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Population dynamics of *Garcinia lucida* (Clusiaceae) in Cameroonian Atlantic forests

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Abstract

Garcinia lucida Vesque (Clusiaceae) is a highly valued non-timber forest tree. The bark and the seeds are exploited and commercialised for medicinal purposes and palm wine processing in Cameroon, Gabon and Equatorial Guinea. The bark is often removed over almost the entire circumference of the stem, leading to high mortality. To identify the processes or the life stages that influence the population dynamics and to forecast the potential effects of harvesting, a demography study was carried and a matrix model was constructed to characterise the population dynamics of *G. lucida* in the South Cameroonian Atlantic humid forests. The study revealed that height and diameter growth values were very low and may constitute biological disadvantages for the dynamics of the species. The flowering and fruiting model, the absence of seed dormancy, and the high germination and seedling survival rates constituted advantages for the population dynamics, which is characterised by effective regeneration strategies. Rates of growth, survival and fecundity allowed calculations of transition probabilities of the matrix model. The value of the dominant eigenvalue (λ) was 1.063, slightly higher than the value expected for stable populations. The sensitivities of λ to changes showed that the population growth was most sensitive to changes in tree growth, particularly in the seedling stage. Elasticity analysis showed that growth and fecundity elements had much lower contributions to λ , indicating that the harvesting of seeds may have a low impact on population growth. However, the population growth was highly sensitive to changes in survival probability, particularly among trees of 5–10 cm, diameter at breast height (dbh). The last stages, containing the large reproductive individuals over 10 cm dbh, which are interesting for the bark extraction, accounted for lowest elasticity, indicating that the extraction of bark may have at least a low impact on population growth. Thus, there maybe a good scope for sustainable extraction of *G. lucida* bark in these stages. The size-class 5–10 cm dbh proved by loop analysis to be the most important reproductive stage for population maintenance. However, individuals in this size-class are also exploited by forest gatherers, and increased exploitation pressure on trees in this size-class is likely to have a considerable impact on the population growth and to compromise the scope for sustainable exploitation of this resource.

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1. Introduction

Among the diversity of forest resources and services, there has been growing interest in the extraction of non-timber forest products (NTFPs) as an alternative to the increasingly high rates of tropical deforestation (Hall and Bawa, 1993; Peters, 1996; Toledo et al., 1992 in Phillips, 1992). Unfortunately, many NTFPs share with timber the problem of finding extraction rates that are both biologically sustainable and profitable (LaFrankie, 1994). There are many examples of non-timber resource depletion as a result of over-exploitation (Varquez and Gentry, 1989; Browder, 1992; Nepstad and Schwartzman, 1992; Cunningham and Mbenkum, 1993). Economic pressure, poor investment in designing and implementing forest management, inadequate legislation concerning sustained non-timber resource exploitation, as well as the lack of sufficient knowledge about the resources themselves are the most important causes of this resource depletion (Wickens, 1991). Quantitative information related to the entire life cycle of non-timber species, their present and future productivity, as well as the impact of exploitation on population dynamics are poorly documented (Peters, 1991; Zuidema, 2000; Soehartono and Newton, 2001). One practical approach to assess the impact of exploitation is to predict future population size based on current population structure, growth and fecundity. Therefore, demographic studies are essential to simulate species dynamics over time. Since the nature, the use and the importance of NTFPs are so closely related to local ecological, economic and socio-cultural conditions, most research will need to be location-specific (de Beer and McDermott, 1989; Wickens, 1991). Such large-scale field or case studies on exploited tropical species are scarce, but essential to understand the population dynamics of species and therefore, the impact of exploitation on population dynamics.

In this paper, the natural population dynamics of *Garcinia lucida* in the south Cameroonian Atlantic humid forests are analysed using matrix models. The bark of this species is one of the most valued NTFP in Cameroon, Gabon and Equatorial Guinea (Mollet et al., 1995; van Dijk, 1999). According to van Groenendael et al. (1988) and Boot and Gullison (1995), matrix models can be used in attempts to forecast population dynamics and to evaluate the long-term

consequences of hypothetical changes in the life cycle. *G. lucida* is a small evergreen dioecious tree, reaching 25–30 cm in diameter at breast height (dbh) and 12–15 m in height. It grows in high-density stands in hilly moist forests. The geographical distribution is limited to parts of Cameroon, Equatorial Guinea and Gabon (Bamps, 1970). The bark is used as an additive to palm wine production and in distilling fermented palm wine to produce liquor. The bark and the seeds, dried or fresh, are widely used for medicinal purposes to prevent food poisoning and to cure stomach and gynaecological pains, as well as to cure snake bites (van Dijk, 1999; Sunderland and Obama, 1999). Traditionally, bark exploitation involves debarking only one side of reproductive individuals, but very often the bark is removed over almost the entire circumference of the stem, especially when the bark is thick and can be easily detached from the wood, regardless of whether it is a young or an old mature tree. This practice leads to a high mortality of trees (Guedje and Nkongmeneck, 2001; Guedje and Fankap, 2002). The present investigation aimed at characterising the population dynamics of *G. lucida* in order to identify the processes or the life stages that are regulating or limiting the population dynamics and therefore, to forecast the potential effects of bark and seed harvesting in south Cameroon.

2. Study site

The study was carried out within the Tropenbos Cameroon Programme (TCP) research area. The study sites are located near the villages Nyangong (2°56.04'N, 10°49.62'E) and Ebom (3°06.04'N, 10°46.28'E) in the South Province of Cameroon (Ebolowa district), some 100 km east of the coast (Fig. 1). The climate is humid tropical with two rainy and two drier seasons, with a yearly rainfall of about 2000 mm, and with an average annual temperature of around 25 °C (Olivry, 1986). The landscape consists of mountains and abrupt hills. The studied plots are located at approximately 500 m a.s.l., but some mountains in the vicinity exceed 1000 m. The substratum consists of Precambrian metamorphic rocks and old volcanic intrusions. The soils have been classified by van Gemerden and Hazeu (1999) as well drained, deep to very deep soils, moderately well drained soils and poorly to very

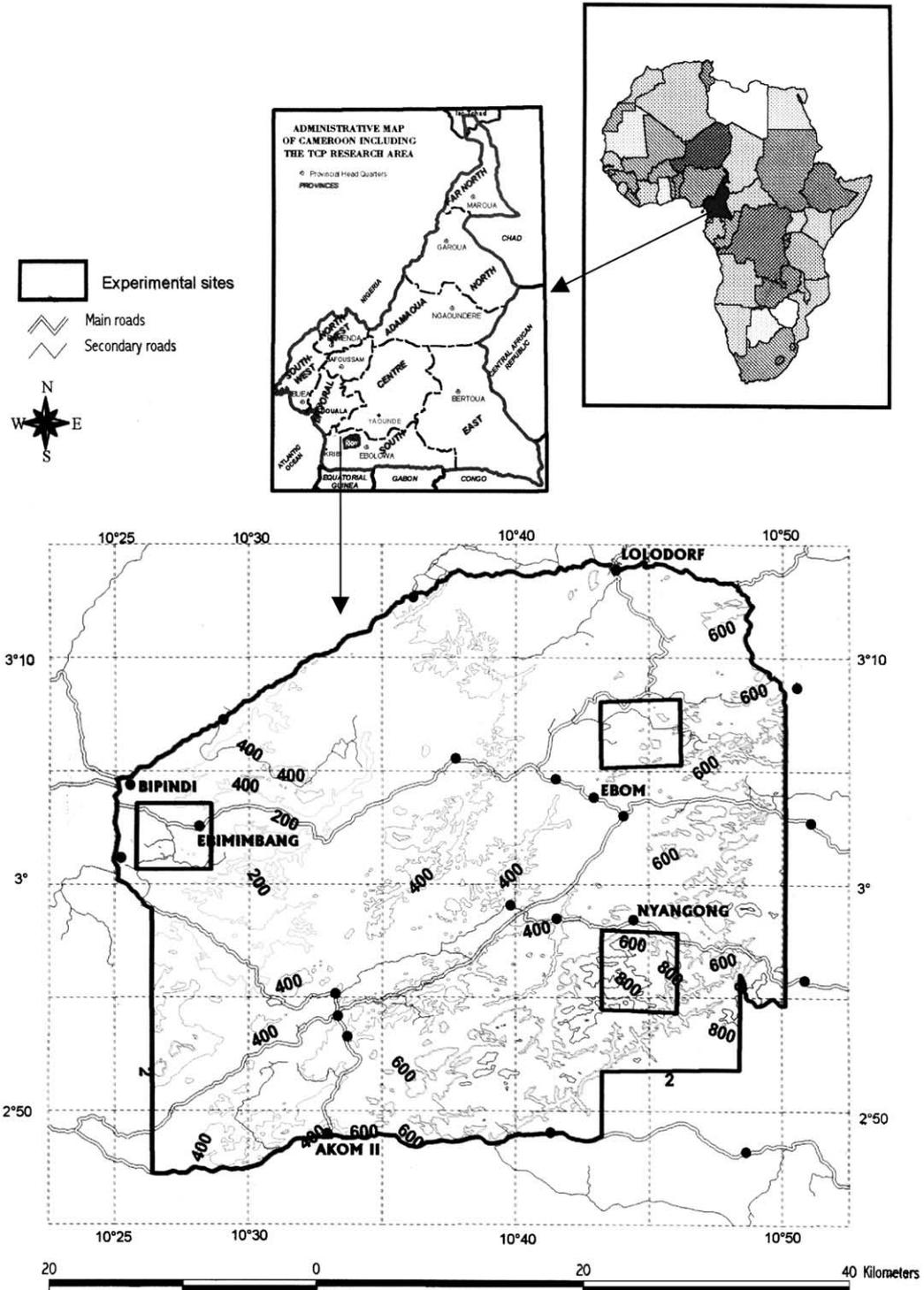


Fig. 1. Location of Cameroon in Africa and map of the Bipindi-Akom II region.

poorly drained soils. According to FAO (1988), the first type is classified as Xanthic Ferralsols, the second as Acric-plinthic Ferralsols and the third as Dystric Fluvisols. According to Letouzey (1985), the vegetation can be characterised as mid altitude evergreen forest rich in Caesalpinaceae. Biodiversity in this part of Cameroon ranks among the highest in Africa. The forest cover is still largely intact, but due to human influence, it is alternated with a mosaic of fields, fallow lands, secondary forest, and logged-over forest. Population density is low (5–10 inhabitants/km²) with Bantu and Bagyeli as the main population groups. People earn their livelihood from hunting, fishing, gathering and practising shifting cultivation.

3. Materials and methods

3.1. Data collection

Eight 100 m × 40 m plots were established in 1997 in the forest at two localities in the Bipindi-Akom II region (Akok and Minwo'o) where *G. lucida* occurs (Fig. 1). Due to the high exploitation pressure, untouched stands of *G. lucida* are rarely found in this region.

Within each plot, all *G. lucida* trees >15 cm dbh were measured for size, tagged and mapped to the nearest meter (Dallmeier et al., 1992). Young adults trees (5–15 cm dbh) were measured, tagged and

mapped in five randomly selected sub-plots of 20 m × 20 m within each plot. Saplings (>1 m height and <5 cm dbh) were inventoried in one 10 m × 10 m quadrat randomly established in each sub-plot, while seedlings (<1 m height) were inventoried in one 5 m × 4 m sub-quadrat randomly established in each quadrat.

Size-specific growth and mortality rates were determined over 2 years for a sub-sample of marked individuals of varying size ($n = 747$). The height of the selected seedlings and saplings was recorded every 6 months while stem diameter of the selected juveniles and adults was measured once a year at the same month. The population was grouped into eight life cycle stages (S1–S8) based on plant size (Table 1). The pre-reproductive and juvenile trees were classified as seedlings (S1: 0–100 cm height), saplings (S2: 100–200 cm height and S3: 200–400 cm height), and juveniles (S4: 2.5–5 cm dbh). Adult trees were classified into adult 1 (S5: 5–10 cm dbh), adult 2 (S6: 10–15 cm dbh), adult 3 (S7: 15–20 cm dbh) and adult 4 (S8: ≥ 20 cm dbh).

Phenology (presence of flowers and fruits) was observed once a month over 2 years for a sub-sample of marked individuals of varying size ($n = 180$ individuals). Seed production of female trees was estimated over two fruiting seasons by constructing circular traps under the crowns of 48 reproductive adults of various size. The traps were constructed by villagers using locally available materials. The traps were visited every week, the seeds collected counted

Table 1
Transition matrix parameters and column vector used to analyse *G. lucida* population dynamics^a

Stages	Height/diameter	A_x	N_x	F_x	C_x	T_x	M_x	G_x	P_x
Seedling (S1)	$H \in [0-100[$	100	5613	0	2.28 ± 0.25	43.89	0.0742	0.0211	0.9047
Sapling (S2)	$H \in [100-200[$	100	1533	0	3.81 ± 0.38	26.27	0.0084	0.0377	0.9539
Sapling (S3)	$H \in [200-400[$	200	488	0	6.77 ± 1.00	29.56	0.0066	0.0336	0.9598
Juvenile (S4)	$\emptyset \in [2.5-5[$	2.5	185	0	0.09 ± 0.01	29.19	0.0081	0.0340	0.9579
Adult (S5)	$\emptyset \in [5-10[$	5	348	14	0.09 ± 0.01	53.19	0.0120	0.01857	0.9694
Adult (S6)	$\emptyset \in [10-15[$	5	147	21	0.07 ± 0.01	72.29	0.0127	0.0137	0.9737
Adult (S7)	$\emptyset \in [15-20[$	5	31	32	0.07 ± 0.02	70.90	0.0100	0.0140	0.9760
Adult (S8)	$\emptyset \geq 20$	–	5	33	0.04 ± 0.03	–	0.0100	0.0000	0.9900

^a All rates are expressed on an annual basis; growth rate units (mean values \pm S.E.) are cm per year for all stages; seedling and sapling classes are based on height, while juvenile and adults classes are based on dbh. A_x (cm): class width; N_x : number of individuals/ha; F_x (seedlings per year): fecundity; C_x (cm per year): annual growth rate; T_x (years): time of remaining of individuals in size-class x ; M_x : annual mortality rate; G_x : probability of moving into the next stage (derived from growth rates and class widths); P_x : probability of remaining in the same stage.

and removed at each visit. Size-specific fecundity rates were multiplied by the number of reproductive adults in each size-class to estimate the total annual fruit production.

The percentage of germination and survival of seeds was measured in twenty 5 m × 4 m quadrats placed under the crowns of reproductive adults during 2 years. The number of germinated seeds was recorded twice a week. Seeds predated by insects were collected to rear the larvae and to identify the insect species.

3.2. Transition matrix construction and analysis

A transition matrix model of the form initially described by Lefkovitch (1965) and subsequently modified by Caswell (1989) was used to analyse *G. lucida* population dynamics.

The matrix is of the form: $n_{t+1} = A \times n_t$, where A is a square matrix containing transition probabilities among categories during one time-step and n is a vector containing the number of individuals in each category at time t and $t + 1$. In this equation, the population structure at time $t + 1$ is obtained by multiplying the structure at time t with the transition matrix that contains information on the dynamics of the population, assuming environment factors to be constant in time. Repeated multiplication of the column vector in the transition matrix with the current population eventually produces the dominant latent root or dominant eigenvalue of the transition matrix (λ), which is equal to the asymptotic population growth rate and which is, together with the stable stage population structure (the right eigenvector w), the inherent characteristics of the matrix (Caswell, 1989).

The followings elements of the transition matrix were calculated using data collected over a 2-year-period from the eight 0.4 ha plots.

Fecundity F_x (seedlings per year) was expressed as the mean number of seedlings produced annually per tree in size-class x . The value of F_x was determined by multiplying the size-specific seed production by the number of seedlings that emerged yearly per seed produced, considering that the percentage of germination and seedling survival rate are not related to the tree size-class.

Mortality M_x was calculated as $m_i = 100[\ln(n_0/(n_0 - d_i))/t_i]$ (Hall and Bawa, 1993), where n_0 is

the number of trees at the first enumeration, d_i the number of trees that died during an interval and t_i is the number of years between enumeration.

The mean annual proportion of individuals growing (G_x) from one size-class into the next was based upon the growth curve obtained from the 2 years of field measurements. $G_x = (1 - M_x)/T_x$, where T_x represents the time for an individual to grow through size-class x . T_x is calculated as $T_x = A_x/C_x$. A_x (in cm) is the class width or size-class amplitude and C_x (cm per year) is the average increment or mean annual growth rate recorded in size-class x .

The mean annual proportion of individuals remaining in the same size-class (P_x) was calculated as $P_x = 1 - M_x - G_x$.

RAMAS stage (Ferson, 1990) was used to calculate the value of λ . The estimate of variance or confidence intervals of λ was based on the approach described by Caswell (1989), relying on the eigenvalue sensitivity formula to develop an approximate expression for the variance in λ and using normal distribution theory to translate this variance into confidence interval. Furthermore, sensitivity and elasticity analyses were carried out to determine the sensitivity of the asymptotic population growth rate to changes in different elements of the transition matrix. Sensitivity analysis (Caswell, 1978) examines the effect on λ of small changes of fixed size in the demographic parameters while elasticity analysis (de Kroon et al., 1986) provides valuable information on the dependence of population growth on proportional changes in survival, growth and reproduction at different stages in the life cycle. Loop analysis (van Groenendael et al., 1994) evaluates the contributions of alternative life history pathways within the life cycle graph to population growth rate, based on the elasticities of the transition elements of matrix. The life cycle graph is broken down in different unbranched loops and each loop will have one unique transition elasticity, the characteristic elasticity of the loop. The mathematical basis for the calculation of the elasticities of the loops is rooted in the following properties: (1) for each stage in the life cycle graph, the summed elasticity of incoming transitions equals the summed elasticity of outgoing transitions; (2) the elasticity of the loop is equal to the characteristic elasticity multiplied by the number of transitions of the loop.

4. Results

4.1. Size distribution, growth and survival

The actual distribution or initial abundance of *G. lucida* populations observed in the South Cameroonian Atlantic humid forests is characterised by a relatively high density of seedlings and saplings compared to the density of adults trees (Table 1). Mean rate of height growth varies from 2.3 to 6.8 cm per year, increasing with tree-size from seedlings to large saplings, while mean rate of diameter growth varies from 0.04 to 0.09 cm per year. The standard error (S.E.) values indicate that height and diameter growth rates are variable from one tree to another. Mean rate of mortality varies from 1 to 7%. There is a tendency for mortality to decline with increasing height or diameter. This indicates a relatively high survival rate and a good adaptation of trees after the critical transition from seed to seedling and a successful establishment under the canopy, where competition for light is an important regulating factor.

4.2. Phenology, seed and seedling ecology

G. lucida trees flower and produce fruit for the first time when they reach 3 cm dbh. However, trees regularly produce fruits at 5 cm dbh. Although female and male trees exhibit flowers during any month of the year, two flowering peaks can be distinguished (April–June and October–January) in the South Cameroonian Atlantic humid forests. One important fruiting peak occurs between July and December, during the main rainy season. *G. lucida* fruits are medium-size (13 cm × 11 cm), ellipsoidal or globular form and green to green-golden in colour. The fruits contain one to four seeds wrapped with a thin and white-yellowish pulp. The number of seeds (mean values ± S.E.) produced by female trees amounts to 35 ± 7 seeds per tree per year in size-class 5–10 cm, 53 ± 7 seeds per tree per year in size-class 10–15 cm, 82 ± 5 seeds per tree per year in size-class 15–20 cm and 85 ± 6 seeds per tree per year in size-class >20 cm dbh. Seed fecundity apparently increased with tree size. Based on these values, seed production estimated from the 48 reproductive adults is on average of 11,584 seeds/ha per year, assuming equal probability ratio of female and male trees in the natural population.

G. lucida seeds are medium-size (4 cm × 3 cm × 2 cm to 8 cm × 6 cm × 4 cm), reddish-purple in colour and of semi-ellipsoidal form. When ripe, the seeds drop from the fruit or with the fruit on the ground beneath the parent tree, seed dispersal is essentially barochore. However, the giant Gambian rat (*Cricetomys gambianus*, Cricetidae) and the so-called brush-tailed porcupine (*Atherurus africanus*, Hystricidae) eat the fallen seeds or transport and store them in caches, thereby scattering the seeds away from the parent tree. Those seeds are either eaten and destroyed by these rodents or left in a forgotten cache where they eventually germinate. The mean percentage (44%) of observed seeds ($n = 271$) removed by these rodents from the twenty 5 m × 4 m survey quadrats during each fruiting period, as well as the proportion (60%) of seeds partially eaten ($n = 20$) found in 10 Gambian rat caches indicate that the predominant role of these animals seems to be predator rather than disperser. However, the observation of abandoned seeds scarcely eaten at some distance from the mother tree, as well as the proportion (35%) of intact seeds forgotten in the 10 Gambian rat caches also indicate that these rodents may act in a short-distance dispersal of *G. lucida* species. In addition, *Leguminivora ptychora* (Lepidoptera, Tortricidae) was identified as an insect destroyer of *G. lucida* seeds, 19% of seeds collected on the ground forest in traps showed holes produced by this insect.

The seeds have little dormancy, and germinate within a few weeks of falling. The percentage germination of the different cohorts of seeds observed was high, varying between 71 and 97%, with an overall average of 82% ($n = 271$). Mean annual rate of seedling survival was 39%.

4.3. Matrix model analysis

The data presented in Table 1 provide the information on which the calculations of the coefficients of the projection matrix for *G. lucida* populations was based (Table 2). Value of the dominant latent root λ or the population growth rate was 1.063. Based on the standard error (0.009) of λ given by the square root of $V(\lambda)$, the 95% confidence interval gives an interval estimate of the rate of increase as $\lambda = 1.063 \pm 0.018$. Thus, it can be concluded that λ is slightly higher than the value (1.0) expected for stable populations.

Table 2
Projection matrix for *G. lucida* population dynamics^a

	S1	S2	S3	S4	S5	S6	S7	S8
S1	0.9047	0	0	0	14	21	32	33
S2	0.0211	0.9539	0	0	0	0	0	0
S3	0	0.0377	0.9598	0	0	0	0	0
S4	0	0	0.0336	0.9579	0	0	0	0
S5	0	0	0	0.0340	0.9694	0	0	0
S6	0	0	0	0	0.0186	0.9737	0	0
S7	0	0	0	0	0	0.0137	0.9760	0
S8	0	0	0	0	0	0	0.0140	0.9900

^a Flux probabilities have been rounded off to four digits.

The stable stage distribution (SSD) resulting from the model resembled the observed population structure (Fig. 2), although the relative SSD abundance of large trees was lower. Sensitivity analysis was used to measure the importance of any element of the transi-

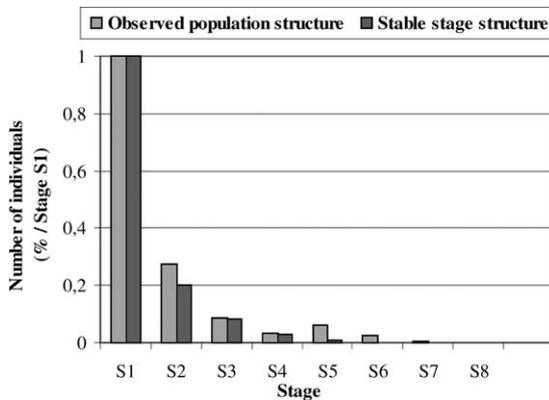


Fig. 2. Comparison of SSD and observed distribution (OD).

tion matrix to the population growth rate. Table 3 presents the result of this analysis in a matrix where each element represents the sensibility of the population growth rate to the associated transition probability. One of the sensitivity analysis limitations is the impossibility to distinguish the observed transition probabilities (the values printed in italics in Table 3) from those who exit only in theory. The results of this table show that the population growth rate is more sensitive to changes at the level of these unrealistic or hypothetical transition probabilities. At the level of the observed transition probabilities, the population growth is more sensitive to changes in growth than to changes in survival and fecundity throughout the entire life cycle. In addition to the unrealistic transitions, the sensitivity value of a matrix element depends also on the actual value of that element, which maybe different for fecundity and survival especially. Small changes in survival rate have much more influence than a similar change in a fertility rate. The interpretation of the sensitivities requires some care. Then,

Table 3
Sensitivity values for the population matrix model of *G. lucida*

	S1	S2	S3	S4	S5	S6	S7	S8
S1	0.1279	0.0247	0.0090	0.0029	0.0010	0.0002	0.0000	0.0000
S2	0.9617	0.1854	0.0675	0.0215	0.0078	0.0016	0.0003	0.0001
S3	2.7919	0.5382	0.1960	0.0624	0.0226	0.0047	0.0007	0.0001
S4	8.6044	1.6588	0.6039	0.1924	0.0696	0.0145	0.0023	0.0004
S5	26.6865	5.1446	1.8730	0.5968	0.2160	0.0448	0.0070	0.0013
S6	38.5286	7.4276	2.7042	0.8616	0.3118	0.0646	0.0102	0.0019
S7	56.0766	10.8105	3.9358	1.2541	0.4538	0.0942	0.0148	0.0028
S8	57.5407	11.0927	4.0386	1.2868	0.4657	0.0966	0.0152	0.0029

Table 4
Elasticity values for the population matrix model of *G. lucida*^a

	S1	S2	S3	S4	S5	S6	S7	S8
S1	0.10882	0	0	0	0.01363	0.00424	0.00101	0.00020
S2	0.01908	0.16631	0	0	0	0	0	0
S3	0	0.01908	0.17687	0	0	0	0	0
S4	0	0	0.01908	0.17334	0	0	0	0
S5	0	0	0	0.01908	0.19690	0	0	0
S6	0	0	0	0	0.00545	0.05924	0	0
S7	0	0	0	0	0	0.00121	0.01355	0
S8	0	0	0	0	0	0	0.00020	0.00269

^a The life cycle graph is broken down into four unbranched loops and each loop will have one unique transition elasticity. The characteristic elasticity of the loop. Loop elasticity is then the number of transitions in the loop times its characteristic elasticity. The four loops have the following values: S1–S8: $S1 = (0.01908 \times 4) + 0.00545 + 0.00121 + 0.0002 + 0.0002 = 0.08338$; S1–S7: $S1 = (0.01908 \times 4) + 0.00545 + 0.00121 + 0.00101 = 0.08399$; S1–S6: $S1 = (0.01908 \times 4) + 0.00545 + 0.00424 = 0.08601$; S1–S5: $S1 = (0.01908 \times 4) + 0.01363 = 0.08995$.

elasticity analysis or proportional sensitivity analysis is used to measure the proportional contribution of the matrix elements to the population growth rate. Table 4 presents the result of this analysis in a matrix where each element represents the proportional sensitivity of the population growth rate to the associated transition probability. Values, which contribute more than 10% to the population growth rate, are printed in italics. Giving that all the elasticities in the matrix sum to one, matrix elements were summed to obtain a measure of the relative importance of progression or growth (e_G), survival or stasis (e_L) and fecundity (e_F). Growth (0.08) and fecundity (0.02) elements have relatively low contributions to λ , suggesting that the harvesting

of seeds may have a low impact on *G. lucida* population dynamics. By far the largest proportion of total elasticity is confined in stasis elements (0.90). Moreover, Fig. 3 shows that there is a peak (0.20) in stage 5 (adults between 5 and 10 cm dbh), indicating the importance of individual survival, especially in this stage for the self-maintenance of the population. Stages 6–8, containing the largest reproductive individuals (above 10 cm dbh), which are interesting for the bark extraction by local population, accounted only for 0.08 of the total elasticity, suggesting that bark exploitation may have at least a low impact on the population dynamics of *G. lucida*. Loop analysis (Table 4) showed that size-class 5–10 cm dbh has the highest loop elasticities, suggesting that this size-class is the most important reproductive stage for population maintenance.

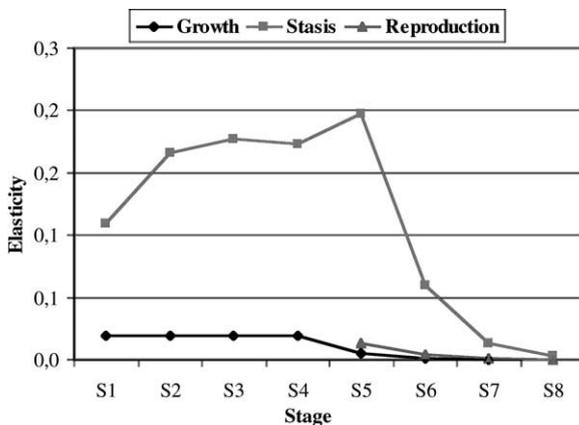


Fig. 3. Elasticity of λ to changes in reproduction, survival and growth for *G. lucida*.

5. Discussion and conclusions

The actual size-class distribution of *G. lucida* populations is comparable to those obtained by LaFrankie (1994) and Murali et al. (1996) for other NTFP yielding species. *G. lucida* exhibits higher rates of growth in pre-reproductive stages, while the mean yearly increment in diameter is very low compared to the value of 0.2 cm per year recorded for *Psidium acutangulum* (Myrtaceae), a typical understorey tree like *G. lucida* (Worbes, 1989 in van Groenendael et al., 1996). In general, the height and diameter growth

values of *G. lucida* are very low and may constitute biological disadvantages for the dynamics of the species. Management strategies improving growth of *G. lucida* in its natural habitat as well as in other environments where the species could be introduced will be favourable to the dynamics of this species.

The timing of flowering and fruiting in terms of duration tends to be staggered over the year. However, two flowering peaks and one fruiting peak have been recorded. The production of *G. lucida* fruits occurs during the main rainy season as for many tropical trees (Mori and Prance, 1987; Zhang and Wang, 1995). *G. lucida* seeds exhibit a high and rapid germination rate with a mean value of 50% of seeds exhibiting complete germination within 2 or 3 weeks after seedfall. These results indicate that the flowering and fruiting model, the absence of seed dormancy, the germination rate and the seedling survival rate constitute biological and ecological advantages for the population dynamics of this species, which is characterised by effective regeneration strategies.

The matrix model approach used here has been applied earlier to describe the population dynamics of large tropical trees (Hartshorn, 1975; Enright and Ogden, 1979; Debroux, 1998), several palms (Bullock, 1980; Enright and Watson, 1992; Bernal, 1998), as well as NTFP species (Peters, 1991; Soehartono and Newton, 2001). The finite rate obtained is close to the value reported for *Roupala montana* (Zuidema, 2000) and for *Brosimum alicastrum* (Peters, 1991), but higher than those reported for other species (Hartshorn, 1975; Enright and Ogden, 1979; Debroux, 1998). The largest contribution of stasis elements to the total elasticity value of *G. lucida* matrix is typical in long-lived species (Silvertown et al., 1992, 1993 in Silvertown et al., 1996). The relatively low contributions of stages 6–8 (the largest reproductive individuals which are interesting for bark extraction) to the total elasticity value, suggest that there is a good prospect for sustainable extraction of *G. lucida* bark. However, young reproductive individuals in size-class 5–10 cm dbh, which proved to be the most important reproductive stage for population maintenance, are also exploited by forest gatherers, especially when the bark of these trees is thick and can be easily detached from the wood. An increased exploitation pressure on trees in this size-class is likely to have a considerable impact on the population growth and to

compromise the scope for sustainable exploitation of this resource.

The methodological advantages of matrix models are the flexibility of their mathematical formulation and their capacity to summarise complex demographic information contained in the life cycle diagram into a few summary statistics. As pointed out by Enright and Ogden (1979), these models allow investigators to predict at least the direction of future trends, and help them to set limits on the probable magnitude of future changes. However, as highlighted by Soehartono and Newton (2001), the model predictions should be viewed with caution. Assessments of demographic parameters were in the present study limited to 2-year-period and the density-dependent processes were omitted. As values of growth, survival and fecundity may vary among individuals or populations and in time, measurements over longer periods may provide more precise values (Enright and Ogden, 1979; Soehartono and Newton, 2001). Investigation about the effects or the role of density-dependence in the population dynamics of *G. lucida* may allow to improve the model developed in the present study. Such density-dependent models are constructed by writing the matrix elements a_{ij} as functions of density, just as they were written as functions of time in basic matrix models (Caswell, 1989). Population models that include population regulation have, however, only been developed for a few species (Alvarez-Buylla, 1994; Silva Matos et al., 1999). As highlighted by Boot and Gullison (1995) and Zuidema (2000), a disadvantage of matrix models is that they are time-invariant, assuming that the conditions of the studied population will continue forever, while demography can be influenced by variation in climatic conditions or by the effect of harvest. Several modifications to the basic matrix models have been developed in order to cope with such problems (Caswell, 1989, 2000; Horvitz and Schemske, 1995). The resulting time-varying and stochastic models describe the demographic consequences of a sequence of environments by the sequence of projection matrices. The results of the present study have direct bearing on attempts to manage *G. lucida* in order to contribute to the long-term exploitation and conservation of tropical forests. Furthermore, the impact of different harvesting and management scenarios should also be assessed using these matrix models.

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