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ORIGINAL PAPER

Interspecific differences in the oleoresin production of *Copaifera* L. (Fabaceae) in the Amazon rainforest

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Abstract
• ***Context*** *Copaifera* species produce an oleoresin of commercial importance that is widely extracted in Amazon communities.

• ***Aims*** This paper addresses two questions. (1) What are the morphological characteristics of *Copaifera* species that influence oleoresin production? (2) How do different *Copaifera* species respond to repeated harvests?

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Contribution of the co-authors Karina Martins: designing the experiment, collecting data, running the data analysis writing the paper
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- ***Methods*** We performed a large-scale experiment in the Brazilian Amazon. We tapped 110 *Copaifera* trees belonging to four species, and several morphological tree characteristics were measured to determine their effect on oleoresin production.
- ***Results*** The proportion of *Copaifera reticulata* and *Copaifera paupera* trees that yielded more than 1 ml oleoresin was higher than the other species. The oleoresin volumes from yielding *Copaifera pubiflora* trees were significantly higher than those from *C. reticulata* and *C. paupera*, with *Copaifera multijuga* yielding intermediate values. Interestingly, none of the studied morphological tree characteristics had a significant effect on the proportion of yielding trees. Hollowed trees yielded significantly smaller volumes than non-hollowed trees. Both the proportion of yielding trees and oleoresin volumes decreased from the first to the second harvests for *C. reticulata* and *C. paupera*; however, the opposite pattern was observed for *C. pubiflora*.
- ***Conclusions*** Oleoresin production capacity varies by species, and management protocols should account for these differences.

Keywords Brazilian Amazon · Copaiba · Extractivism · Forest management · Non-timber forest products · Sustainability

1 Introduction

Understanding the morphology and yield of different oleoresin-producing species is crucial for developing sustainable management practices, particularly in tropical forests where non-timber forest products (NTFPs) are subject to little or no regulation with regard to yield due the lack of knowledge of the behavior of the species involved.

The commercial exploitation of NTFPs is often touted as a way to reconcile rural development with the conservation of tropical forests, and hundreds of millions of people worldwide exploit NTFPs, either alone or combination with timber logging, for subsistence and income (Ahenkan and Boon 2011; Arnold and Pérez 2001; FAO 2008; Guariguata et al. 2010; Herrero-Jáuregui et al. 2009; Shanley et al. 2012; Ticktin 2004). In the Amazon forest, the knowledge of NTFP harvesting techniques and applications is found in ancient and local communities, primarily among indigenous people and rubber tappers. Clearly, the appropriate management and harvest of many NTFPs are important for sustaining the rural economies that rely on them.

Copaifera species (Leguminosae: Caesalpinioidae) produce an oleoresin popularly known as "óleo-de-copaíba" (hereafter referred to as oleoresin), an important NTFP from the Brazilian Amazon. The oleoresin is found in the interconnecting secretor channels located throughout the tree, particularly in the trunk where it accumulates (Martins-da-Silva 2006). In local communities, copaiba oleoresin is a multipurpose home remedy that is used as an anti-inflammatory and to treat wounds and skin problems. Oleoresin is also sold in Brazilian markets and exported to various countries where it is used in medicinal and cosmetic applications (Veiga Junior and Pinto 2002). *Copaifera* species are also commercially harvested for their timber in several Amazonian countries (Herrero-Jáuregui et al. 2011, 2012). The Amazon region is the primary supplier of oleoresin (Cascon and Gilbert 2000): 580 t of copaiba oleoresin was produced in Brazil in 2010, representing US$ 2,416,186 (IBGE 2010).

Copaiba oleoresin is commercially harvested in natural forests. In the past, trees were felled, or large holes were fashioned in the trunk with an axe or a chainsaw to tap the oleoresin (Plowden 2001). However, current management practices consist of making a hole of only approximately 1.91 cm diameter in the trunk to drain the oleoresin and then sealing the opening with wood.

Information about the productive capabilities of source trees under varying environmental conditions and the ecological effects of harvesting on plant populations is scarce (Ticktin 2004), and there is concern about supplying sufficient quantities of oleoresin to meet the market demand. Previous studies suggest that oleoresin production differs by species (Newton et al. 2011; Rigamonte-Azevedo et al. 2006); however, this variation is given little consideration in the design of sustainable management policies and guidelines (Leite et al. 2001) for oleoresin production in the region.

Although the process of oleoresin production and accumulation within trees is poorly understood, it is known that *Copaifera* trees can regenerate oleoresin. Because a sustainable means of oleoresin production is desired, permanent production from the same tree requires consecutive harvests. However, these harvesting practices consist of re-opening the hole or re-drilling the tree, and the available reports differ with respect to the frequency that individual trees can be tapped. Indeed, the responses of different *Copaifera* species to consecutive harvests are still not understood. Alencar (1982) reported higher oleoresin volumes in the second harvest than in the first, with declining volumes in the third. Decreased production in the second harvest has also been documented, and oleoresin can only be harvested once from some trees (Herrero-Jáuregui 2009; Martins et al. 2008; Plowden 2003; Rigamonte-Azevedo et al. 2006; Silva-Medeiros and Vieira 2008). Therefore, studies of the factors affecting oleoresin production that incorporate a uniform experimental design are needed to develop economically and ecologically sound strategies of copaiba oleoresin production.

Our goal is to evaluate oleoresin production in different *Copaifera* species on a large geographical scale. We address the following questions: (1) what are the tree morphological characteristics that influence oleoresin production? and (2) how do different *Copaifera* species respond to initial and consecutive harvests?

2 Methods

2.1 *Copaifera* spp.

Amazonian *Copaifera* species are typically light-demanding, canopy trees occurring in humid, dense or open tropical forests of a wide variety of forest types, including upland, lowland, and inundated habitats, in clayey or sandy soils (Alencar 1982; Carvalho 1994; Plowden 2004). We studied four species of *Copaifera*. *Copaifera paupera* (Herzog) Dwyer occurs in Brazil, Bolivia, and Peru; it is observed in the southwestern region of the Brazilian Amazon, particularly in Acre where it is widely distributed. *Copaifera reticulata* Ducke occurs only in the Brazilian Amazon. It is commonly distributed in the east, particularly in Pará State; although rare in the western and northeastern Amazon regions, it is more abundant in the southwest of Amazonas, southeast of Roraima and northern Mato Grosso. *Copaifera pubiflora* Benth occurs in Brazil, Colombia, Guyana, and Venezuela; in the Brazilian Amazon, it has only been collected in the northern state of Roraima and is common to this location. *Copaifera multijuga* Hayne occurs in Brazil and Bolivia; in the Brazilian Amazon, it is widely distributed in the central and western Amazon regions, particularly in Amazonas State, northern and southern Rondônia, and northwestern Mato Grosso. Detailed botanical descriptions and information on the geographical distributions of these species can be found in Martins-da-Silva et al. (2008).

2.2 Study sites and sampling

This study was performed in natural *Copaifera* populations in forests of four Brazilian Amazonian states (Fig. S1). In the state of Acre, the work was conducted in the Porto Dias Agro-Extractive Settlement Project (PAE), located in the municipality of Acrelândia. PAE community inhabitants have previous experience extracting copaiba oleoresin, and, based on their knowledge of the forest, two local extractors helped us to map *C. paupera* trees above 40 cm DBH (diameter at breast height) in three adjacent rural properties inside the PAE. The total sample area in Acre was 396,200 ha. In Pará State, oleoresin samples were collected in two areas of the National Tapajós Forest in the municipality of Belterra, comprising a total of 200 ha. One area is home to the community of Pedreira, a traditional riverside community where the extraction of *Copaifera* oleoresin is common (100 ha), and the other area lies inside an experimental area with no recorded history of timber or NTFP extraction (100 ha). In each area, *C. reticulata* trees above 40 cm DBH, with no evidence of prior drilling, were marked, georeferenced and drilled. In the state of Rondônia, the fieldwork was conducted at Brazilian Agricultural Research Corporation's (EMBRAPA) research station, located in the northwestern municipality of Machadinho D'Oeste; there is no history of commercial extraction of *Copaifera* oleoresin in this area. All mature *C. multijuga* trees of ≥40 cm DBH were mapped in three 1.5 ha (100× 150 m) permanent plots that were randomized within the larger experimental area. In Roraima State, the collection was performed within the legal reserve (93.68 ha) of the GS farm in Mucajaí county, in the central-eastern region of the state. All the *C. pubiflora* trees in the reserve were mapped, and we selected 35 *C. pubiflora* trees of DBH ≥30 cm, with no apparent signs of prior extractions.

A total of 110 *Copaifera* trees representing four species were sampled. The chosen DBH criterion was based on the protocols of Good Forest Management Practices in Brazil (Leite et al. 2001; Pinto et al. 2010) and is currently employed by local extractors in Acre. In Roraima State, seven trees had DBHs of between 30 and 40 cm.

2.3 Data collection

All the sampled trees were mapped using a GPS receiver, number tagged with an aluminum plate, and measured with respect to the following traits: crown form and position, DBH, total height, first branch height, and presence of hollows, termites, or lianas. The trees were then drilled for oleoresin extraction. The trees were identified to the species level by a professional taxonomist from the EMBRAPA Amazonia Oriental Herbarium (indexed as IAN) in Belém, Pará. The crown form categorization was adapted from Synnott (1979), as follows: (1) full circle and irregular circle (good), (2) half-crown (tolerable), (3) less than half-crown (poor), and (4) one or few branches (very poor). The crown position was scored as (1) dominant (entirely above the canopy and receiving sidelight), (2) co-dominant (receiving full overhead light), (3) intermediate (receiving some overhead light or sidelight), or (4) suppressed (no direct light). Hollows, termites, and lianas were recorded as binary variables; i.e., present/absent. The experimental oleoresin harvest was conducted between October 2006 and December 2008.

2.4 Harvest procedure

The sampled trees were drilled using the same procedure in all four Amazonian states using a procedure that was similar to that employed by the local extractors in Acre State. The harvesting techniques were designed in consultation with an expert extractor of copaiba oleoresin in Acre State. The trunks were drilled at approximately 1.3 m height using a 1.91-cm metal borer; each tree was drilled to a depth at which the oleoresin flowed naturally, with the hole depth not exceeding half the diameter of the tree. A 1.27-cm diameter PVC pipe was fitted to the hole; the oleoresin was collected after 24 h, and the pipe was closed with a screw cap. The pipe of every tree was left open for 24 h, even for the nonproductive trees, and the oleoresin no longer flowed after the 24 h period. The trees were drilled only once (no additional holes were drilled in nonproductive trees). The oleoresin volume was then measured using graduated cylinders. To investigate the influence of the season on the oleoresin production at the first harvest, 48 trees were drilled at the end of the dry season and 62 at the end of the rainy season.

2.5 Consecutive harvests

Eighty-two trees were reharvested; of these, 40 (30 *C. paupera* and 10 *C. reticulata*) were revisited after 18 months, 29 (19 *C. reticulata* and 10 *C. pubiflora*) after 12 months, and 13 (*C. multijuga*) after 22 months. The procedure consisted of opening the PVC pipe and letting the oleoresin flow for 24 h.

2.6 Statistical analysis

The influence of the *Copaifera* species and morphological characteristics on the production capacity and response to consecutive harvests was investigated.

We tested for normality and homoscedasticity using the Kolmogorov–Smirnov and Levene tests. As all explanatory numeric variables followed a normal distribution, with homoscedasticity observed only for the DBH, the effect of the mean species DBH was tested using an ANOVA, with post hoc comparisons conducted using Tukey's tests. Even after Ln transformation, the total height and first branch height were not homoscedastic; therefore, the variation among the species was tested using the nonparametric Kruskal–Wallis *H* test, with post hoc comparisons conducted using Mann–Whitey *U* tests between species pairs. Seven *C. pubiflora* and two *C. multijuga* trees with DBH <40 cm were omitted from the DBH comparisons among the species. Other attributes, such as the crown form, crown position, and presence of hollows, termites, and lianas were evaluated using Chi-square tests.

To evaluate the effects of the tree morphology and season of tapping on oleoresin production, the production was coded as a categorical, binominal variable scored as either "physiological" (>1 ml production) or "commercial" (>50 ml). Following Plowden (2001) and Herrero-Jáuregui (2009), production of >50 ml was designated as commercially viable. We used Chi-square tests and logistic regression to evaluate the effects of multiple predictors on production. For the logistic regression model, the DBH, total height, first branch height, species, and season of tapping were the predictors. We also evaluated the volume of oleoresin produced, excluding the non-productive trees. We used parametric (ANOVA, linear regression, *t* test) and nonparametric tests (Kruskal–Wallis *H* test, *t* test, Mann–Whitney *U* test), depending on the type of predictor variable and the characteristics of the data.

We tested for differences in the number of trees yielding oleoresin in successive harvests using a sign test and tested for differences in the amount of oleoresin produced in the reharvested trees using a repeated-measures ANOVA. The statistical analyses were performed using SPSS v. 15.0.

3 Results

3.1 Proportion of productive trees

The proportion of trees producing oleoresin (>1 ml) were significantly higher for *C. reticulata* (62.1 %) and *C. paupera* (46.7 %) than *C. pubiflora* (31.4 %), and *C. multijuga* (18.8 %; χ^2=10.23, P=0.017, df=3) (Table 1). However, no species differences were observed when considering only commercial production (>50 ml; χ^2=0.94, P=0.816, df=3): only 28.8 % of the *C. reticulata* and 31.4 % of the *C. paupera* trees produced >50 ml oleoresin, whereas the proportions of the other two species were unchanged.

As the species varied in their DBH and total height (Table 2), logistic regression was used to determine whether these morphological variables correlated with the physiological production of oleoresin (>1 ml); however, no significant effect of either was identified. Logistic regression testing for the effects of species and DBH found a marginally significant effect of the species on physiological production (P=0.079). When considering only the effects of species and tree height on production, only the species effect was significant (P=0.02), with *C. reticulata* having the greatest proportion of yielding trees.

When considering the physiological production (>1 ml) of all species, the proportion of trees yielding oleoresin was marginally significantly higher for the trees drilled in the rainy season (50 %) than those drilled in the dry season (31 %; χ^2=3.177, P=0.054, df=1). However, when analyzing the species individually, such seasonal differences were only apparent for *C. paupera* (χ^2=4.286, P=0.058, df=1), with 60 and 20 % of the trees drilled in the rainy and dry seasons, respectively, being productive. When considering the commercial production (>50 ml) of all the species, no

Table 1 Percentage of trees yielding oleoresin, considering physiological (>1 ml) and commercial (>50 ml) production

Species	Number of productive trees (# of trees; % of trees)		Average volume[a] (ml; SE)	Minimum volume (ml)	Maximum volume (ml)
	(>1 ml)	(>50 ml)			
Copaifera reticulata	18 (62.1)	8 (27.6)	452.9 (184.7) b	4.0	2,760.0
Copaifera paupera	14 (46.7)	9 (30.0)	521.5 (219.7) b	5.0	2,935.0
Copaifera pubiflora	11 (31.4)	11 (31.4)	1,701.5 (567.7) a	200.0	5,510.0
Copaifera multijuga	3 (18.8)	3 (18.8)	656.7 (391.8) a, b	70.0	1,400.0
Total	46 (41.8)	31 (28.2)	–	–	–

The average yield per tree at the first harvest and the standard error are shown, together with the minimum and maximum volumes drilled for each species at the first harvest

[a] Only trees that produced >1 ml of oleoresin at the first tapping were considered. Different letters indicate that species differ significantly using Mann–Whitey *U* test between pairs of species

significant seasonal effect on the proportion of productive trees was detected (rainy season, 33.9 % and dry season, 20.8 %; χ^2=1.674, P=0.142, df=1). Neither tree morphology (crown form and position) nor the presence of either termites, hollows, or lianas significantly influenced tree productivity. However, when analyzing the species individually, 74.2 % of the *C. pubiflora* trees with good crowns did not produce oleoresin (χ^2=7.458, P=0.024, df=1).

3.2 Tree morphological characteristics

A total of 110 trees were evaluated; of these, 30 were located in Acre (*C. paupera*), 29 in Pará (*C. reticulata*), 35 in Roraima (*C. pubiflora*), and 16 in Rondônia (*C. multijuga*). The variation in the number of individuals among the areas was due to the scarcity of trees found in each area. *C. paupera* and *C. reticulata* had higher mean DBH values

Table 2 Summary of parameters (numerical and categorical variables) for *Copaifera* species sampled in *terra firme* forest in four states of the Brazilian Amazon

Species	*Copaifera reticulata*	*Copaifera paupera*	*Copaifera pubiflora*	*Copaifera multijuga*
State	Pará	Acre	Roraima	Rondônia
No. of trees drilled in rainy season	19	20	21	2
No. of trees drilled in dry season	10	10	14	14
Average DBH (cm; ±SE)[a, b]	69.64a (3.12)	67.68a (3.73)	59.46ab (2.27)	54.91b (2.90)
Total height (m; ±SE)	31.20b (1.35)	37.90a (1.04)	29.79bc (0.66)	25.81c (0.84)
1st branch height (m; ±SE)	18.20a (1.25)	17.60a (0.71)	14.28b (0.65)	–
Lianas (% of trees)	50.0	73.3	28.6	31.3
Hollows (% of trees)	29.6	6.7	0.0	0.0
Termites (% of trees)	73.3	30.0	–	25.0
Crown position (% of trees)				
Dominant	93.3	43.3	94.3	62.5
Co-dominant	6.7	50.0	5.7	25.0
Intermediate	0.0	6.7	0.0	12.5
Crown form (% of trees)				
Good	90.0	3.3	3.3	3.3
Tolerable	90.0	10.0	0.0	0.0
Poor	88.6	8.6	2.9	0.0
Very poor	81.3	12.5	6.3	0.0

Standard errors are in parenthesis

[a] Different letters indicate significant differences at 5 % using Tukey's test for DBH and Mann–Whitney *U* test between pairs of species for the total height and first branch height

[b] The data refer only to the population of >40 cm DBH. For DBH comparisons sample sizes were *C. reticulata* (29) *C. paupera* (30), *C. pubiflora* (28), and *C. multijuga* (14)

than *C. multijuga*, whereas *C. pubiflora* exhibited intermediate DBH values (Table 2). The crown position differed significantly among the species (χ^2=32.21, *P*=0.000, *df*=6). In more than 90 % of the *C. reticulata* and *C. pubiflora* trees, the crown position was categorized as dominant; in contrast, no dominant crowns were recorded for the other two species (Table 2). More than 80 % of the trees had crowns with good architecture, with no significant differences among the species (χ^2=5.78, *P*=0.762, *df*=9). The species varied significantly with regard to liana infestation (χ^2=14.83, *P*=0.002, *df*=3), the presence of hollows (χ^2=18.78, *P*=0.000, *df*=3), and the presence of termites (χ^2=14.05, *P*=0.001, *df*=2). More than 50 % of the *C. paupera* and *C. reticulata* trees were infested with lianas; for the other two species, approximately 30 % were infested (Table 2). *C. reticulata* exhibited the highest percentage of hollows and termite infestation.

3.3 Oleoresin yield

The average oleoresin volumes obtained in the first harvest varied among individual trees, as shown by the standard error and the minimum and maximum volumes collected (Table 1). The average oleoresin volume of the productive *C. pubiflora* trees was significantly higher than those of *C. reticulata* and *C. paupera* (Kruskal–Wallis *H*=11.12, *P*=0.011). *C. multijuga* yielded intermediate volumes and did not differ significantly in average oleoresin volume from the other species. The high average volume of *C. pubiflora* reflects the high (>5 l) yield of two of the 11 productive trees. In contrast, the greatest volume obtained from the *C. paupera* and *C. reticulata* trees was less than 3 l (Table 1).

The average production per tree did not differ significantly (*t*=−0.408, *P*=0.685) by season (dry, 945.1±343.8 ml SE; rainy, 708.5±213.7 ml SE). Of the variables measured, only the presence of hollows had an effect (negative) on the volume of oleoresin obtained (*t*=2.272, *P*=0.028). Hollows were recorded in only eight *C. reticulata* individuals and two *C. paupera* individuals (Table 2).

3.4 Consecutive harvests

Consecutive tapping events did not significantly decrease the proportion of yielding *C. paupera*, *C. reticulata* and *C. multijuga* trees (Fig. 1) (sign test—*P*=0.375, 0.125, and 0.625, respectively). However, for *C. pubiflora*, only two of ten trees yielded oleoresin at the first tapping, whereas eight were productive at the second tapping 12 months later (sign test—*P*=0.031; Fig. 1). Only three *C. multijuga* trees yielded oleoresin at the first harvest, yet only one was productive at the second harvest. Due to the small number of yielding trees and low oleoresin volumes, the data from repeated harvests are not shown for *C. multijuga*.

The average volume per yielding tree was lower at the second harvest than at the first for *C. paupera* and *C. reticulata* (Fig. 2). Due to the high variation among trees within each species (Fig. S2), the decrease in the oleoresin volumes between harvests was marginally significant only for *C. paupera* (paired *t* test=2.167, *P*=0.058), whereas the increase in oleoresin yield for *C. pubiflora* was not significant (paired *t* test=0.500, *P*=0.705).

4 Discussion

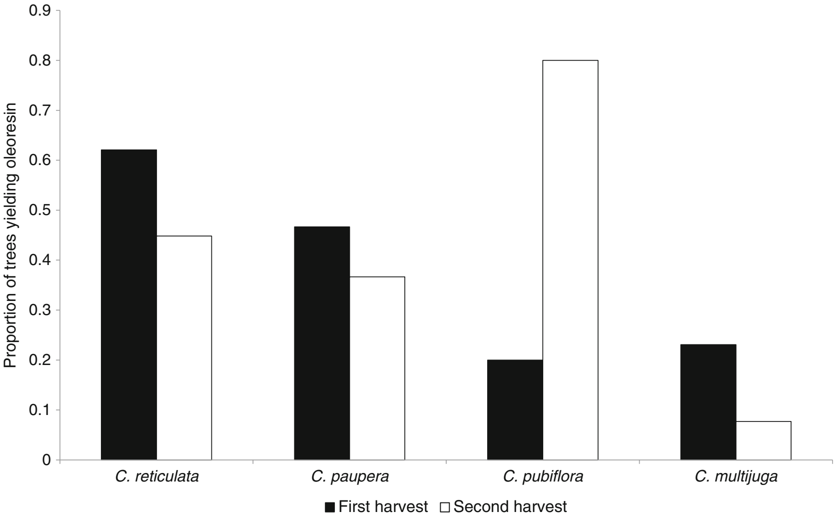
4.1 Factors influencing oleoresin production

Like other studies (Alencar 1982; Ferreira and Braz 2001; Martins et al. 2008; Rigamonte-Azevedo et al. 2006), we found no effect of DBH on the yield of oleoresin. However, there is evidence to suggest that trees with intermediate DBHs (55 to 60 cm) yield higher volumes of oleoresin (Plowden 2003; Silva-Medeiros and Vieira 2008; Herrero-Jáuregui 2009). In our study, the *C. reticulata* and *C. paupera* trees had significantly larger DBHs than *C. pubiflora* and *C. multijuga*. Interestingly, *C. reticulata* and *C. paupera* had the highest number of yielding trees (>1 ml), though *C. pubiflora* yielded higher oleoresin volumes. Perhaps interactions among different environmental and tree variables, potentially including variables not evaluated in this study, are more significant in explaining production than a single variable. Comparative evaluations of trunk anatomy in productive and non-productive trees would be useful to better understand oleoresin production and accumulation.

Some studies have shown that the presence of hollows (Alencar 1982; Herrero-Jáuregui 2009; Newton et al. 2011; Plowden 2003; Rigamonte-Azevedo et al. 2006) and termite infestation (Herrero-Jáuregui 2009; Silva-Medeiros and Vieira 2008) negatively influence oleoresin production; however, we only found an effect for the presence of hollows. Plowden (2003) found a positive relationship between tree size and hollowness. Although we did not evaluate this relationship, the hollow trees in the present study had an average DBH of 78.1 cm and were primarily represented by *C. reticulata* (80 %). A positive correlation between DBH and the presence of hollows could explain our observed lack of correlation between DBH and production. Although larger and older trees might accumulate larger volumes, hollows are also more common to such trees, potentially negatively affecting their production of oleoresin.

Silva-Medeiros and Vieira (2008) found that most termite-infested *C. multijuga* trees were productive and that no nonyielding trees showed evidence of termite infestation; these authors suggested that oleoresin might act as a defensive mechanism against termite infestation. However, our results are inconsistent with their findings, as 15 of 32

Fig. 1 Proportion of productive trees at the first and second tapping (*C. reticulata*, *n*=29; *C. paupera*, *n*=30; *C. pubiflora*, *n*=10; and *C. multijuga*, *n*=13)



infested trees and 19 of 41 uninfested trees yielded oleoresin, i.e., we did not observe a positive relationship between termite infestation and oleoresin production. Some authors have also suggested that termite infestation (along with fungal infection and the activity of other insects) can induce hollow formation (Lindenmayer et al. 2000), which, in turn, negatively influences oleoresin production. If this were the case, termites would initially act as oleoresin inducers, but subsequent hollow formation and decreases in oleoresin production would ensue.

Among the variables analyzed in the present study, the presence of hollows appears to be the only factor found to negatively affect oleoresin production across multiple studies. Although most studies also report declining oleoresin volumes over successive harvests, no patterns have been identified thus far that can advise management protocols. Long-term experiments and the use of progeny tests are necessary to identify the genetic basis (if any) of oleoresin production.

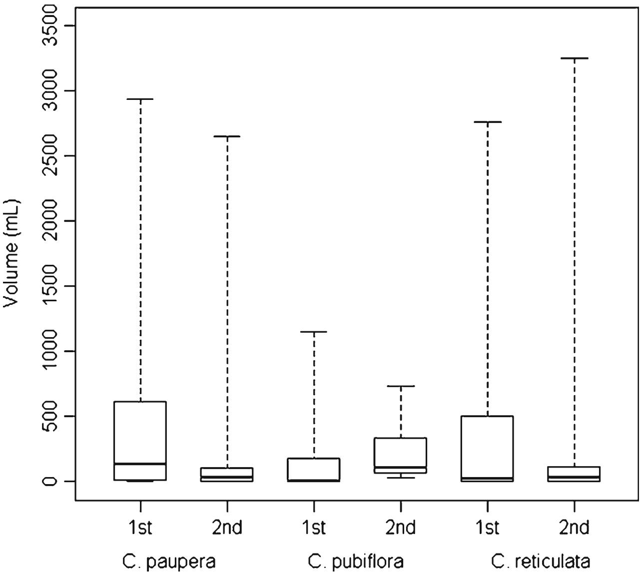


Fig. 2 Variation in oleoresin volumes obtained at the first tapping and second tapping (after 12 or 18 months). Only trees that yielded >1 ml at the first and/or second tapping were considered. *Boxes* indicate ±1 standard error and are bisected by the median value; *whiskers* indicate minimum and maximum volumes

It remains unclear whether there is an optimal season for harvest (e.g., dry or rainy). We found a higher proportion of yielding (>1 ml) trees at the end of the rainy season (particularly for *C. paupera*), but the oleoresin volume was only slightly higher (and not significantly) at the end of the dry season. Ferreira and Braz (2001) evaluated oleoresin production in Acre State and found that 72 % of the trees harvested in the middle of the dry season (July and August) were productive and yielded higher volumes than those harvested between October and November (at the beginning of the rainy season). However, other studies have not found statistically significant differences in the average yield between harvest seasons (Herrero-Jáuregui 2009; Plowden 2003; Silva-Medeiros and Vieira 2008). The inconsistencies across studies might reflect that lack of a direct relationship between seasonality and oleoresin production, and it is possible that seasonal influences interact with other factors to influence production. For example, the higher humidity during the rainy season favors fungal and bacterial infestation and herbivore attack, factors that could influence oleoresin production. Because rainfall varies among years and regions, future studies should measure the correlation between the local rainfall levels and oleoresin yield to evaluate whether water availability might influence the production of oleoresin.

4.2 Interspecific *Copaifera* oleoresin production

Our results demonstrate that the *Copaifera* species of the Brazilian Amazon differ with regard to the proportion of productive trees and their oleoresin yield. Despite the differences in methodology, our results are consistent with those of the previous studies (Table 3). The trees in Acre State yielded larger volumes than those in the other areas, and *C. pubiflora* yielded higher, and *C. multijuga* yielded smaller, average volumes than the other two species. Although oleoresin production has not previously been studied in *C. pubiflora*, our data suggest that this species is a promising potential supplier of oleoresin. Among the yielding trees, the volumes obtained from this species were higher than those of the other *Copaifera* species (Table 1). Furthermore, *C. pubiflora* occurs at higher densities (2.11 adult trees/ha in Mucajaí, RR (Costa et al. 2007)) than the other species (typically, <1 adult/ha).

As the time and human effort invested in drilling non-productive trees would be costly for copaiba oleoresin management, the most profitable species would be those that have both a high individual yield and a high proportion of productive trees. Our study also suggests that commercial production (>50 ml) may be an effective indicator of oleoresin production, as it is less variable among species than other criteria and is of economic relevance to the producer; it may also serve as an appropriate parameter in future studies.

We contend that the high individual variation in oleoresin production and the small samples size of our study and most others (Table 3) hinder the accurate estimation of oleoresin production and the development of standard management indicators for particular species or regions. Unfortunately, studies of oleoresin production based on large samples are rare (but see Martins et al. 2008 and Rigamonte-Azevedo et al. 2006), primarily due to the low population density of most target species. We suggest that sample sizes of at least 100 should be adequate to draw more robust conclusions, representing a compromise between the sampling effort and robustness of the results. The high variation in oleoresin yield reported by different authors likely reflects, in part, methodological differences: in some studies, oleoresin production was measured in previously undrilled trees; in other studies, the trees had been previously drilled. Despite of the importance of consecutive tapping on yield (discussed below), most studies do not address this issue.

A limitation of our study is the confounding of site with species, as each species was sampled at a different site. However, all sites belong to the Amazonian rainforest, and, despite the intrinsic differences among sites, such features as rainfall, vegetative structure and soil composition are similar among the sites. We, therefore, contend that most of the observed differences are due to differences among the species and not the sites.

Table 3 Average volumes of oleoresin produced for different *Copaifera* species in the Brazilian Amazon (Pará (PA), Amazonas (AM), Acre (AC), Rondonia (RO), and Roraima (RR))

Species	State	No. of drilled trees	Yielding trees (%)	Average volume (ml)/yielding tree	Maximum volume (ml) 1st tapping	Reference
Copaifera sp.	PA	57	31.5	230	n.i.	Plowden (2003)
Copaifera reticulata	PA	48	47.9	250	2,760[a]	Herrero-Jáuregui (2009)
	PA	29	62.1	452.9	2,760	this study
Copaifera multijuga	AM	43	63.0	970	7,200	Silva-Medeiros and Vieira (2008)
	AM	82	34.1	620	2,850	Alencar (1982)
	AM	54	70.0	510	4,246	Newton et al. (2011)
	RO	16	18.8	656.7	1,400	this study
Copaifera paupera	AM	18	28.8	114.9	268	Newton et al. (2011)
Copaifera cf *paupera*[b]	AC	27	81.5	1,640	4,600	Rigamonte-Azevedo et al. (2006)
	AC	246	28.0	3,100	21,000	Martins et al. (2008)
	AC	30	46.7	521.5	2,935	this study
Copaifera reticulata[c]	AC	361	27.0	2,920	18,000	Rigamonte-Azevedo et al. (2006)
Copaifera sp.	AC	62	50.0	1,810	n.i.	Ferreira and Braz (2001)
Copaifera pubiflora	RR	35	31.4	1,701.5	5,510	this study
Copaifera piresii	AM	17	24.0	16.9	28	Newton et al. (2011)
Copaifera guyanensis—terra firme	AM	19	16.0	15.2	27	Newton et al. (2011)
Copaifera guyanensis—várzea	AM	57	37.0	139.2	1,036	Newton et al. (2011)

n.i. not included

[a] Data supplied by the author

[b] Popularly known as copaiba mari-mari

[c] Subsequent evaluations have shown that the species occurring in Acre is *C. paupera* (Martins-da-Silva et al. 2008)

4.3 Management

Although the average volume per yielding tree was lower at the second harvest than at the first in two species (Fig. 1), the variation among the trees was large for all the species. An individual-based analysis (Fig. S2) showed that those trees yielding higher volumes at the first tapping had larger decreases in oleoresin production at the second tapping. This observation supports the hypothesis that oleoresin accumulates over time and suggests that a 12- or 18-month interval between successive harvests would be insufficient for the restoration of oleoresin to the original levels.

Oleoresin appears to be produced discontinuously and at different rates within trees. Some individuals produced oleoresin in the past and accumulated large volumes over time, yielding large volumes when drilled. However, the oleoresin volumes were low at the second harvest, likely because the trees were no longer producing at the maximum levels. Other individuals may have still been in full production and able to accumulate large volumes in a short period of time; these trees could provide a stable supply of oleoresin over consecutive harvests. Another possible explanation of our results is that not all of the oleoresin was harvested during the first harvest, with the remainder accumulating in the pipe immediately after the cap was affixed (after 24 h). There are anecdotal reports of trees with oleoresin flowing for two or more days. In our study, the flow always ceased within 24 h. However, upon the second harvest, it is difficult to distinguish between oleoresin regenerated by the tree during the interim months and that simply accumulating in the pipe immediately after the first harvest. This difficulty is common to all studies involving copaiba oleoresin reharvest that have been conducted to date.

Recommendations for management practices consider 3 to 4 years as an economically viable interval between the tapping of individual trees (Leite et al. 2001; Pinto et al. 2010); however, no studies have confirmed the economic viability of this practice. The decrease in average oleoresin production between the first and second harvest was 38 % for *C. reticulata* and 44 % for *C. paupera*. A decrease of 80.3 % was observed by Plowden (2003) in a study in which the trees were re-tapped every 6 months in Pará State, Brazil. Other authors have also noted a decrease in oleoresin production upon the second tapping, with some trees yielding oleoresin only upon the first tapping (Herrero-Jáuregui 2009; Martins et al. 2008; Newton et al. 2011; Plowden 2003; Rigamonte-Azevedo et al. 2006; Silva-Medeiros and Vieira 2008). However, in the present study, some trees yielded more oleoresin at the second harvest than the first, an observation also reported by Alencar (1982) and Newton et al. (2011) for *C. multijuga*. These results reinforce the hypothesis that oleoresin production differs among trees.

Silva-Medeiros and Vieira (2008) found that *C. multijuga* trees with DBH at >40 cm produced more oleoresin at the first tapping than those with DBH between 30 and 40 cm; however, the decrease was greatest in the larger DBH trees at the second harvest. It is possible that smaller (and presumably younger) trees are more regular in their production. As natural populations include trees of varying age and in varying physiological stages, we cannot recommend a specific interval between successive harvests. Indeed, further assessments of whether the oleoresin renewal rates differ among species are required.

5 Conclusions

As *Copaifera* oleoresin is harvested in natural forests, the increasing demand for this product has generated concern on how to adequately supply the market. The few studies of the productive potential of *Copaifera* have attempted to identify the factors influencing oleoresin production. However, due to the lack of a common methodology, high inter- and intraspecific variation in oleoresin production and small samples sizes, no robust conclusions have yet been possible. We found no apparent effect of termite infestation, liana load, crown form, crown position, or DBH on the productivity and average yield of *Copaifera* trees. Only the presence of hollows was explanatory, negatively affecting the average oleoresin yield.

Our study reinforces the hypothesis that the productive potential varies by species; therefore, harvest intensity should be based on the species. *C. paupera* had the highest number of yielding trees, but the average volume was highest for *C. pubiflora*. The oleoresin yield might also be influenced by consecutive harvests from the same tree and the interval between harvests.

A 12- or 18-month interval between successive harvests is likely to be insufficient for the restoration of the original oleoresin levels in *C. reticulata* and *C. paupera*. However, *C. pubiflora* demonstrated higher oleoresin production at the second harvest. Management practices should consider the differences among species to achieve sustainable oleoresin production.

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