

POSSIBLE MECHANISMS FOR THE COEXISTENCE OF CONGENERIC (*POUROUMA*, CECROPIACEAE) AMAZONIAN TREE SPECIES

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Abstract. The distribution, architecture, and foliar pest damage of ten species of *Pourouma* (Cecropiaceae) were investigated in a 50-ha plot of old-growth tropical rainforest in the Yasuní National Park, Ecuador. Individuals were censused and ecological and architectural data recorded along three 500 x 20 m transects (totaling 203 individuals). There were differences between the species in topographic preference. Additionally, in two taxa (*P. bicolor* and *P. guianensis* ssp. *guianensis* var. 2) there were ontogenetic changes in topographic preference. Architectural differences between the species indicated that one species, *P. minor*, was more shade-tolerant than the others. The level of pest damage was frequency-dependent, the more abundant species also being most attacked. Within species, small individuals were most severely damaged by pests. Thus differences in microhabitat preferences and frequency-dependent herbivory probably both contribute to the coexistence of the studied *Pourouma* species in the 50-ha plot in Yasuní. Accepted 11 December 2001.

Key words: Amazonian Ecuador, congeneric species, frequency-dependent herbivory, niche differentiation, species richness, *Pourouma*.

INTRODUCTION

The maintenance of high tree species richness in tropical lowland rainforests is an important, much debated topic in ecology (e. g., Janzen 1970, Hubbell 1979, Connell *et al.* 1984, Denslow 1987, Condit *et al.* 1992, Phillips *et al.* 1994, Dalling *et al.* 1998, Kobe 1999, Svenning 1999). The investigation reported here was made to explore mechanisms that may maintain the high tree diversity found in lowland tropical rainforest of Amazonian Ecuador (e. g., Balslev & Renner 1989, Valencia *et al.* 1994). An inventory of trees and shrubs in 2 ha of the Yasuní National Park indicates that the tree diversity in the area is among the highest in the world (Romoleroux *et al.* 1997). By mid-2000 the inventory had been expanded to 25 ha with preliminary identification of 1152 tree species (Center of Tropical Forest Science (CTFS), unpubl. data). I compared tree and shrub species records from Yasuní with five 50-ha tropical forest plots from other parts of the world (CTFS., unpubl. data). Mean species number within the 0.01% most species rich genera at the five sites was highly correlated with total number of species at the sites (Pearson $r = 0.99$, $P = 0.0002$, $n = 6$). Thus, genera containing many species contribute much of the spe-

cies richness at these tropical forest sites. Few studies have focused on the ecology of such sympatric congeneric species (though see Davies *et al.* 1998, Davies 2001). Due to ecological similarity one would expect closely related species to have had or have more interspecific competition than more distantly related species (e. g., Darwin 1859, Webb 2000). Consequently, understanding the coexistence of congeneric species may be the key to understanding the existence and maintenance of high tropical tree diversity overall. The tree genus *Pourouma* is an example of a species-rich genus, with 10 species growing sympatrically within 50 ha of *terra firme* forest in Yasuní. I investigated the following hypotheses:

(1) The distribution of the *Pourouma* species is influenced by microhabitat heterogeneity. One of the main hypotheses concerning maintenance of species richness in lowland tropical rain forest states that microhabitat niche differentiation is an important mechanism (Connell 1978, Wright 1999). Numerous studies have investigated this hypothesis (e. g., Tuomisto *et al.* 1995, Clark *et al.* 1998, Svenning 1999, Svenning 2000). I tested specifically, if *Pourouma* species were differently distributed with respect to topographic position and canopy openness. (2) Differences in branching architecture may reflect adaptation to differing light environments (King 1990, Leigh

1999, Valladares 1999). Tree juveniles exhibit two basic crown building strategies to cope with the low light availability in the understory: shade avoidance (no or few branches) or shade tolerance (many branches) (Valladares 1999). If *Pourouma* species have different branching strategies, this would be consistent with microhabitat niche differentiation with regard to light availability. (3) An important alternative hypothesis for the maintenance of species richness suggests that distance-, density-, or frequency-dependent pests and pathogens are able to keep the density of tropical tree species at relatively low levels, precluding the dominance of just a few species (Gillet 1962, Connell 1970, Janzen 1970). Negatively density-dependent recruitment and performance have received increasing empirical support (Wills *et al.* 1997, Harms *et al.* 2000), although it has not yet been shown that the general agents creating the patterns are indeed pests (Wright 1999). Here I have recorded the percentage of leaves damaged by pests in the *Pourouma* species, and compared the observed levels of foliar damage to the abundance of each species.

MATERIAL AND METHODS

Study area and species. The study site was a permanent 50-ha plot established in old-growth tropical rain forest by the Yasuni Forest Dynamics Project (Romero *et al.* 1997). The plot is located in Amazonian

Ecuador in the Yasuní National Park in *terra firme* forest (0°40'20"S, 76°23'45"W) (Svenning 1999) and includes three hills with poorly drained bottomland areas between (Fig. 1). The altitude is ca. 230 m with the maximum elevation difference within the plot being 32 m. Fieldwork was carried out during August–October 1995 in three 500 × 20 m transects within the plot (Fig. 1). One transect included mainly hilltop, one mainly bottomland, while the last one was cross-country. Twenty-seven species of *Pourouma* (Cecropiaceae) are recognized from the Neotropics, and 14 occur in Amazonian Ecuador (Berg & RosSELLI 1992). Some species, as defined in Berg & RosSELLI (1992), seem to contain several biological species. These were recognized at the Yasuní study site and analyzed as distinct species in the present study. Species identification was carried out following the field key in Appendix 1. The key includes all subspecific taxa that apparently represent distinct biological species (Table 1). From hereon, I will refer to these subspecies and varieties as species.

Field measurements. All *Pourouma* individuals encountered within 5 m of the midline of each transect were recorded. In addition I also recorded all *Pourouma* individuals taller than 10 m within 10 m of the transect midline.

Ontogenetic stage and morphology of each individual were recorded as follows:

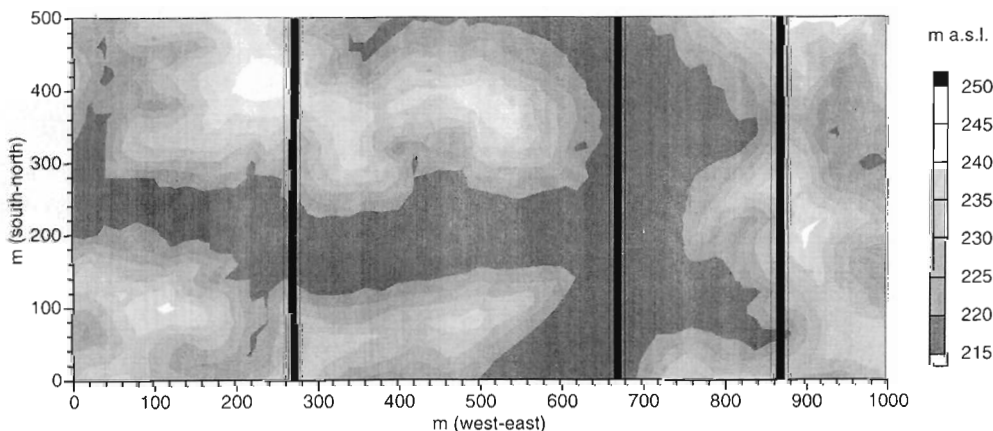


FIG. 1. Location of the three transects in the Yasuní Forest Dynamics Project's 50-ha plot. The central (black) part of each transect was sampled for *Pourouma* individuals of all heights, while the outer parts were only sampled for individuals >10 m tall.

TABLE 1. *Pourouma* (Cecropiaceae) species found within the 50-ha study area in the Yasuni National Park, Ecuador. Species names and authors from Flora of Ecuador (Berg & Rosselli 1992). Concerning *in vivo* vouchers, # refers to the permanent number of an individual in the Yasuni Forest Dynamics Project. All herbarium vouchers (EMY numbers) are deposited at the Herbarium Jutlandicum (AAU), University of Aarhus, Denmark. One further species, *P. melinonii* (Benoist), occurred within the 50-ha plot, but not in study transects.

<i>Pourouma</i> species	Voucher	Sample size
<i>P. bicolor</i> Martius	EMY73	108
<i>P. cecropiifolia</i> Martius	EMY91	2
<i>P. cucura</i> Standley & Cuatrec.	EMY80	3
<i>P. guianensis</i> subsp. <i>guianensis</i> Aublet var. 1	#101490	9
<i>P. guianensis</i> subsp. <i>guianensis</i> Aublet var 2.	EMY70	18
<i>P. minor</i> Benoist	EMY74	22
<i>P. napoensis</i> C.C. Berg	EMY120	3
<i>P. petiolulata</i> C.C. Berg	#53800	6
<i>P. tomentosa</i> subsp. <i>persecta</i> C.C. Berg & van Heusden	EMY75	4
<i>P. tomentosa</i> subsp. <i>tomentosa</i> Quatrec.	EMY81	28
<i>P. melinonii</i> Benoist	-	0
Total: 10		203

(a) Height. For individuals ≤ 8 m, height was estimated by eye using a pole of 1.3 m length as help. For individuals > 8 m, height was measured with clinometer and measuring tape.

(b) Branch height. Estimation of height to the first branching from the main stem was made applying the same methods as in a.

(c) Number of branches. Number of branches from the main stem was counted, if necessary using binoculars.

(d) Herbivory. I estimated the percentage of the leaves that had been pest-damaged as 0%, $< 25\%$, $\geq 25\%$ – 50% , or $\geq 50\%$. By pest-damaged is meant that part of the leaf was eaten, leaving a hole, thus I did not count leaves with slight color changes caused by fungi, etc.

I also recorded the following environmental data for each individual:

(a) Topographic position. For every individual the topographic position was recorded using three categories (bottomland, slope, hilltop).

(b) Crown position index. I estimated the amount of light available to a given individual using the method of Clark & Clark (1993). Five categories were used: 1 = no direct light or one small lateral gap; 2 = several small or one medium-sized lateral gap; 2.5 = several medium-sized lateral gaps; 3 = 10–90% gap,

vertically above the crown; 4 = 90–100% gap, vertically above the crown.

Analytical methods. Likelihood ratio tests (G^2) were used to test for differing distributions over topographic positions between six species and between height classes within four species (due to sample size). In all analyses expected counts < 1 were not allowed. In within-species analyses height was transformed and represented as a nominal variable with two classes. Five analyses were made for each species using five different height class limits: \leq or > 1 , \leq or > 2 , \leq or > 3 , \leq or > 4 , and \leq or > 5 m. This was done to investigate at which height, if any, change in topographic preference occurred.

Using logistic regression I examined if presence or absence of branches was related to height of individual, crown position index, and species. I also tested whether total number of branches on individuals was related to the same three parameters using ANCOVA. In both of the above two tests only the five most abundant species were included (Table 1). Only one interaction term (species \times height) could be allowed in the models. Using ANCOVA I also analyzed if crown depth was related to height of individual, crown position index, and species. Crown depth was obtained by subtracting height to first branch from height of

individuals. Only the four most abundant species were analyzed (Table 1). The ANCOVA included main effects and the species \times height interaction. Backward elimination was used to find a model with only significant effects. In all ANCOVAs height of individuals and number of branches were square root transformed to approximate normality.

Ordinal logistic regression was used to examine if crown position index or pest damage were related to height or species identity. Only the six most abundant species were included (Table 1). Significance of whole-model and single effects in the logistic regressions were tested using likelihood ratio tests.

RESULTS

The three transects contained 203 *Pourouma* individuals, representing 10 of the 11 locally occurring species (Table 1).

Topography. There were differences in topographic preference among the six species tested ($G^2 = 20.729$, d.f. = 191, $P = 0.023$; Fig. 2). The most distinct species were *P. bicolor* with relatively few individuals in bottomland and many on hilltops, *P. minor* with many individuals in bottomland and on hilltops, and *P. petiolata* with relatively high numbers of individuals on the slopes. An identical test without the abundant *P. bicolor* still indicated that the remaining species were differentially distributed, although with borderline significance ($G^2 = 14.796$, d.f. = 83, $P = 0.06$). In *P. bicolor* and *P. guianensis* ssp. *guianensis* var. 2, individuals ≤ 3 m tall differed from individuals > 3 m tall in their

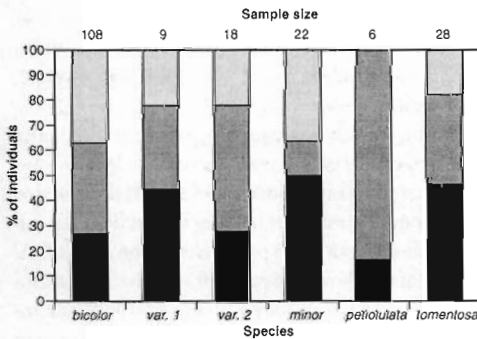


FIG. 2. The percentage of individuals (all height classes) of eight *Pourouma* species located in bottomlands (black), on slopes (dark gray), or on hilltops (light gray).

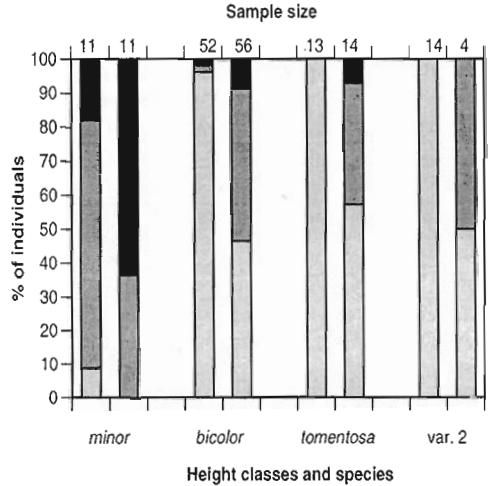


FIG. 3. The percentage of individuals of four *Pourouma* species within two height classes (individuals ≤ 3 m in first column and individuals > 3 m tall in second column) with 0-1 (light gray), 2-5 (dark gray), or ≥ 6 branches (black).

distribution among topographic positions (*P. bicolor*: $G^2 = 9.546$, d.f. = 108, $P = 0.009$ and *P. guianensis* ssp. *guianensis* var. 2: $G^2 = 7.841$, d.f. = 18, $P = 0.020$). Using height class limits of 4 m and 5 m gave similar results, while limits of 1 m and 2 m resulted in no significant differences. Conversely, short and tall individuals of *P. tomentosa* ssp. *tomentosa* and *P. minor* did not differ in topographic distribution regardless of class limits (results not shown).

Morphology. Presence/absence and number of branches were strongly related to species, height, and crown position index, with the height effect differing between species while (Fig. 3, Table 2). Total height was the most important descriptor of crown depth, but there was also an indication that crown depth varied between species (Table 2).

Herbivory. The level of foliar pest damage differed between species, was related to height, and the damage - height relation differed between species (Fig. 4, Table 3).

Light. Crown position was only related to the height of the individual and did not differ between species (Table 3).

TABLE 2. Total number of branches (ANCOVA), crown depth (ANCOVA), and presence/absence of branches (logistic regression) as a function of individual height, crown position index, and species identity (final models). *Pourouma bicolor*, *P. tomentosa* ssp. *tomentosa*, *P. guianensis* ssp. *guianensis* var. 2, and *P. minor* were included in all analyses, while *P. guianensis* ssp. *guianensis* var. 1 was not included in the analysis of crown depth.

SQUARE ROOT NUMBER OF BRANCHES	df	P
Whole Model	148	< 0.0001
Species	4	< 0.0001
Square root height	1	< 0.0001
Crown position index	6	0.0029
Species * square root height	4	0.0073
BRANCHES PRESENT OR ABSENT	df	P
Whole model	11	< 0.0001
Species	4	0.000
Square root height	1	0.000
Crown position index	6	0.012
CROWN DEPTH	df	P
Whole Model	78	< 0.0001
Species	3	0.09
Square root height	1	< 0.0001

TABLE 3. Ordinal logistic regression shows tests of the influence of individual height and species identity on crown position index and foliar pest damage (final models).

FOLIAR PEST DAMAGE	df	P
Whole model	11	< 0.0001
Species	5	0.0021
Height	1	0.0002
Species * height	5	0.0015
CROWN POSITION INDEX	df	P
Whole model	11	< 0.0001
Species	5	0.6079
Height	1	0.0049
Species * height	5	0.4825

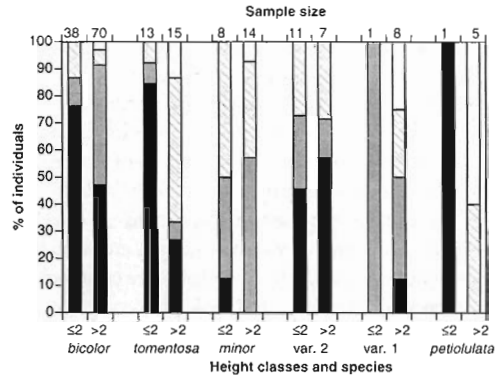


FIG. 4. The percentage of individuals of six *Pourouma* species within two height classes (individuals ≤ 2 m in first column and individuals > 2 m in second column) with $\geq 50\%$ (black), $\geq 25\%$ – 50% (dark gray), 1–25% (striped), or 0% of leaves damaged by pests (white).

DISCUSSION

There were differences in topographic distribution between the six most abundant *Pourouma* species. Two species, *P. bicolor* and *P. guianensis* ssp. *guianensis* var. 2, showed increasing topographic specialization through ontogeny. Large individuals of both species were more likely to be found in bottomland, whereas smaller individuals were more evenly distributed over all topographic positions. This increasing specialization is consistent with environmental sorting acting on stages between establishment and maturity (cf. Svenning & Balslev 1999). These differences in topographic preferences provide some support for the niche diversification hypothesis (e. g., Connell 1978). Other studies have found similar levels of specialization along small topographic gradients for herbs, shrubs, palms, and trees in tropical rain forests (e. g., Tuomisto *et al.* 1995, Clark *et al.* 1998, Svenning 1999). Numerous environmental factors (e.g., gap formation rates, canopy height, and water availability) have been shown to vary among topographic positions (Becker *et al.* 1988, Poorter *et al.* 1994, Clark *et al.* 1996). Thus, the differences in topographic preferences found for the *Pourouma* species may reflect differential specialization with regard to nutrients, water conditions, and/or light conditions. Notably, other studies have shown that *P. bicolor*, while relatively

shade-tolerant as a small juvenile and maybe even shade-demanding for germination, needs canopy gaps for later growth and survival (King 1993, Van der Meer *et al.* 1998, Svenning 2000). The bottomland has more low canopy areas than the hills in the Yasuní plot (Svenning 1999). Thus, *P. bicolor*'s increasing preference for bottomland most likely reflects the greater availability of canopy gaps there.

The *Pourouma* species had varying crown architecture, in terms of presence and absence of branches, numbers of branches, and possibly crown depth. *Pourouma minor* was the most deviant species, having more branches and a deeper crown than the other species throughout ontogeny. Thus it appears that *P. minor* exhibits a shade-tolerant crown-building strategy, while the other species studied, allocating more resources to height growth than to lateral branching, demonstrate a shade-avoidance strategy (Valladares 1999).

Despite their architectural differences the *Pourouma* species did not differ in crown position. Davies *et al.* (1998) found a significant variation in crown position among 11 sympatric *Macaranga* (Euphorbiaceae) species on Borneo. The 11 pioneer *Macaranga* species ranked from extremely light demanding to quite shade tolerant. By contrast, Clark & Clark (1993) found that mean Global Site Factor (GSF is a measure of the relative level of photosynthetically active radiation at a site) of seven non-pioneer tree species in Costa Rica were very similar. The eight *Pourouma* species in this study are not true pioneer species either (mean crown position index had a range of 2.1–3.2). Thus the lack of differences in crown position index could reflect the relatively crude estimation of light availability that the crown index provides, the static nature of the data, and/or small sample sizes. Thus, while *P. minor* seems to be more shade tolerant than the other *Pourouma* species in Yasuní, the difference in shade tolerance must be quite subtle.

The *Pourouma* species differed in their level of foliar pest damage. The differences found here are strongly suggestive of positively frequency-dependent herbivory: the most common species had most leaves damaged by pests, whereas the rarest species had fewest leaves damaged (Fig. 4). Numerous studies have documented negative density- or distance-dependent recruitment and seedling performance within species (e. g., Connell *et al.* 1984, Wills *et al.* 1997, Harms *et al.* 2000), but there is much less evidence for negative frequency-dependent perfor-

mance among species (but see Connell *et al.* 1984). Further studies are needed to determine whether the differential levels of damage resulted in negatively frequency-dependent performance. At least the two commonest species, *P. bicolor* and *P. tomentosa* spp. *tomentosa*, had their youngest individuals most heavily attacked (ca. 80% of small individuals had more than 50 % of their leaves attacked). This observation agrees with the results of Connell *et al.* (1984) from an Australian tropical forest and the Janzen-Connell hypothesis in general (Janzen 1970, Connell 1971). Thus the herbivory pattern documented for the *Pourouma* species supports the notion that negatively frequency-dependent performance due to pests promotes species coexistence in tropical forests.

Clear indications of microhabitat specialization among the *Pourouma* species and frequency-dependent pest pressure have been found. Thus both mechanisms are probably involved in the maintenance of the high number of congeneric species found in this small area in the Amazonian lowland forest. There is increasing empirical evidence that processes of negatively density-dependent performance (Wills *et al.* 1997, Harms *et al.* 2000), nichespecialization (Clark & Clark 1993, Tuomisto *et al.* 1995, Svenning 1999, Svenning 2000), and dispersal processes (Dalling *et al.* 1998, Hubbell *et al.* 1999) all contribute to the coexistence of numerous plant species in tropical forests. Consequently there is a need for further investigation concerning the relative importance for tree species coexistence of all these processes.

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APPENDIX 1: Field key to adult *Pourouma* species in the 50-hectare plot in Yasuní (this key was developed by the author before data collection. Taxonomy work took place in the 50-ha plot in Yasuní and in two herbaria in Quito (Herbario Nacional QCNE and Herbario QCA).

- 1: Leaves entire and mostly unlobed:
- 2: Leaves lanceolate: *P. minor*
- 2: Leaves ovate:
- 3: Stipule inside densely hairy:
- 4: Hairs on venation and petiole sparse, fine, and uniform: *P. bicolor*
- 4: Hairs on venation and petiole dense and of different lengths: *P. cucurva*
- 3: Stipule inside sparsely hairy, outside with uniform white hairs: *P. melinonii*
- 1: Leaves compound:
- 2: Petiolules with long, fine hairs; stipule outside with sparse yellow hairs: *P. tomentosa* subsp. *persecta*
- 2: Petiolules without hairs, stipule outside with dense long, soft hairs: *P. petiolulata*
- 1: Leaves entire and mostly lobed:
- 2: Stipule outside white tomentose: *P. tomentosa* subsp. *tomentosa*
- 2: Stipule outside hairy:
- 3: Hairs dense long, thick, and fur-like: *P. napoensis*
- 3: Hairs thin, soft, and abscising:
- 4: Leaves deeply lobed; usually 5-9 lobes; lobes lanceolate: *P. guianensis* subsp. *guianensis* var. 2
- 4: Leaves not deeply lobed; usually 3 lobed; lobes ovate: *P. guianensis* subsp. *guianensis* var. 1
- 2: Stipule inside densely hairy: *P. cecropifolia*