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The Amazon flood plain forest tree *Maquira coriacea* (Karsten) C.C. Berg: aspects of ecology and management

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Abstract

Maquira coriacea is a commercial tree species growing throughout the Amazon flood plain forests. Densities up to 14/ha of individuals, ≥ 10 cm diameter at breast height (DBH) were observed, corresponding to a basal area of 2 m²/ha and a volume of 38 m³/ha. The primary period of fruiting coincided with the annual flooding, but fruits were also produced in other parts of the year. Seedlings with densities up to 150/m² were concentrated around mother trees, and the stocks fluctuated much over the year due to mortality caused by flooding and wilting in dry periods. Growth data mainly from nine 1 ha permanent sample plots were used to develop models of the height–diameter relationship and diameter increment. These relationships indicated that the optimal felling limit for maximum volume production was 120–130 cm DBH, which can be obtained in 150–260 years. Since seed production has been observed in much smaller individuals, such diameter limits should not be detrimental to regeneration. © 2001 Elsevier Science B.V. All rights reserved.

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1. Introduction

Tropical rain forests are characterized by a complex structure and ecology, and much knowledge on how these ecosystems function and respond to interventions is still lacking. This often complicates forest management. Recently, the need for more profound knowledge on ecology of single tree species has been stressed (e.g. Hubbell and Foster, 1986; Bawa et al., 1990; Gómez-Pompa and Burley, 1991; Hubbell, 1995; Whitmore, 1995), and several workers have described aspects of autecology of tropical forest tree

species from various points of view and using different methods (e.g. Henriques and Sousa, 1989; Viana, 1990; Peters, 1990; Clark and Clark, 1992; McCormick, 1995; Zagt, 1997).

In this study we focused on one commercial timber tree species growing in Peruvian flood plain forests. The objective was to describe aspects of its biology and ecology, and to provide useful information for its management.

2. Materials and methods

The study of *Maquira coriacea* (Karsten) C.C. Berg was based on field data from flood plain forests in the vicinity of Jenaro Herrera (4°55'S, 73°44'W) located at the lower Río Ucayali in the lowland Peruvian

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Amazon. General aspects of Peruvian flood plain forests were described by Kvist and Nebel (2001), while specific details on the study site were given by Nebel et al. (2001a,b,c,d).

2.1. Data collection

All individuals equal to or above 10 cm diameter at breast height (DBH) were recorded in nine 1 ha permanent sample plots (overstorey; Nebel et al., 2001a), while individuals from 1.5 m height up to 10 cm DBH were recorded in sub-plots covering an area of 0.64 ha (understorey; Nebel et al., 2001b). The nine 1 ha plots were equally distributed in the three forest types of high restinga, low restinga, and tahuampa, while understorey sub-plots were only established in the restinga forests. After plot establishment in late 1993 felling at two intensities were carried out. In each forest type one plot was kept untreated, while the remaining two plots were treated with a moderate and a heavy felling, respectively. All individuals were remeasured in 1994, 1995, and 1997. Ingrowth was registered in 1995 and 1997. Recordings included measurement of DBH, coordinates, and estimate of height (Nebel et al., 2001a). Data of *M. coriacea* were used to describe (1) its position in different forest types, (2) its population structure, and (3) its population dynamics. A total of 432 growth registrations from 147 *M. coriacea* individuals were useful for modeling.

In late 1994, the presence of *M. coriacea* seedlings (height < 1.5 m) was evaluated in the high and low restinga sample plots. Densities of seedlings were estimated within sub-plots of 20 m × 20 m, and these data were used to evaluate dispersion of seedlings, and to assess regeneration success.

In late 1996 previously unrecorded *M. coriacea* understorey individuals were registered in the 1 ha plots, but individuals were only recorded in high restinga forest plots, and in two of the three plots located in low restinga forest. DBH and total height were measured. A total of 312 individuals were registered and the data were used to analyze dispersion patterns.

In late 1996 and early 1997 additional permanent sample plots were established in high restinga forest. Plots were formed as 40 m wide transects extending a total length of 2.4 km, thus covering an area of 9.6 ha.

A total of 444 individuals of *M. coriacea* above 1.5 m height were recorded. Registrations included measurements of DBH, coordinates, total and commercial height. Thirty-nine individuals representing the entire diameter range were selected, and their fruiting was evaluated each month in the period from March 1997 to December 1998. Data were used to describe the height–DBH relationship and the fruiting pattern.

Before and after the inundation in 1998 seedling stocks were evaluated in permanent sample plots established in four perpendicular directions away from the boles of five relatively isolated mature female *M. coriacea* individuals. In each direction, 25 plots with a length of 2 m were established. In segments of five plots, starting from the bole of the tree, the plots had widths of 1–5 m. The data were used to evaluate the seedling stocking in relation to distance from mother trees.

2.2. Data analysis

Species importance values (SIVs) were calculated for the overstorey and the understorey as the sums of the relative densities, relative frequencies, and relative dominances of the species. The method accorded to Curtis and McIntosh (1950, 1951; formulae given by Nebel et al., 2001a).

The dispersion patterns of *M. coriacea* individuals belonging to the understorey and overstorey were evaluated for the high and low restinga forest types. To quantify the degree of clumping at different levels, Morisita's index of dispersion was calculated for varying plot quadrat sizes (side length 5, 10 and 20 m, respectively)

$$I_{\delta} = \frac{\sum_{i=1}^q n_i(n_i - 1)}{N(N - 1)} q \quad (1)$$

where n_1, \dots, n_q are the numbers of individuals observed in each of q quadrats and N is the total number of individuals observed. The departure from randomness ($I_{\delta} = 1.0$) was tested by a F -test (Greig-Smith, 1983). Likewise, the distribution of seedlings in each forest type was examined, using a quadrat with length of 20 m only. To assess the impact of the 1993/1994 felling treatments, data from the untreated plots were subsequently analyzed separately. In this way it was determined if the establishment and survival of

seedlings had been altered, resulting in a distorted seedling dispersion pattern as compared to original stand conditions.

All volumes are for stems and calculated using a form factor of 0.5 determined by Cannell (1984) for a number of tropical tree species.

3. Distribution, morphology, wood properties, and extraction

The genus *Maquira* (Moraceae) comprises four Neotropical species occurring mainly in northern South America, all of which are found in the Amazon basin. *M. coriacea* inhabits flood plain forests throughout the Amazon basin, the Orinoco basin, and the upper Río Paraguay basin, while the other species usually occur in non-inundated forests (Berg, 1972; Berg and Rosselli, 1996). *M. coriacea* is known as Capinurí in Peru (Gentry, 1993) and together with *M. sclerophylla* (Ducke) C.C. Berg as Muiratinga or Capinurí in Brazil (Chichignoud et al., 1990).

M. coriacea is a large-buttressed tree reaching 45 m in height. It has a smooth-barked cylindrical and conspicuously self-pruning trunk, and reaches diameters of 1.3 m or more. The latex is cream colored and occurs in the wood, bark and leaves. It is dioecious with masculine flowers (4–10 mm in diameter) in bunches 1–6, while the female flowers occur singly or in pairs, forming ellipsoid or subglobose fruits around 1 cm in diameter (Berg, 1972; Gentry, 1993).

The wood of *M. coriacea* has a white to yellowish-brown color with a green weight of 1050 kg/m³, and a specific gravity of 470 kg/m³ at 12% moisture content. Tangential shrinkage is 6.7–9.4%, whereas the radial shrinkage is in the range 3.4–4.2%. Sawing is easy but creates a wooly surface, and the high silica content causes blunting. Veneer can be produced by peeling or slicing at room temperature. The wood can be dried in 2 days with a slight risk of distortion and checking. The natural durability of the wood is poor, and the major use is for plywood, with some use for other cheap wood products (Teixeira et al., 1988; Chichignoud et al., 1990).

Ros-Tonen (1993) considered *M. coriacea* as one of the most important species extracted from várzea flood plains in Brazil. Together with *Ceiba pentandra* (L.) Gaertner and *Virola surinamensis* (Rolander) Warburg

it is of major importance for production of veneer and plywood in Brazil, which provided export earnings of around US\$ 178 million in 1989. In the Peruvian Loreto department *M. coriacea* is used in the plywood industry. According to unpublished data from the Banco Central de Reserva del Peru it accounted for around 2500 m³ (10%) of the plywood production in 1996, while the rest was produced from *C. pentandra* (Kvist and Nebel, 2001).

4. Results

4.1. Reproduction

Female trees of *M. coriacea* can have a prolonged and abundant fruiting, but considerable variation takes place over time. One and two periods of fruiting were observed in 1997 and 1998, respectively (Fig. 1). In both seasons fruiting took place from around December to May, and a high quantity of fruits were produced in these periods, which partly coincided with the annual flooding (March to May). In 1997 a less vigorous fruiting event also took place from June to August, but in 1998 fruiting was absent in this period, perhaps due to unusual dry weather restraining fruit development. Fruiting was observed for trees from 42 cm DBH upwards. Only 32% of the individuals in this size category did not fruit at all.

Large animals take fruits of *M. coriacea*. However, judging from the presence of seedlings, the vast

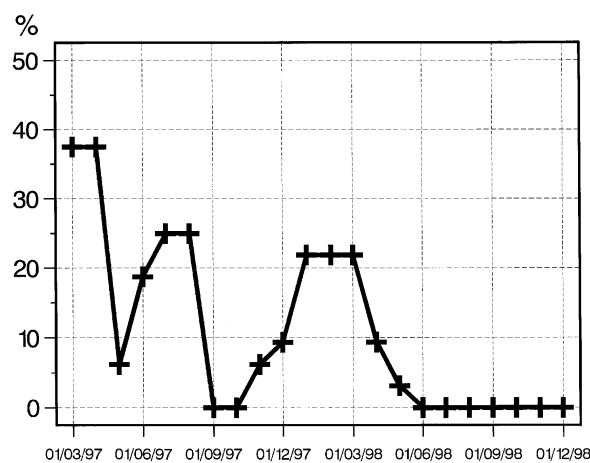


Fig. 1. Percentage of fruiting trees among 28 individuals of *M. coriacea* with DBHs above 42 cm.

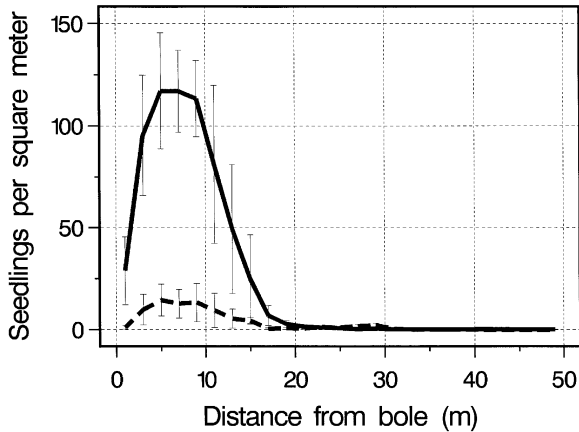


Fig. 2. Seedling densities observed in plots located at different distances from the boles of five isolated mother trees of *M. coriacea*. Mean and 95% confidence limits for seedling density before (solid line) and after inundation (dashed line).

majority of fruits is left below the crowns of fruiting trees, and only a small proportion is carried away from mother trees (Fig. 2). In this case, seedlings typically occur in aggregations of 20–50 individuals, which

may have been dropped on the site by resting or defecating animals. Fruits falling during the inundation germinate when the water recedes, and form carpets of seedlings with densities up to 150/m² under the crowns of mother trees (Fig. 2). Post-dispersal seed predation may be high, and is probably due to rodents. Pest attacks on seedlings are rare, but longer dry periods cause many seedlings to die off. Almost all surviving seedlings are killed by the subsequent inundation (Fig. 2). Preliminary observations from an experiment exposing seedlings to different flooding periods indicated that they start dying after approximately 1 month of total inundation.

4.2. Population structure and dynamics

M. coriacea attained considerable SIV's in the overstorey and understorey in all forest types (Fig. 3). In the overstorey, the relative dominance was higher than the relative density, indicating that individuals had diameters higher than the forest averages. Conversely, in the understorey its relative

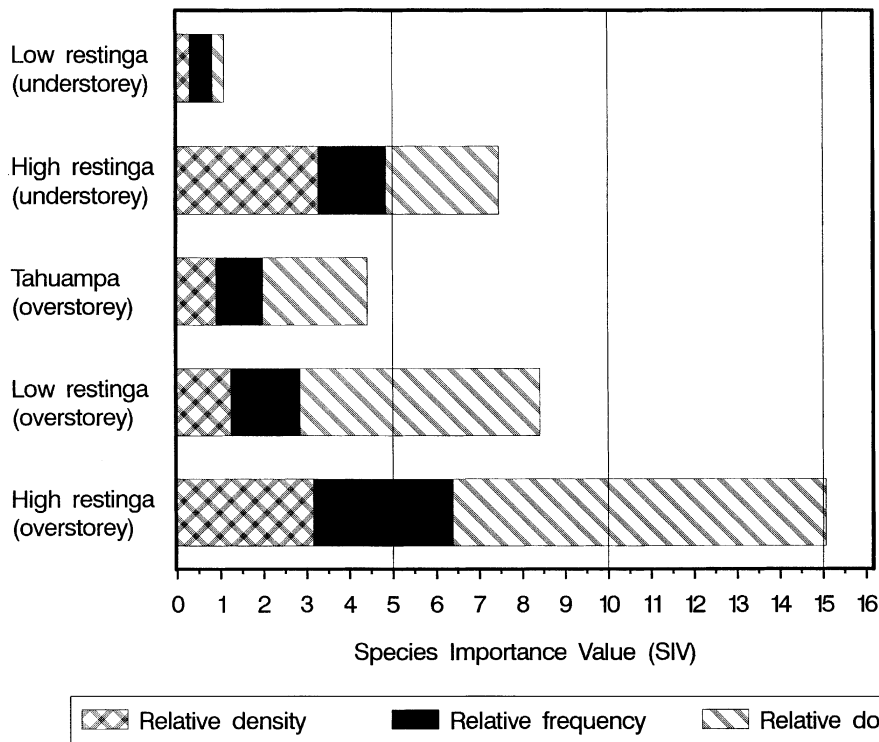


Fig. 3. Species importance values for *M. coriacea* in different forest types and stand components. By definition, the sum of SIVs for all species in a forest or stand component must equal 300.

dominance was equal to or lower than its relative density, indicating average or below average tree sizes.

A tree position map outline showed that *M. coriacea* individuals in the understorey of the high restinga had a heterogeneous, swarm-like distribution, whereas no pattern was evident for individuals in the overstorey of the high restinga or among the few individuals in the low restinga. This was also evident from the relative frequency/relative density ratio (Fig. 3). Accordingly, calculation of the Morisita index for high restinga quadrat plots of different lengths (Fig. 4) showed a significant departure ($P < 0.001$) from random dispersion towards clumping ($I_\delta > 1$) in the understorey, whereas in the overstorey the species was more-or-less randomly spaced ($P > 0.05$).

Individuals of *M. coriacea* in the high restinga understorey displayed an approximately exponential decline in I_δ values with increasing plot quadrat area (Fig. 4). Although, the calculation was not carried out for extremely small quadrats, the results suggested a pattern of “point sources” with a high density, surrounded by more diffuse swarms of individuals with density declining more-or-less exponentially from the

population centers (Hubbell, 1979, 1980). This pattern was particularly pronounced when untreated plots were considered individually.

The seedlings recorded in the 1 ha plots presented a pronounced and highly significant ($P < 0.001$) aggregation at the 20 m \times 20 m quadrat level ($I_\delta > 6$ and 12 for the high and low restinga, respectively). When analyzed separately, the seedlings in the untreated plots failed to show significant departure from random distribution. However, the seedlings here occurred in so large numbers that the Morisita index may not be appropriate to assess the distribution pattern at a 20 m \times 20 m quadrat level (Greig-Smith, 1983). In fact, the seedling density in the untreated plots in 1994 averaged approximately 10,000 and 4000/ha on the high and low restinga, respectively, compared to 250 and 100 in the treated plots. However, whether opening up the canopy causes less regeneration success cannot be concluded from the results mentioned, as other factors such as the density of mother trees and a temporary reduction in fruiting (due to disturbance) may have been decisive.

The density decreased with increasing diameters, showing a so-called reverse J pattern as regards the diameter distribution (Table 1).

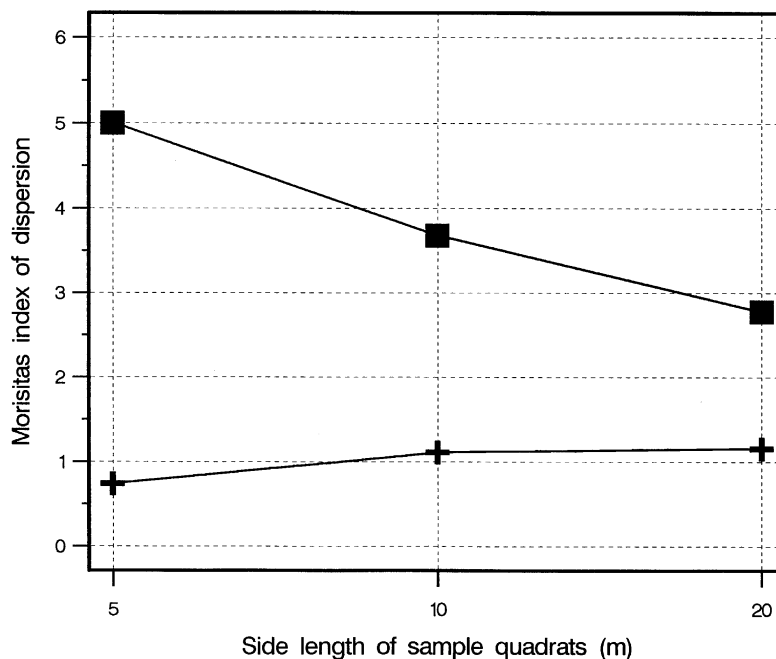


Fig. 4. Morisita index of dispersion (I_δ) for *M. coriacea* in high restinga overstorey (line with pluses) and understorey (line with squares). The abscissa is on an exponential scale as regards area of sample plots.

Table 1
Diameter distribution of *M. coriacea* individuals in flood plain forests^a

DBH (cm)	High restinga	Low restinga	Tahuampa
<9	418	35	– ^b
10–19	18	5	6
20–29	8	5	2
30–39	6	2	–
40–49	2	1	2
50–59	2	–	1
60–69	2	3	1
70–79	1	4	1
80–89	1	–	1
90–99	1	1	–
110–119	1	–	–
>120	1	–	–

^a Data from 3 ha were included for each forest type.

^b Data not available.

The tree height–DBH relationship was modeled using the Mitscherlich or monomolecular equation (Fig. 5)

$$h = 44.55(1 - 0.9725 e^{(-0.02361d)}) \quad (2)$$

where h is the height (m) and d is DBH (cm).

The high restinga had the highest stocking of *M. coriacea*, both in terms of density and basal area,

while growth (both basal area and volume) in the period 1993–1997 was highest in the low restinga (Table 2).

The highest mean annual diameter growth of individual trees occurred in the 50–70 cm class (2.2 cm per year), but there was a considerable variation (Table 3). Mean relative basal area and volume growth within size classes ranged from 5 to 45%. The time for trees to reach 130 cm DBH is 112 and 33 years given mean and maximum DBH growth rates, respectively.

Diameter increment of *M. coriacea* was generally high, but varied considerably with DBH. Two models based on the Wykoff equation (cf. Vanclay, 1994, p. 166) were fitted using the DBH variable. The first model was fitted to data from untreated plots using the DBH variable (3), while the second model was fitted to data from the treated plots again using the DBH variable (4)

$$\Delta d = \sqrt{e^{(-9.521892+3.063883 \ln(d)-0.000489d^2)}} \quad (3)$$

$$\Delta d = \sqrt{e^{(-9.480924+3.105072 \ln(d)-0.000509d^2+15.346986 e^{(-\sqrt{d})})}} \quad (4)$$

where Δd is the diameter increment (cm), and d the

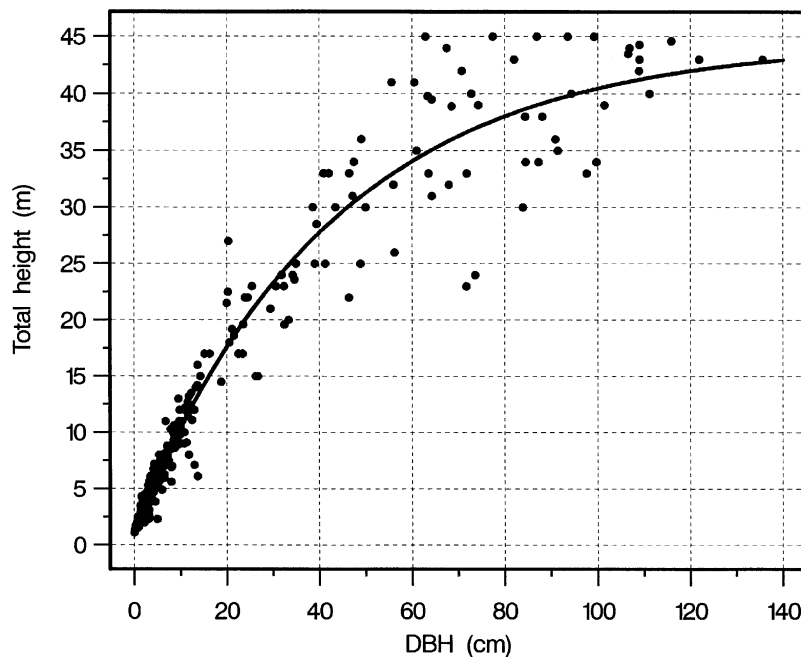


Fig. 5. Total height vs. DBH of *M. coriacea*: observations and relationship (model (2)).

Table 2
Stocking and growth of *M. coriacea* in flood plain forests^a

	High restinga	Low restinga	Tahuampa
Density (per ha)	14.3	7.0	4.7
Basal area (m ² /ha)	2.1	1.4	0.7
Stem volume (m ³ /ha)	37.9	23.8	11.1
Diameter (cm) corresponding to average basal area of stand	30.7	41.8	36.3
Average annual basal area growth (m ² /ha per year)	0.085	0.087	0.025
Average annual volume growth (m ³ /ha per year)	1.46	1.68	0.47

^a Growth data were from plots where different felling treatments were applied. Volumes were calculated on basis of the height model (1).

DBH (cm). Standard *F*-tests showed relatively good fit of all models ($R^2 = 0.45$ (2), 0.54 (3), $P < 0.0001$). Model (3) predicted that annual current DBH increment peaks around 55 cm DBH, and is relatively low for small diameters, resulting in a low mean annual DBH increment culminating at around 120 cm DBH

(Fig. 6a). Model (4) also predicted a peak in annual current diameter increment at around 55 cm DBH, but shows higher increments at smaller diameter sizes, resulting in an earlier and more pronounced peak in the annual mean DBH increment at around 100 cm DBH (Fig. 6b).

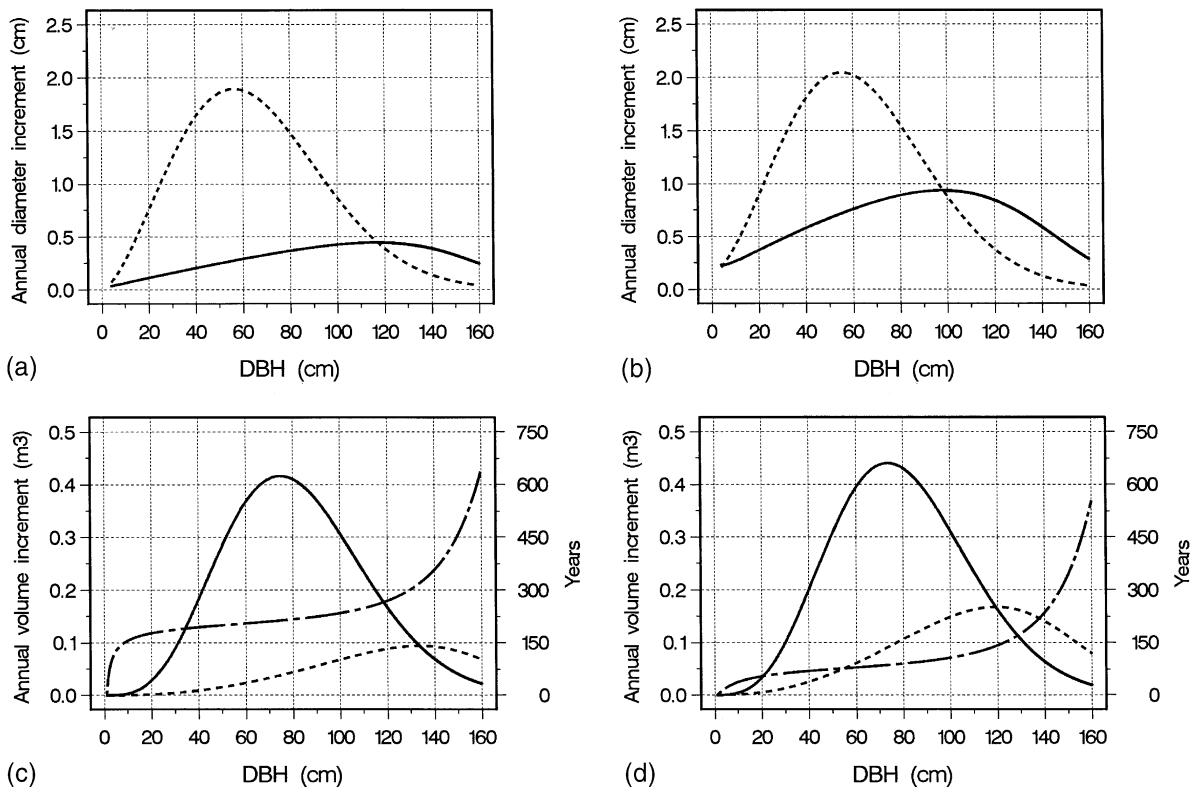


Fig. 6. Current (solid line) and mean (dashed line) annual diameter and volume increments for *M. coriacea* individuals as a function of DBH; time required for a tree to reach the nominated diameter (long dashes, right axis): (a) diameter development predicted from data collected in untreated plots (model (3)), (b) diameter development predicted from data collected in treated plots (model (4)), (c) volume increment predicted by combining models (2) and (3), (d) volume increment predicted by combining models (2) and (4).

Table 3
Growth of *M. coriacea* individuals in diameter classes^a

DBH (cm)	Number of growth registrations	DBH growth (cm per year)		Relative basal area growth (% per year)	Relative volume growth (% per year)	Time to grow through diameter class (years)	
		Mean \pm 95% confidence limits	Maximum	Mean \pm 95% confidence limits	Mean \pm 95% confidence limits	Mean growth rate	Maximum growth rate
≤ 1	11	0.02 \pm 0.05	0.17	21 \pm 10	26 \pm 12	– ^b	– ^b
1–5	115	0.21 \pm 0.02	0.98	31 \pm 5	45 \pm 9	19	4
5–10	67	0.27 \pm 0.04	0.96	8 \pm 1	11 \pm 2	19	5
10–20	100	0.66 \pm 0.06	3.47	12 \pm 1	18 \pm 2	15	3
20–30	41	1.75 \pm 0.13	3.65	17 \pm 1	23 \pm 2	6	3
30–50	45	1.66 \pm 0.17	3.84	10 \pm 1	13 \pm 2	12	5
50–70	19	2.21 \pm 0.29	5.76	8 \pm 1	10 \pm 1	9	3
>70	34	1.78 \pm 0.21	5.81	5 \pm 1	6 \pm 1	34 ^c	10 ^c
Sum/mean	432	0.83 \pm 0.05	–	16 \pm 2	23 \pm 3	112	33

^a Data for individuals over and below 10 cm DBH were derived from plots of different sizes, i.e. individuals under 10 cm DBH were monitored on 0.64 ha, while individuals over 10 cm DBH were monitored on 9 ha. Data were from plots where different felling treatments were applied.

^b Periods to grow to 1 cm DBH are not included, because the value calculated from the mean is unrealistically high.

^c Periods are to reach a DBH of 130 cm.

5. Discussion

M. coriacea has wood properties suitable for plywood production, and is extracted throughout much of its natural habitat (flood plains in tropical South America; Berg, 1972; Teixeira et al., 1988; Chichignoud et al., 1990; Ros-Tonen, 1993). In the Peruvian flood plain forests, it is generally numerous, frequent and dominant, although it apparently prefers the restinga forests that are inundated more briefly, and becomes less dominant in tahuampa forests flooded for longer periods. The relative overall importance (SIVs) of *M. coriacea* corresponded to 1.5–5% of all species in the overstorey and 0.3–2.5% in the understorey (Fig. 3), which is high for a single species in a tropical rain forest. Applying an appropriate management, this figure can perhaps be increased if requested.

Phenological studies of *M. coriacea* in 1997–1998 showed that the major fruiting took place from around December to May, coinciding with the annual flooding. However, in 1997 trees also fruited from June to August, while no fruiting was observed in this period in 1998, perhaps due to the occurrence of an unusual dry period restraining fruit development (Fig. 1). These observations are in accordance with Berg (1972), who stated that the species probably flowers

throughout the year. Similarly, Pekka Soini (personal communication) informed that *M. coriacea* in the Pacaya-Samiria National Reserve is an important food source for mammals and larger birds because of its abundant and prolonged production of fruits. Since most other flood plain trees only fruit during or just after the inundation, it is important to retain fertile individuals of *M. coriacea* in the forests as sources for food for animals and birds.

Seedlings of *M. coriacea* were abundant, but the stocks varied considerably (Fig. 2). Wilting during prolonged dry periods and drowning in connection to longer inundations seemed to be the major causes of mortality, resulting in fluctuations of seedling stocks over time (Fig. 2). Restrictions in space also occurred, as the densities of seedlings were clearly highest below the crowns of mother trees (Fig. 2), where they established under closed canopy conditions. Although the presence of seeds and seedlings fluctuated in time and space, the reproductive pattern was positive from a forest management point of view. An abundant recruitment can be expected close to mother trees in a substantial part of the year. However, observations in our treated plots suggested that seed germination or seedling establishment and growth may be impeded by direct and sudden exposure to high light conditions.

In areas with longer flooding periods, where seedlings are killed except in years with brief floods, planting of large sized seedlings may be a way to get the species established, as flooding tolerance generally increases with size of individuals (Gill, 1970). From a seedling establishment point of view, logging operations should preferably be carried out just after inundation to allow growth of seedlings before the next inundation. This may, however, conflict with the technical advantage of felling trees just before inundation and floating the logs to the mills together with drifting species. Larger juveniles were abundant in the forests studied, but decreased with the duration of flooding (Table 1). Management should aim at recruiting these juveniles, which are so abundant in the high restinga that the risk of genetic erosion should be small if they are successfully recruited.

The different dispersion patterns of *M. coriacea* in the understorey and overstorey in high restinga (Fig. 4) can be interpreted in several ways. The patchy distribution of understorey individuals may reflect corresponding variation in microsite conditions and biological processes crucial to the establishment and survival of seedlings. The reduction in clumping with increasing size may be indicative of self-thinning, density dependent mortality, or incomplete colonization of the site (Hubbell, 1979, 1980; Greig-Smith, 1983; Henriques and Sousa, 1989). In the high restinga, the growth conditions were rather homogeneous in terms of drainage and soil fertility, implying that other factors caused the clumping of juveniles. However, light conditions were patchy, but there was no tendency towards a more random dispersion in the plot where firm feelings were carried out, resulting in more homogeneous light conditions. It is more likely that the restricted dispersal of seeds was the major reason for the patchy distribution of juvenile individuals, which due to density dependent mortality developed to a more random dispersion among larger individuals (Fig. 4).

Calculation of growth of *M. coriacea* in diameter classes (Table 3) appeared to be a feasible approach to growth and yield modeling for the species. However, compared to predictions of the developed growth models ((3) and (4)), the results of the growth in diameter classes indicated a relatively fast development, especially when based on the maximum growth. The height and diameter increment models combined

predicted culmination of mean annual volume increment at approximately 130 cm DBH when data from the untreated plots were used (Fig. 6c), and at around 120 cm DBH in the treated plots (Fig. 6d). These points also indicated the optimal felling diameter limit for maximum volume production, which was reached in around 260 and 150 years, respectively. The considerable difference between the two models was mainly due to the slow juvenile development in the untreated plots, indicating that felling treatments can have a desirable effect on the growth of *M. coriacea*. Thus, the diameter limit for optimal volume production is in the range 120–130 cm DBH depending on which model is used, and is reached in 150–260 years. Whether these limits are also economically optimal depends on other factors. Since fruiting has been observed in individuals of 42 cm DBH, and may be abundant in trees of 60–100 cm DBH, a diameter cutting limit in the range 120–130 cm DBH should not have repercussions on the regeneration of the species. As indicated by the observed maximum growth rates (Table 3), the growth performance may perhaps be even better with optimal thinning treatments.

The relatively high stocking of *M. coriacea* (Table 2) was rather unusual for a single commercial tree species in the species rich Neotropical rain forests (e.g. Lamprecht, 1989, 1993; Silva, 1989). Furthermore, its growth rates were relatively high (Table 2, Table 3, Fig. 6). Combined with its reproductive features, which from a forest management point of view are relatively positive, it implies that many forest management options exist. Despite the tendency to clumping of seedlings and juveniles (Figs. 2 and 4), the horizontal and vertical distribution of larger individuals was relatively homogeneous, which is desirable for implementation of a polycyclic silvicultural system, especially in the high restinga. The abundant and reliable regeneration would on the other hand probably also be sufficient to accomplish the establishment of a monocyclic silvicultural system focusing on the species. Either approach would be feasible, depending on the aims of the enterprise. However, the polycyclic system may be more consistent with maintaining the many other services provided by the flood plain forests. As they are by nature adapted to large perturbations (Foster et al., 1986; Salo et al., 1986; Foster, 1990a, 1990b; Worbes et al., 1992; Salo and

Kalliola, 1993; Worbes, 1997), they can probably accommodate the disturbance involved in timber harvesting, especially the rapidly responding restinga forests. *M. coriacea* could contribute significantly to the timber harvest in such systems.

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