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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).

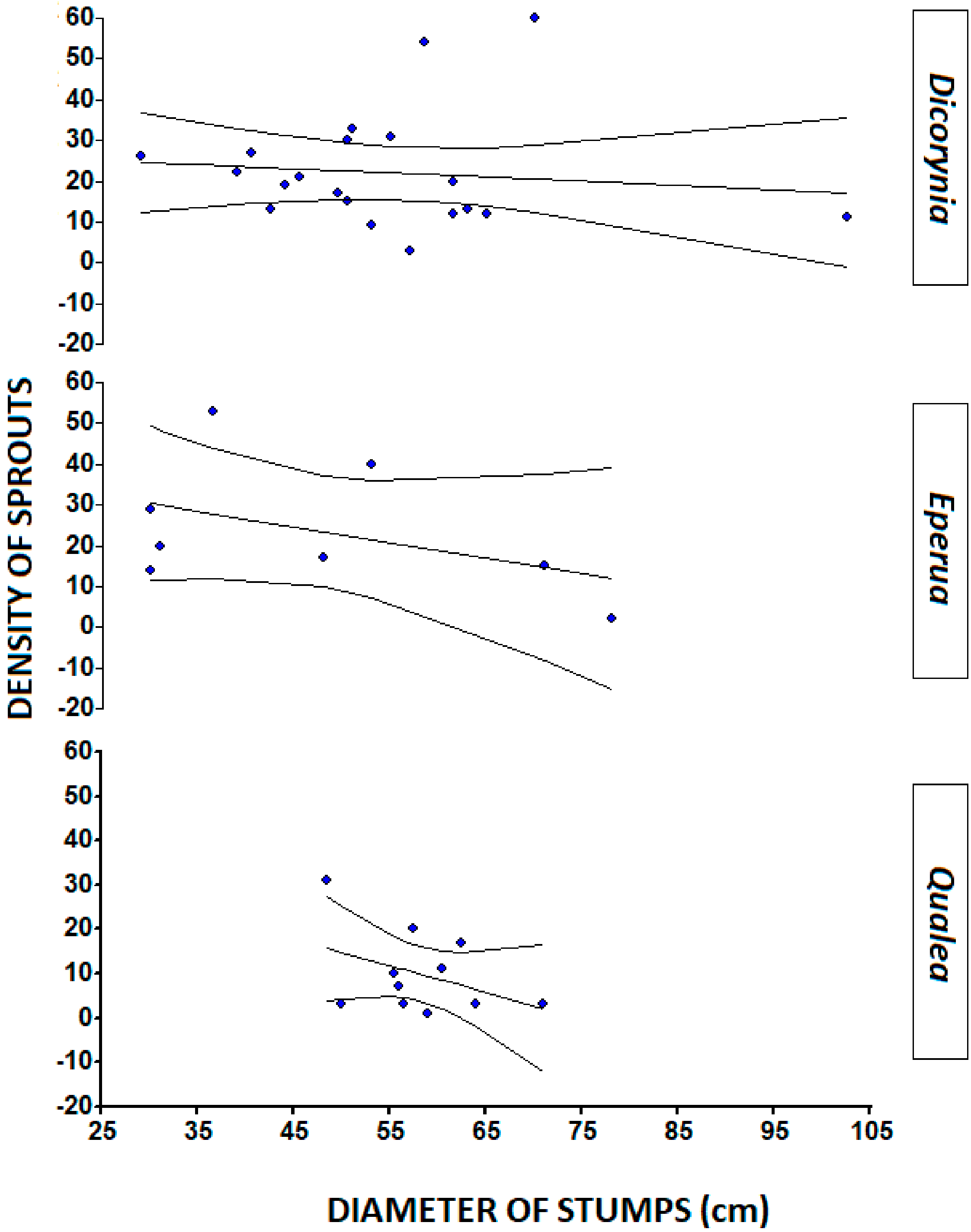

Figure 2. Sprout density (i.e., number of sprouts per stump) as a function of stump diameter (*Dicorynia* = 27.6 − 0.10 × diameter (N = 21; p = 0.57, R^2 = 0.02); *Eperua* sprout density = 41.8 − 0.38 × diameter (N = 8; p = 0.27, R^2 = 0.20); *Qualea* sprout density = 44.9 − 0.60 × diameter (N = 11; 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).

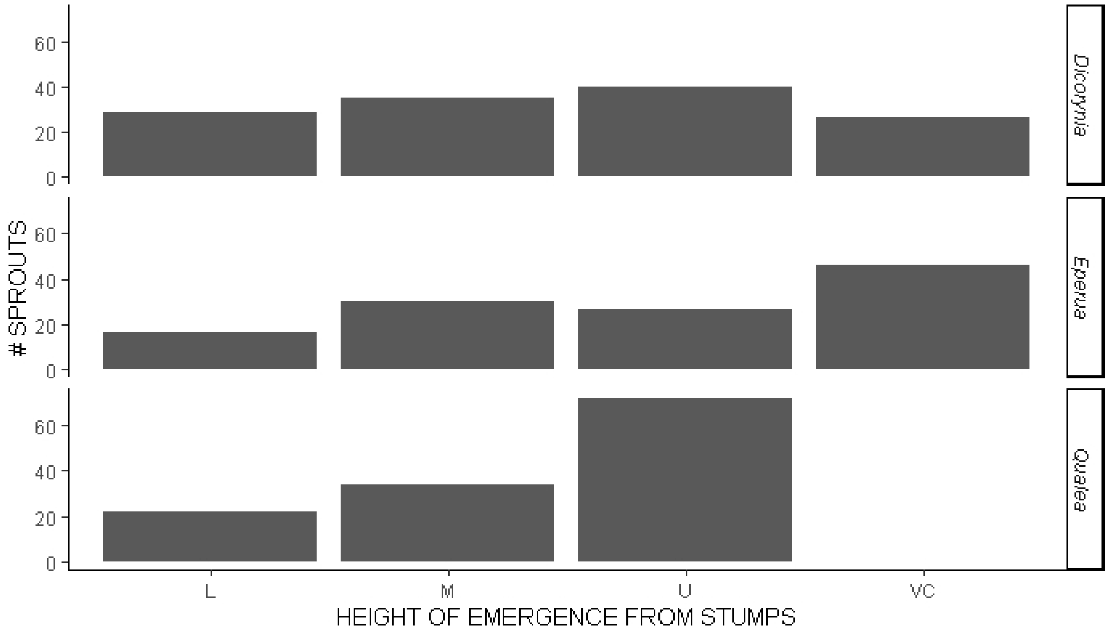

Figure 3. Point-of-origin percentages of sprouts from stumps of *Dicorynia*, *Eperua*, and *Qualea* by percentage (L = lower third of stump, M = middle third, U = upper third, VC = from under the bark at the top of the cut stump, i.e., from the vicinity of the vascular cambium).

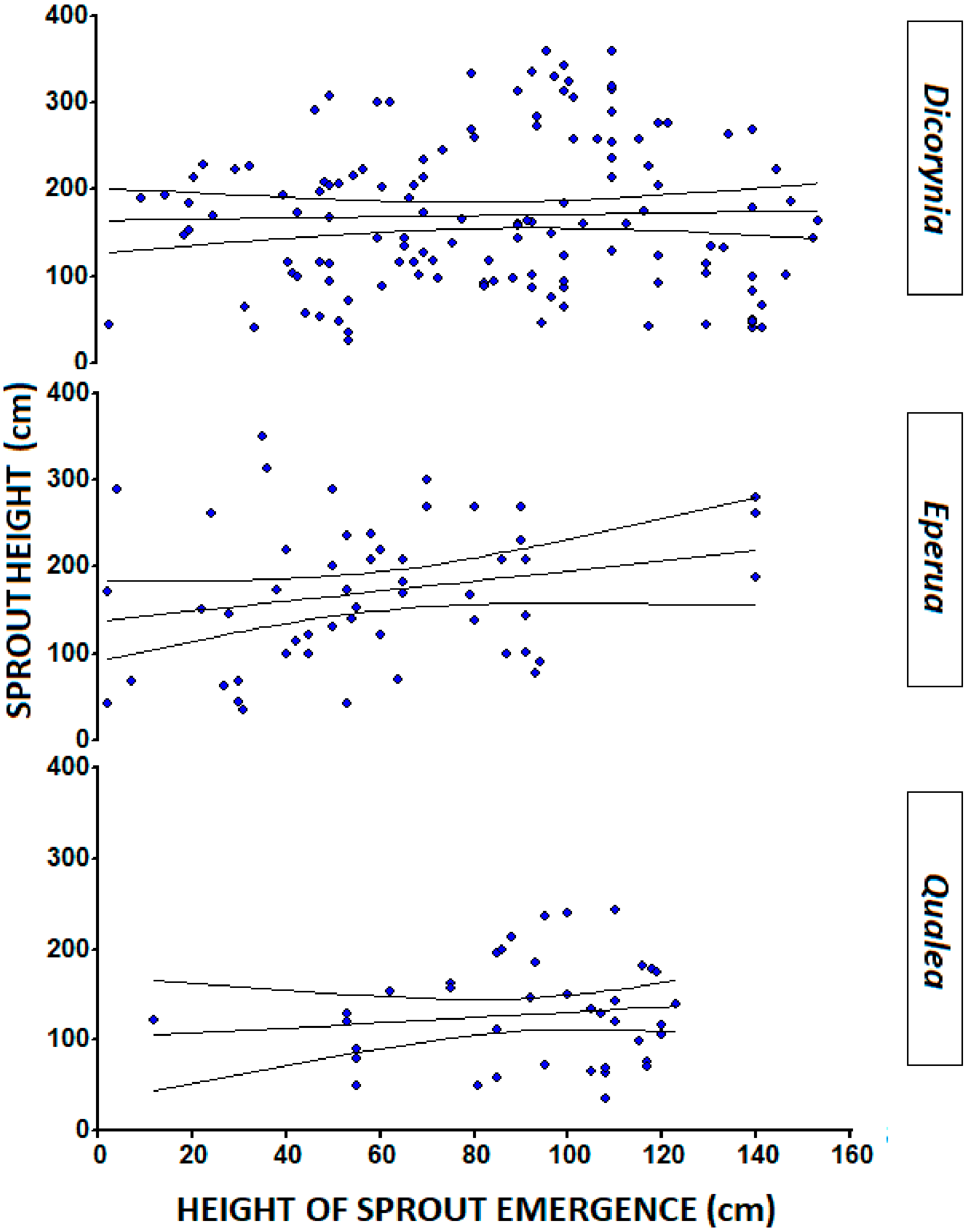

Figure 4. Height (i.e., length) of sprouts as a function of the height on the stump from which they emerged (*Dicorynia* = 161.0 + 0.07 × emergence height (N = 133; p = 0.73; R^2 = 0.001); *Eperua* = 137.67 + 0.58 × emergence height (N = 52; p = 0.10; R^2 = 0.05); *Qualea* = 101.68 + 0.29 × emergence height (N = 41; p = 0.42; R^2 = 0.02)). Regression lines bounded by 95% confidence intervals.

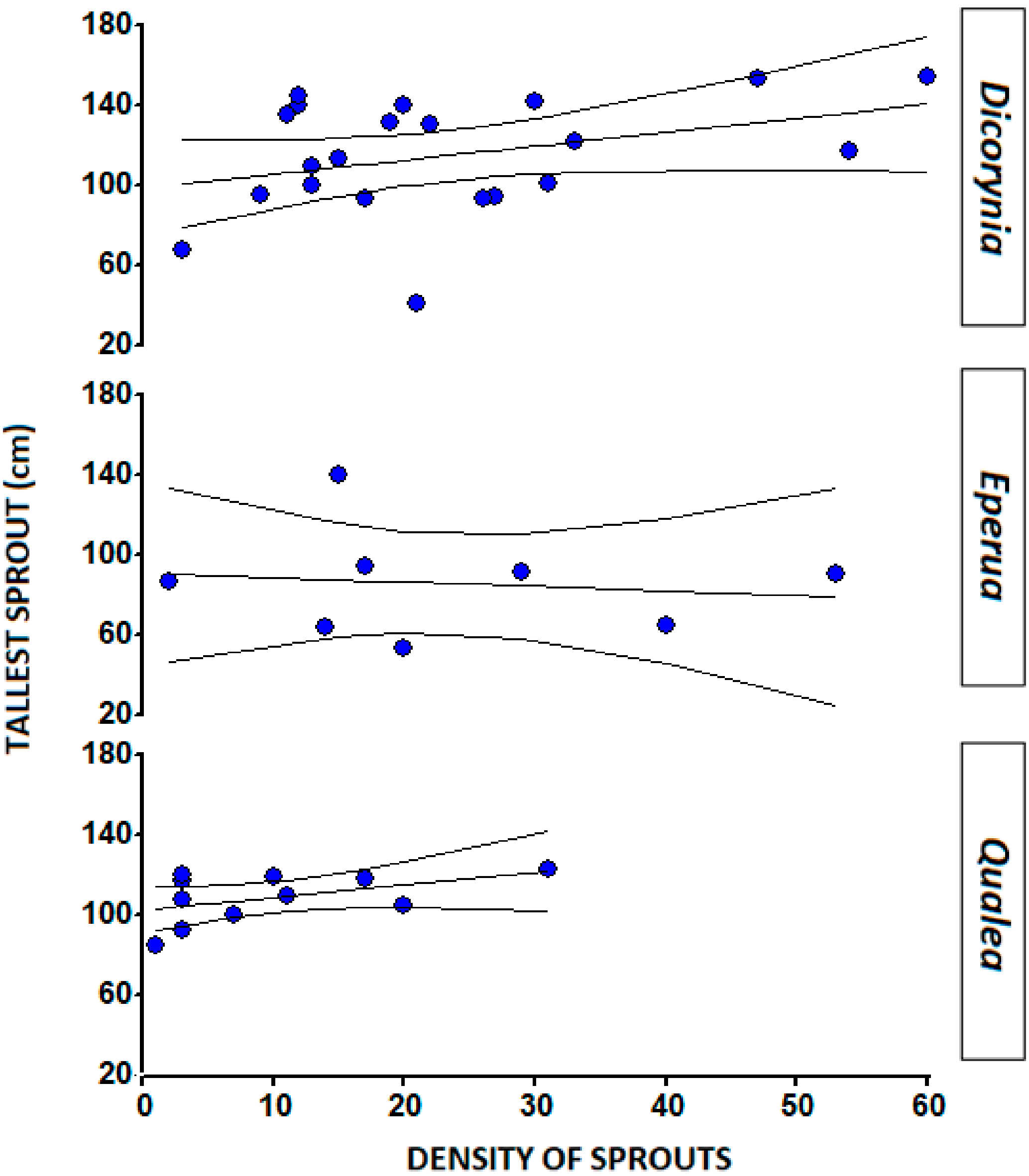

Figure 5. Relationship between the length of the tallest sprout and sprout density on each stump (*Dicorynia* sprout length = 98.51 + 0.70 × density (N = 21; $p = 0.11$, $R^2 = 0.13$); *Eperua* sprout length = 90.73 − 0.22 × density (N = 8; $p = 0.75$, $R^2 = 0.02$); *Qualea* sprout length = 102.56 + 0.63 × density (N = 11; $p = 0.14$, $R^2 = 0.23$)). Regression lines bounded by 95% confidence intervals.

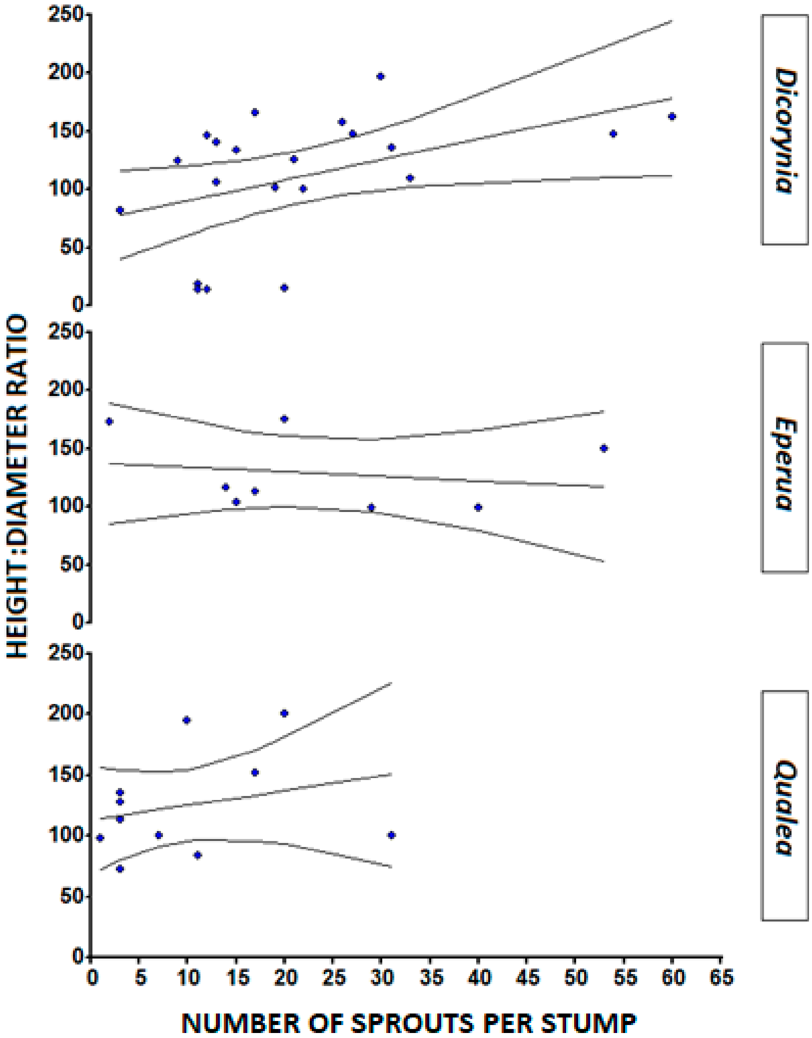

Figure 6. Height:diameter (H:D) ratios of the tallest sprouts as a function of numbers of sprouts per stump of *Dicorynia* (H:D = 72.96 + 1.77 × sprout density (p < 0.05, R^2 = 0.21; N = 21)], *Eperua* (H:D = 137.97 − 0.38 × sprout density (p = 0.64, R^2 = 0.04; N = 8)) and *Qualea* (H:D = 113.42 + 1.2 × 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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