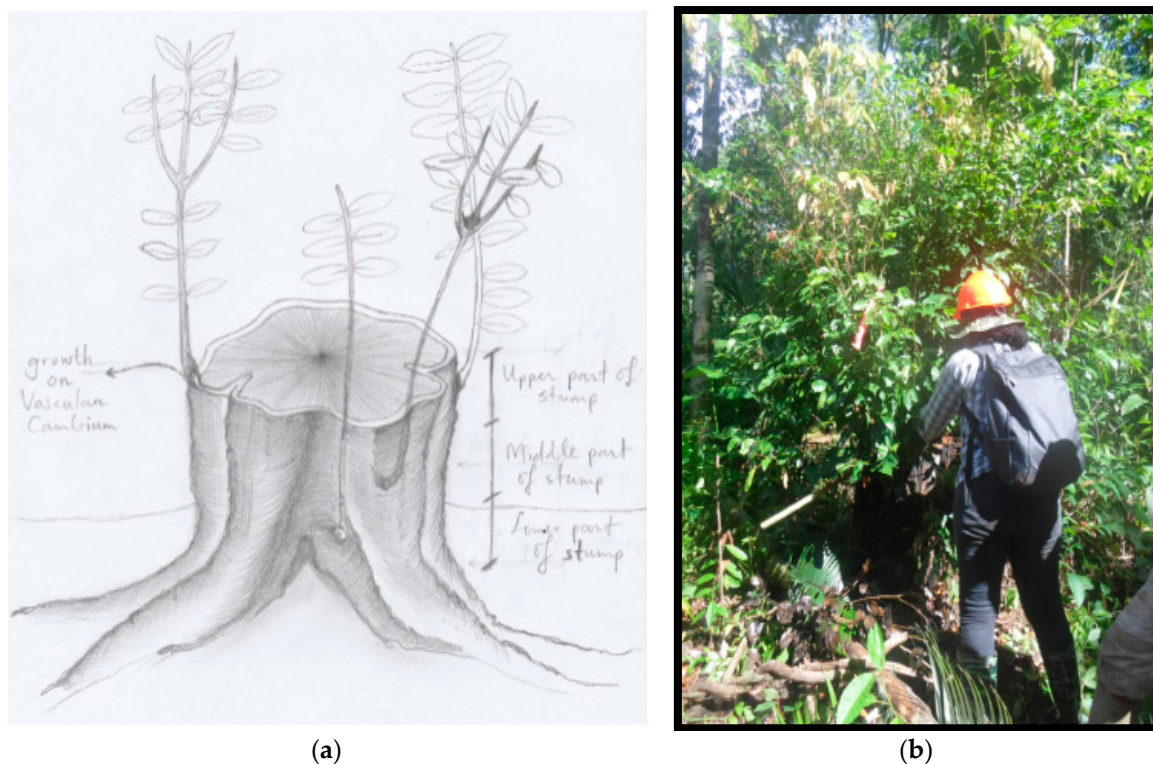
Figure 1. Diagrammatic representation of a stump showing the four possible sprout origin locations (**a**) and a sprouted stump being measured in the field (**b**).

3. Results

3.1. Stump Characteristics

Qualea stumps were smaller in diameter than those of the other two species but there was substantial overlap in their ranges (F = 28.8, $p < 0.01$; Table 1). The species also differed in regard to the number of sprouts per stump (F = 20.3, $p \leq 0.0001$), with *Dicorynia* and *Eperua* producing the most and

Qualea the least (Table 1). There was no relationship between sprout density and stump size in any of the three species (Figure 2).
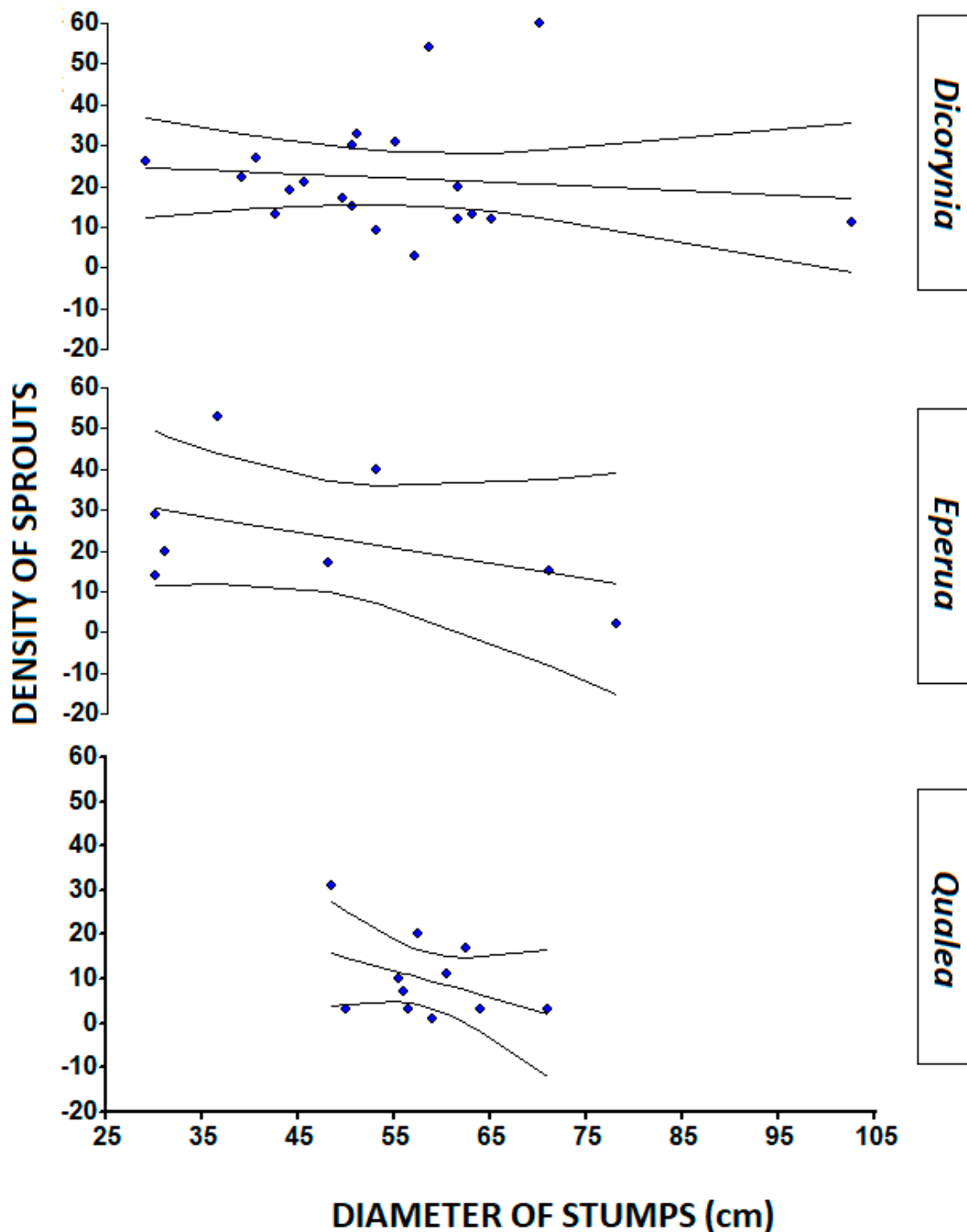

Figure 2. Sprout density (i.e., number of sprouts per stump) as a function of stump diameter (*Dicorynia* = $27.6 - 0.10 \times$ diameter (N = 21; $p = 0.57$, $R^2 = 0.02$); *Eperua* sprout density = $41.8 - 0.38 \times$ diameter (N = 8; $p = 0.27$, $R^2 = 0.20$); *Qualea* sprout density = $44.9 - 0.60 \times$ diameter (N = 11; $p = 0.22$, $R^2 = 0.16$)). Regression lines bounded by 95% confidence intervals.

Table 1. Stump diameters and densities of three commercial timber species. For among species contrasts, means followed by different letters differed (least significant difference tests, $p < 0.05$).

| Species	N	Mean Stump Diameter (cm)	S.D.	Range (cm)	Mean # Sprouts Per Stump	SD	Range (#)
Dicorynia guianensis Amsh.	19	61.79 [b]	16.14	29–102.5	23.73 [a]	14.46	3–60
Eperua falcata Aubl.	5	48.60 [c]	18.56	31–75.5	23.75 [a]	16.26	2–53
Qualea rosea Aubl.	10	71.55 [a]	17.83	51.50–110	4.17 [b]	3.49	1–11

The locations on the stumps from which sprouts emerged varied among the three species only insofar as no sprouts emerged from the vicinity of the vascular cambium on *Qualea* stumps (Figure 3). Sprout lengths did not vary with height on the stump from which they emerged (Figure 4). Length of the tallest sprout per stump increased slightly but not significantly with sprout densities in both *Dicorynia* and *Qualea* but not at all in *Eperua* (Figure 5). Similarly, the height:diameter ratio of the tallest sprout increased with sprout density in *Dicorynia* but not in the other species (Figure 6).
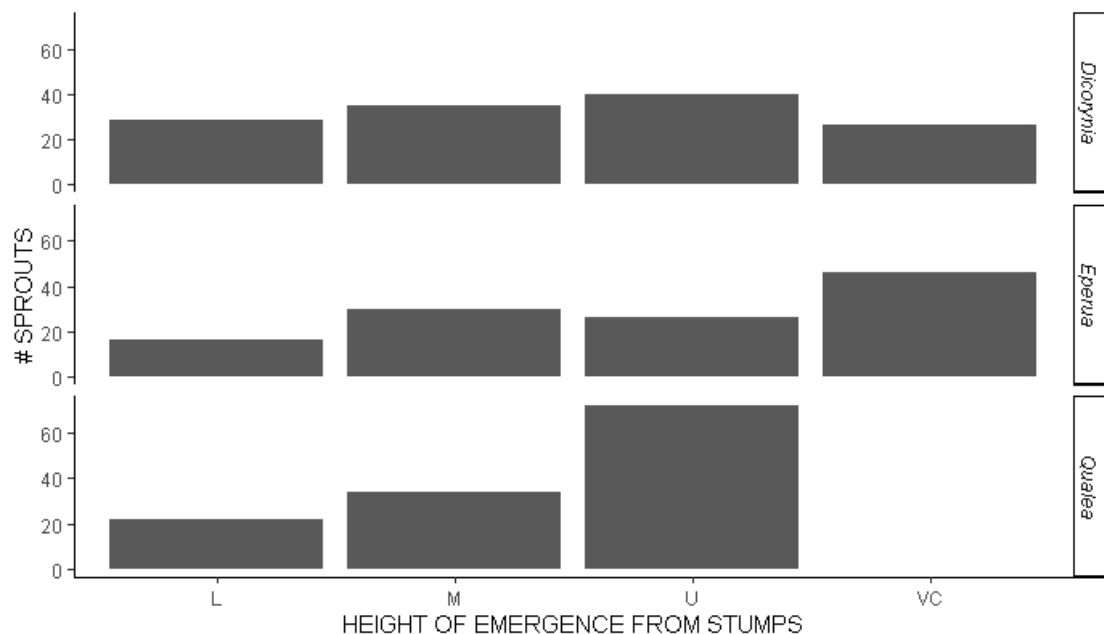
Figure 3. Point-of-origin percentages of sprouts from stumps of *Dicorynia*, *Eperua*, and *Qualea* by percentage (L = lower third of stump, M = middle third, U = upper third, VC = from under the bark at the top of the cut stump, i.e., from the vicinity of the vascular cambium).
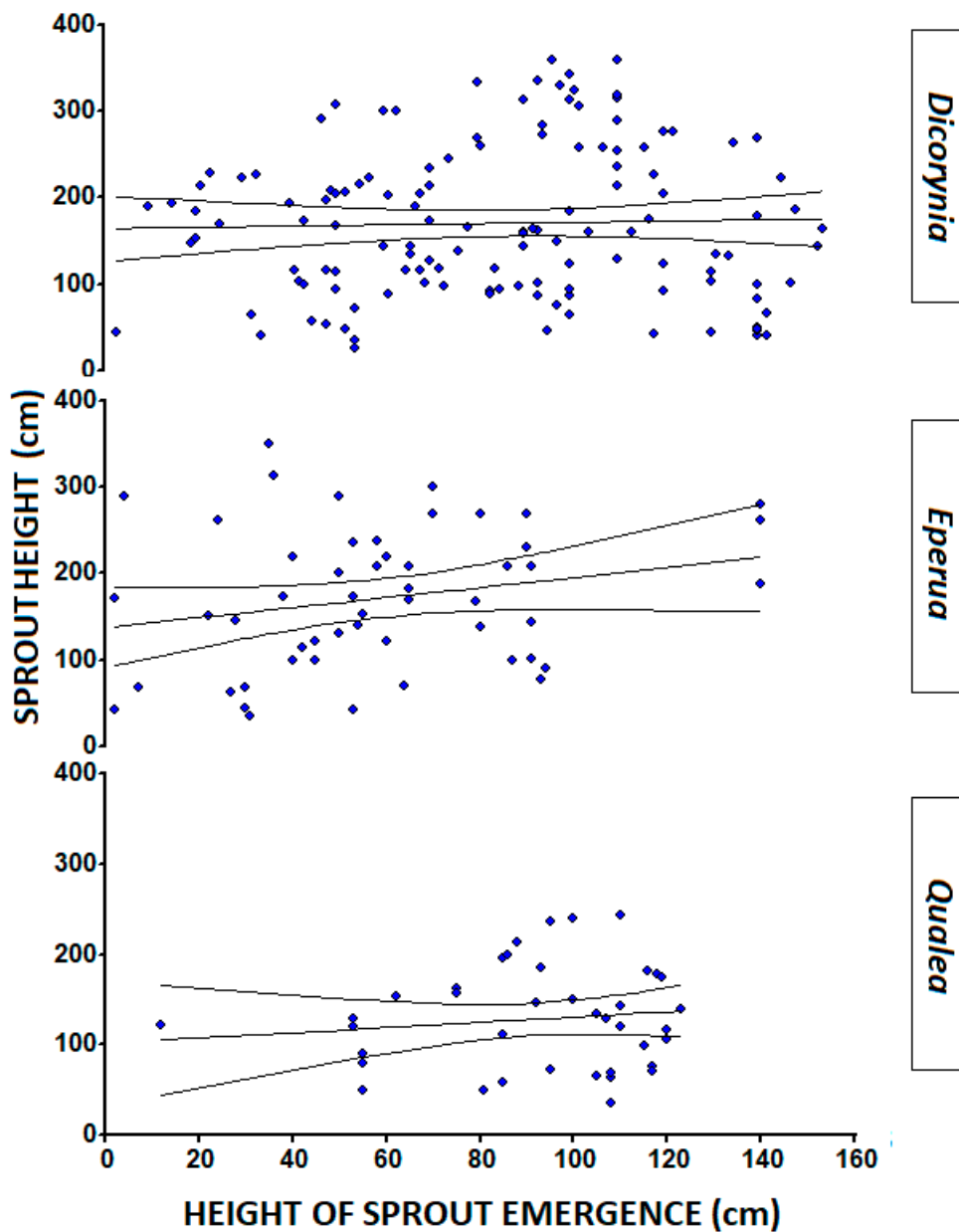
Figure 4. Height (i.e., length) of sprouts as a function of the height on the stump from which they emerged (*Dicorynia* = 161.0 + 0.07 × emergence height (N = 133; p = 0.73; R^2 = 0.001); *Eperua* = 137.67 + 0.58 × emergence height (N = 52; p = 0.10; R^2 = 0.05); *Qualea* = 101.68 + 0.29 × emergence height (N = 41; p = 0.42; R^2 = 0.02)). Regression lines bounded by 95% confidence intervals.
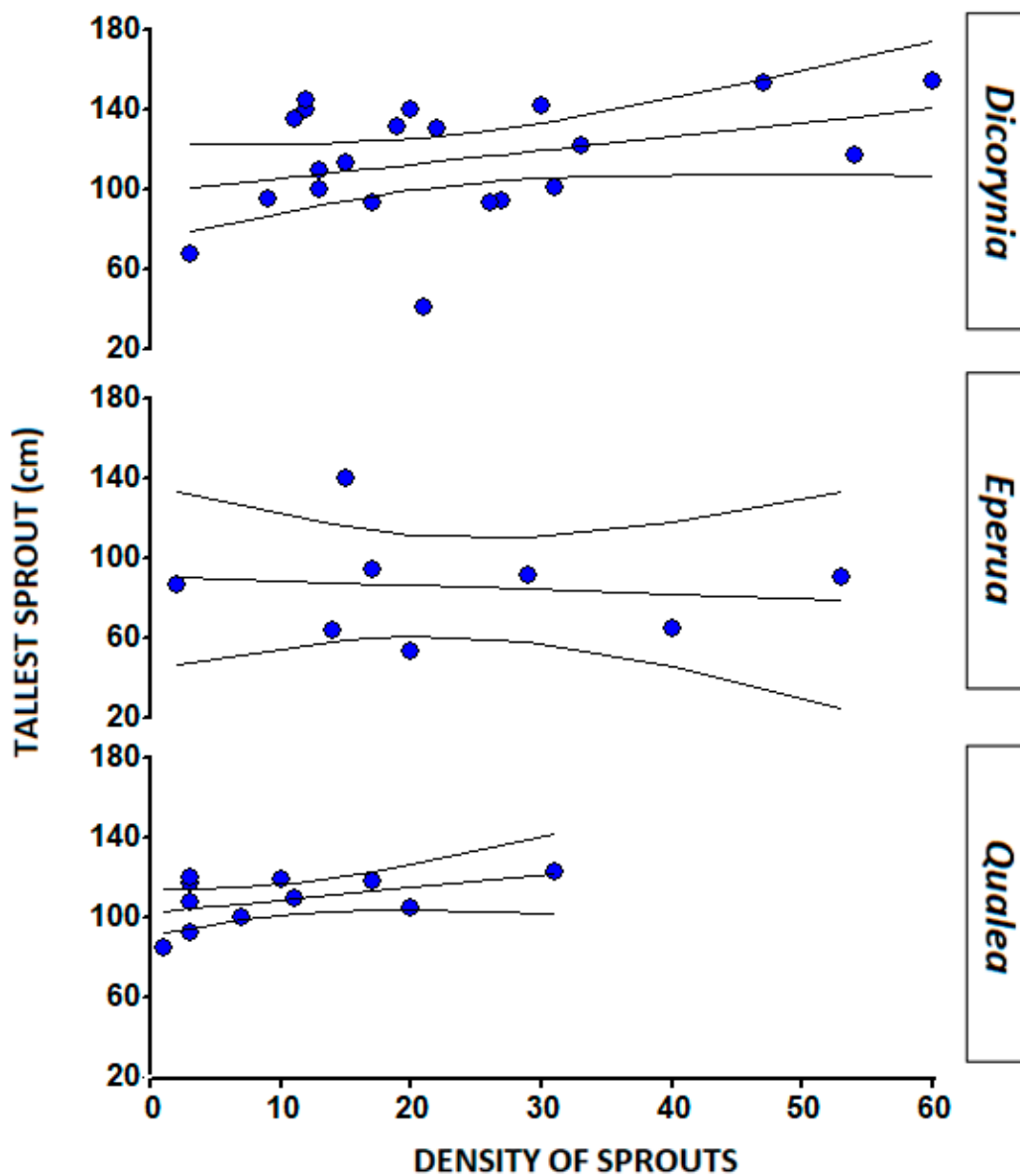
Figure 5. Relationship between the length of the tallest sprout and sprout density on each stump (*Dicorynia* sprout length = 98.51 + 0.70 × density (N = 21; p = 0.11, R^2 = 0.13); *Eperua* sprout length = 90.73 − 0.22 × density (N = 8; p = 0.75, R^2 = 0.02); *Qualea* sprout length = 102.56 + 0.63 × density (N = 11; p = 0.14, R^2 = 0.23)). Regression lines bounded by 95% confidence intervals.
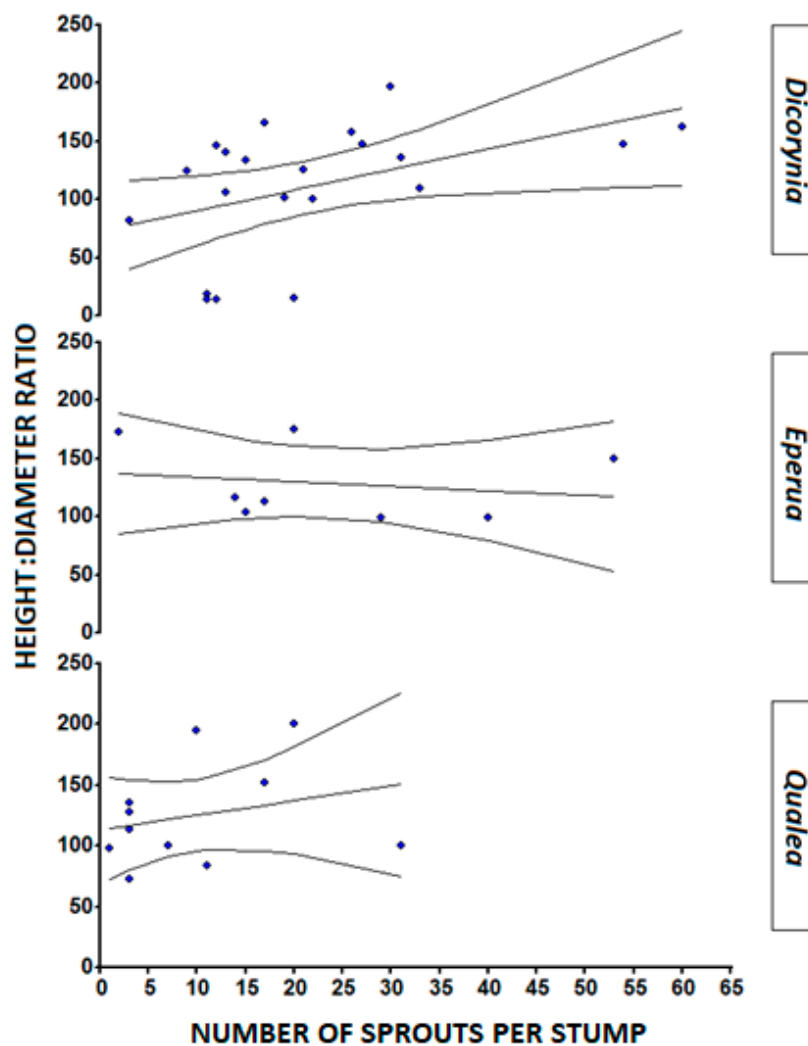
Figure 6. Height:diameter (H:D) ratios of the tallest sprouts as a function of numbers of sprouts per stump of *Dicorynia* (H:D = 72.96 + 1.77 × sprout density ($p < 0.05$, R^2 = 0.21; N = 21)], *Eperua* (H:D = 137.97 − 0.38 × sprout density (p = 0.64, R^2 = 0.04; N = 8)) and *Qualea* (H:D = 113.42 + 1.2 × sprout density (p = 0.43, R^2 = 0.07; N = 11)). Regression lines bounded by 95% confidence intervals.

3.2. Comparisons of Sprouts and Conspecific Saplings

Sprouts and conspecific saplings of *Dicorynia* and *Eperua* more often differed in functional traits than observed for *Qualea* (Table 2). Sprouts and saplings of none of the three species differed significantly in height:diameter ratios, but there was a strong tendency, especially in *Dicorynia*, for the sprouts to be taller for a given diameter. In the case of the proportion of above-ground biomass allocated to leaves, *Dicorynia* and *Eperua* sprouts invested 21% and 37% more to leaves than stems, respectively, whereas *Qualea* sprouts and saplings did not differ in this trait. Leaf moisture contents were expected to be higher and LMAs were expected to be lower in sprouts than saplings, but none of the species showed differences in these traits. In contrast, leaflets of *Dicorynia* and *Eperua* saplings were 25% and 37% larger on sprouts than on saplings, while *Qualea* sprout and sapling leaves were almost exactly the same size. Wood densities were 18% and 15% lower in *Dicorynia* and *Eperua* sprouts than saplings, respectively, while the woods of *Qualea* sprouts and saplings did not differ.

Table 2. Comparisons of 15–18-month-old sprouts with conspecific saplings of similar stature but unknown age on the basis of the proportion of dry shoot mass invested in leaves (leaf mass ratio, LWA), leaf moisture contents, leaf area, leaf mass per unit area (LMA), and wood density. Individual leaf data for *Dicorynia* and *Eperua* pertain to individual leaflets; leaf area, LMA, and water content values are for lamina only (i.e., petiole and rachis removed).

Species	Sprouts (s.d., N)	Saplings (s.d., N)	t	p
	Height:Diameter			
Dicorynia	139.8 (41.48, 18)	126.6 (18.15, 10)	1.2	0.26
Eperua	132.3 (54.71, 5)	109.3 (27.26, 3)	0.8	0.46
Qualea	116.9 (40.09, 9)	123.2 (26.85, 21)	0.4	0.67
	% Mass in Leaves	**% Mass in Leaves**		
Dicorynia	48.9 (12.34, 18)	33.7 (13.91, 10)	2.9	0.01
Eperua	43.4 (8.546, 5)	16.3 (7.81, 3)	4.6	<0.01
Qualea	47.8 (8.836, 9)	41.2 (12.63, 21)	1.6	0.11
	% H_2O in Leaves	**% H_2O in Leaves**		
Dicorynia	64.4 (4.35, 13)	59.07 (5.82, 6)	2.0	0.08
Eperua	52.756 (3.36, 5)	57.121 (7.24, 3)	1.0	0.41
Qualea	67.397 (8.79, 5)	67.281 (2.14, 5)	0.1	0.98
	Leaf Area (cm^2)	**Leaf Area (cm^2)**		
Dicorynia	224.2 (73.30, 50)	168.8 (20.39, 10)	4.5	<0.0001
Eperua	101.7 (45.27, 20)	64.0 (20.73, 20)	3.1	<0.005
Qualea	65.1 (17.49, 25)	70.2 (8.88, 14)	1.2	0.23
	LMA ($g\ m^{-2}$)	**LMA ($g\ m^{-2}$)**		
Dicorynia	58.9 (11.49, 50)	57.7 (14.99, 10)	0.3	0.08
Eperua	49.9 (21.09, 19)	51.1 (30.94, 9)	0.1	0.91
Qualea	73.5 (38.63, 25)	77.4 (21.13, 14)	0.4	0.68
	Wood Density ($g\ cm^{-3}$)	**Wood Density ($g\ cm^{-3}$)**		
Dicorynia	0.42 (0.06, 39)	0.51 (0.08, 18)	4.5	<0.001
Eperua	0.50 (0.04, 15)	0.59 (0.03, 9)	6.3	<0.01
Qualea	0.41 (0.10, 15)	0.50 (0.07, 15)	2.8	0.41

4. Discussion

In the selectively logged lowland tropical forest we studied in Suriname, of three commercial timber species, the two Fabaceae (*Dicorynia* and *Eperua*) often sprouted in ways that differed from the one sampled Vochysiaceae (*Qualea*). *Dicorynia* was the most prolific sprouter, with up to 60 on a single stump, but even *Qualea*, the least prolific sprouter, averaged nearly 6 per stump. Unexpectedly, sprout density did not vary with stump diameter in any of the species, but at least in *Dicorynia*, the length of the tallest sprout increased with sprout density, which suggests inter-sprout competition or perhaps a thigmomorphogenic response to crowding [22]. This contention is supported by the positive relationship between sprout height:diameter ratio and sprout density in *Dicorynia* and *Eperua* (but not *Qualea*). While sprouts emerged from all heights on the stumps of all three species, sprout lengths did not vary with their emergence heights. Unlike the two Fabaceae, *Qualea* produced no sprouts from the vicinity of the exposed vascular cambium on the cut surface (but twice as many from the top 1/3 of the stump). It is perhaps noteworthy that in the same stand, [23] reported the proportions of sprouted stumps were highest for *Dicorynia* (78%), intermediate for *Eperua* (50%), and low for *Qualea* (15%).

Comparisons of some functional traits of sprouts and conspecific saplings of similar heights revealed patterns similar to those described above for the sprouting process; differences were often clear for the two Fabaceae but not for the Vochysiaceae we sampled. When there were differences, resprouts displayed more acquisitive traits than conspecific saplings. In particular, compared to

saplings, sprouts of both *Dicorynia* and *Eperua* invested much more in leaf mass than in their stems and branches, their leaves were much larger, and their stem wood densities were lower. In contrast, *Qualea* sprouts and saplings did not differ in any of these traits. Given that sprouts can make use of their stump's root system, they have access to more water and soil nutrients than nearby saplings [24]. Presumably, these benefits are enjoyed by sprouts of all three species, but why then did *Qualea* not show a similar response? Might this difference be related to the relatively low densities of sprouts on *Qualea* stumps? More generally, if their use of the stump's extensive root system means that sprouts have access to more water and nutrients than conspecific saplings, then why did none of the species show the expected differences in leaf water contents or LMAs?

Among our sample of only three species, two of which are Fabaceae, functional trait differences between resprouts and saplings did not follow the patterns expected from their life histories. The most and least shade tolerant of the studied species (*Eperua* and *Dicorynia*, respectively) produced more sprouts with more and larger leaves than *Qualea*. Of the three species, nitrogen availability is only elevated in *Eperua* due to its association with non-symbiotic nitrogen-fixing organisms [21], but that species was intermediate in most of the measured traits related to stump sprouting other than its extraordinarily high leaf weight ratios (i.e., leaf mass as percentage of total sprout mass). Clearly, more species need to be sampled in sites that differ in resource availability to assess adequately the hypotheses that functional trait responses to stump sprouting are related to life history traits and environmental conditions.

From a timber stand management perspective, stump sprouting has some positive ecological and silvicultural consequences. Even if sprouts do not survive for an entire cutting cycle, their prolific initial growth contributes to the rapid revegetation of felling gaps, which helps maintain forest microclimates, reduces erosion, and suppresses unwanted pioneer trees, lianas, and other forest weeds [4]. Stump sprouts of commercial species that live long enough to reproduce contribute to the stocking of those species. Finally, even if stump sprouts do not survive for an entire cutting cycle or produce merchantable timber, where there are markets for small stems, coppicing could provide a source of income, but this is not the case in our study area in Suriname.

Stump sprouts have several negative consequences for timber stand management. First of all, prolifically growing stump sprouts are serious above- and below-ground competitors to nearby future crop trees, i.e., individuals of commercial species smaller than the minimum harvest diameter. The total leaf area of a single sprouted stump gives some idea of the potential strength of this competitive effect. Take, for example, an average *Dicorynia* stump with 10 sprouts, each of which has 300 g dry weight of leaves with an LMA of 60 g/m^2; such a stump will support an estimated 50 m^2 of leaves; in contrast, the total leaf area of an average conspecific sapling is <2 m^2. These calculations are admittedly rough, but they are nevertheless illustrative. Furthermore, sprouted stumps with abundant and poorly defended foliage may indirectly increase local herbivore pressure by providing abundant edible leaves. Similarly, for trees connected to conspecific neighbors below ground via root grafts, stumps provide an interchange pathway for heartrots and pathogens. It should also be noted that for root grafted trees, treating stumps with herbicides can have negative consequences if the chemicals are translocated effectively to the connected neighbor.

Monitoring the sprouted stumps over time could be revealing in a number of ways. First of all, we expect thinning of sprouts over time as they compete for limited resources. The surviving sprouts may change their acquisitive functional traits as resources stored in the stump and roots are exhausted. For example, as our 15–18-month-old sprouts age, we would expect them to change their allometries to become more like saplings [25] and to invest relatively less in leaves than in woody support structures, as observed in other woody plants [26]. We also expect leaf sizes in sprouts to decrease until they more resemble those of saplings. Most fundamentally, given our failure to find sprouted stumps from the selective timber harvest from our study area 25 years prior to our entry, we expect a massive die off of sprouted stumps due at least in part to stump decay, which reduces the mechanical stability of the sprouts, perhaps coupled with attacks by pathogens attracted to the abundant foliage and low

density wood of the crowded stump sprouts. In any event, our findings suggest that in studies of plant functional traits, resprouts should be differentiated from individuals of seed origin.

5. Conclusions

In contrast to other reports in the literature, at our study site in Suriname 15–18 months after logging, stump diameter did not have an influence on sprout density nor did the height of sprout emergence from stumps influence their lengths. While we observed some marked differences in leaf and stem functional traits between the sprouts and saplings of *Dicorynia* and *Eperua* with less clear differences for *Qualea*, the patterns were not clearly related to differences in life history characteristics of these three species.

Even if stump sprouts are not long-lived, which is what we expect for those in our study area, prolific initial stump sprouting has both positive and negative ecological and silvicultural effects. By rapidly covering the ground with foliage, resprouting may reduce proliferation of pioneer trees, lianas, and other light-demanding weeds. At the same time, the competitive effects of stump sprouts on future crop trees deserve consideration. Monitoring the fates of stump sprouts over time is needed to determine whether or not their effects are transient.

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