Chapter 8

General discussion and summary

Comparing life history of the study species

Three woody tropical forest species were studied in this thesis: one tree species (*Bertholletia excelsa*, Chapter 2) and two palms (*Euterpe precatoria*, Chapter 3; and *Geonoma deversa*, Chapters 4 & 5). All study species are exploited for non-timber products: Brazil nuts are harvested from *Bertholletia*, palm heart from *Euterpe* and leaves for high quality thatching from *Geonoma*. Both similarities and differences were found among the study species in their demography, the impact of extraction and their scope for sustainable management. In Table 1 the study species are compared with respect to these parameters. The following text explains the information in this table.

The study species differed considerably in adult stature and distribution: *Bertholletia*, an emergent tree that occurs at relatively low densities; *Euterpe*, a (sub)canopy palm that occurs at relatively high densities; and *Geonoma*, an understorey palm that has a strongly clumped distribution in dense stands. Reproductive strategy also differed among the species: *Geonoma* reproduces both vegetatively and by seeds, *Euterpe* and *Bertholletia* by seeds only. The last species depends heavily on small rodents for seed dispersal to open its woody fruits (Chapter 2). For all species, the abundance of seedlings relative to adults was high, and similar (inverse J-shaped) population structures were obtained.

As for the population dynamics, survival was low for seedlings and contrasted with a (very) high survival rate for adults in all species. Low seedling survival is generally found in tropical forest trees, and can be attributed to low understorey light availability (Chapters 2 & 3), vulnerability to herbivores and seed predators (Chapter 2), and vulnerability to damage by falling debris or complete coverage by leaves (Chapter 4). Furthermore, climatic variation influenced seedling survival (Chapters 2, 3 & 4). In all species, survival
probability steeply increased with size from small seedlings to larger seedlings or saplings.

Seedling growth was generally low, and often negative growth rates were found. *Bertholletia* seedlings appeared to suffer less from unfavourable understory conditions, probably as they can make use of a large cotyledon reserve (Zuidema et al. 1999). In contrast, growth of juvenile individuals (*i.e.* non-reproductive individuals with a visible stem or measurable diameter at

<table>
<thead>
<tr>
<th>Parameter</th>
<th><em>Bertholletia</em></th>
<th><em>Euterpe</em></th>
<th><em>Geonoma</em></th>
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<tr>
<td><strong>General characteristics</strong></td>
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<td>Emergent tree</td>
<td>(Sub)canopy palm</td>
<td>Understorey palm</td>
</tr>
<tr>
<td>Adult height</td>
<td>[m] 35-45</td>
<td>15-25</td>
<td>1-4</td>
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<td>Reproduction</td>
<td>Seeds</td>
<td>Seeds</td>
<td>Seeds &amp; clonal</td>
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<tr>
<td>Adult density</td>
<td>[ha⁻¹] c. 1-3</td>
<td>c. 25</td>
<td>c. 1,000</td>
</tr>
<tr>
<td>Seedling density</td>
<td>[ha⁻¹] c. 25-45</td>
<td>c. 200</td>
<td>c. 14,000</td>
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<tr>
<td>Spatial distribution</td>
<td>Clumped</td>
<td>Homogeneous</td>
<td>Strongly clumped</td>
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<td><strong>Population dynamics</strong></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Seedling survival</td>
<td>[% yr⁻¹] c. 55</td>
<td>c. 70</td>
<td>c. 55</td>
</tr>
<tr>
<td>Adult survival</td>
<td>[% yr⁻¹] c. 99</td>
<td>c. 97</td>
<td>&gt; 99</td>
</tr>
<tr>
<td>Seedling growth</td>
<td>Low</td>
<td>Low, often negative</td>
<td>Low, often negative</td>
</tr>
<tr>
<td>Most important life stage</td>
<td>Early reproductive</td>
<td>Late reproductive</td>
<td>Early reproductive</td>
</tr>
<tr>
<td>Most important vital rate</td>
<td>Survival</td>
<td>Survival</td>
<td>Survival</td>
</tr>
<tr>
<td>Importance of survival</td>
<td>[%] 97</td>
<td>96</td>
<td>89</td>
</tr>
<tr>
<td>Regeneration strategy</td>
<td>Gap-dependent</td>
<td>Intermediate?</td>
<td>Shade-tolerant</td>
</tr>
<tr>
<td>Life span</td>
<td>[yr] c. 360</td>
<td>c. 110</td>
<td>c. 300</td>
</tr>
<tr>
<td>Age reaching adult stage</td>
<td>[yr] c. 125</td>
<td>c. 70</td>
<td>c. 25</td>
</tr>
<tr>
<td><strong>Exploitation</strong></td>
<td></td>
<td></td>
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<tr>
<td>Plant part extracted</td>
<td>Seeds</td>
<td>Apical meristem</td>
<td>Leaves</td>
</tr>
<tr>
<td>Product obtained</td>
<td>Brazil nuts</td>
<td>Palm heart</td>
<td>Thatching material</td>
</tr>
<tr>
<td>Abundance of exploited ind.</td>
<td>[ha⁻¹] c. 1-3</td>
<td>c. 25</td>
<td>c. 1,000</td>
</tr>
<tr>
<td>Abundance of product</td>
<td>[ha⁻¹] c. 2,000-4,000</td>
<td>c. 25</td>
<td>c. 35,000</td>
</tr>
<tr>
<td>Impact of extraction</td>
<td>Low</td>
<td>High</td>
<td>Middle</td>
</tr>
<tr>
<td>Recuperation capacity</td>
<td>Probably good</td>
<td>Poor</td>
<td>Good</td>
</tr>
<tr>
<td>Time to recuperate</td>
<td>-</td>
<td>Long (&gt;50 yr)</td>
<td>Short (&lt;5 yr)</td>
</tr>
<tr>
<td>Prospects for sustainable use</td>
<td>Good</td>
<td>Poor</td>
<td>Good</td>
</tr>
</tbody>
</table>

Table 1: Comparison of three species of which study results are included in this dissertation. Note that only mean values are provided and some parameters are highly variable. Densities are given for the study plots and are mostly lower over larger areas; spatial distribution refers to larger areas. Seedlings include small seedlings in the first size category; adults are considered from the first size category with high proportion of reproductive individuals. Survival is for a year with normal precipitation. For *Geonoma* information refers to genets (clones). The importance of life stages and vital rates is based on sensitivity analysis of the matrix models. The importance of survival is expressed as the percentage of total vital rate elasticity that is accounted for by survival (see method section in Chapter 6 for explanation). Product quantities are expressed as nuts, palm heart and leaves, respectively.
1.3 m height) was generally high. In *Bertholletia* and *Euterpe*, individual growth rate rapidly increased from small juveniles, with a maximum value for pre-reproductive individuals. Adults, again had generally low growth rates. This non-linear pattern of growth vs. size is typically found in tropical trees (e.g., Zagt 1997, Clark & Clark 1999, Alder & Silva 2000, Silvie-Gourlet & Houillier 2000). Reproductive status (whether or not reproductive) was closely related to plant size in all species, and was also influenced by light availability in *Bertholletia* and *Euterpe*.

Regeneration strategy varied among the study species: *Bertholletia* is considered to be a gap-dependent species (Mori & Prance 1990), which is confirmed by its strong response to increased light availability (Chapter 2, Kainer et al. 1998, Poorter 1999, M. Peña-Claros personal communication). *Euterpe* is probably less dependent on gaps: seedlings responded less strongly to increased light availability, although enhanced growth was found under high light conditions in other studies (Peña-Claros 1996, Poorter 1999). Lastly, *Geonoma* is an understory specialist, completing its entire life cycle under the dark understory conditions with a canopy openness of <7% (Chapter 4).

In spite of the differences in stature and regeneration strategy, there are remarkable similarities in the life history of the study species: all have a long life span (except for ramets of *Geonoma*, which live for an estimated 37 yr) and have a fairly stable population size (i.e., population growth rate close to 1). In all species, reproductive categories contribute most to population growth and survival is the most important demographic rate.

**Extraction impact and sustainability**

The response to extraction differed considerably among the three study species: in *Euterpe* a very strong impact of extraction was found as those individuals that contribute most to population growth and maintenance are harvested for palm heart, an activity resulting in their death. In *Geonoma*, extraction did have a marked influence on growth and reproduction, but leaf cutting did not increase mortality. In the first two years after leaf removal, sexual and vegetative reproduction were strongly reduced (by 40-70%), whereas growth and leaf production were less affected (by 30-40% and 10-15%, respectively). In *Bertholletia* no signs of overexploitation were found in two sites which have been intensively exploited for a long time: both populations were regenerating and seemed to have stable population sizes. Also, in this species, no negative impact of exploitation is expected for at least 125 yr, the estimated time it takes for an individual to reach maturity in a primary forest.
Recuperation time after extraction is short in the case of harvesting *Geonoma* leaves: 36% and 68% of the number of harvested leaves were recuperated after one and two years following the leaf removal treatment. Complete recuperation of leaf area is expected in three years, after which growth and reproduction may return to their pre-harvest levels. For palm heart extraction from *Euterpe*, however, recuperation time is very long, as cut individuals can only be replaced from seeds, a process that takes almost 100 yr. For Brazil nuts, it is difficult to tell the recuperation time, as no obvious impact of seed extraction was found in the two study sites.

The above factors - impact of extraction and recuperation ability - whether a certain product can be extracted in a sustainable way. For *Bertholletia*, the demographic analysis shows that there is good prospect for sustainable production in spite of the high harvest intensity (c. 90% of the seeds are taken away): there is a continuous recruitment of seedlings, there are no gaps in the population structure, the population model did not predict a decline in population size, and production of seeds is the least important life history process for population maintenance. The unintentional ‘seeding’ by Brazil nut collectors and the hunting pressure on seed dispersing rodents (agoutis) in forests with *Bertholletia* might contribute to the continued regeneration of the species despite extraction. However, these relations are highly speculative, as there is no evidence that these factors play a role. Nevertheless, there are good prospects for sustainable harvest of Brazil nuts, thus providing opportunities for its certification as an environmentally friendly product. Initiatives for Brazil nut certification in Bolivia have already been undertaken (CFV 1999).

The situation for *Euterpe* is clearly different. The individuals used for palm heart extraction are old and their removal has a strong impact on population growth and future palm heart availability. Model simulations showed that heavy harvest intensities (75–100% of adults killed) and short harvesting cycles (4–8 yr) lead to a rapid decline in population size and adult density. But also a mild harvest regime - cutting 25% of the reproductive stems every 32 yr - caused the availability of palm heart to decrease continuously when compared to an undisturbed situation. These results are confirmed by a similar demographic study in populations in flooded forests in Bolivia (Peña-Claros 1996, Peña-Claros & Zuidema 1999). Furthermore, studies on the closely related *Euterpe edulis* which is exploited for palm heart in Argentine and south east Brazil, point in the same direction (Galetti & Fernandez 1998). An adjustment of harvest intensity or frequency in *Euterpe precatoria* was not considered to be economically viable, as this would make the collection of palm heart unprofitable. The conclusions of both Bolivian studies have resulted in the formulation of technical norms for the extraction of palm heart in
Bolivia. An alternative source of palm hearts are plantations with the fast-growing clonal palm *Bactris gasipaes*. Trials with this species in the Bolivian and Brazilian Amazon have been successful, with considerable yields obtained in a short time (PROMAB 1998). From the above it becomes clear that the demographic limitations of the species preclude an economically viable and ecologically sustainable extraction system of palm heart from *Euterpe precatoria*. The exploitation of this species is a typical example of the rapid expansion and decline (“boom and bust”) scenario that is also found for other non-timber products (Homma 1992).

The prospects for sustainable harvesting of *Geonoma* leaves are very positive. Although a considerable decrease in growth and reproduction was observed, plant survival was not affected and the removed leaf area was recovered rapidly. Similar results have been obtained for other understorey palm species (Mendoza *et al.* 1987, Oyama & Mendoza 1990, Chazdon 1991b), indicating that these plants are very tolerant to defoliation. Simulations of leaf extraction revealed that defoliated populations recuperate well after harvest: initial leaf availability at the population level can be maintained with repeated defoliation. Nevertheless, caution should be taken with too frequent harvests: sustained leaf availability is probably assured when cutting takes place once every 10–15 years. The good prospects for sustainable extraction in combination with the species’ high local density and the high quality of the leaves, indicate that there are good opportunities for a more intensive extraction of this product. Currently, *Geonoma* leaves are merely traded at the national level, but dissemination of information on the product’s quality and a certification of its extraction system may increase interest in its use.

**Constructing matrix models**

In the present study, matrix population models have been applied to analyse population dynamics of the investigated species. Without going into too much technical detail, the following sections provide some discussion on the use (construction, variation) and usefulness (for the analysis of demography, for the evaluation of sustainability) of matrix models.

Matrix models have a standard model form which can be adjusted depending on the focal species or researcher’s wishes. For the construction of matrix models, the whole population is divided into size categories (age categories are rarely used for plant species, so the following discussion will be restricted to size categories). The basic information in the model are the transition probabilities among these categories, which are organised in a transition matrix (a square $m \times m$ matrix, with $m$ being the number of categories). In constructing this transition matrix, several decisions have to be
made: (1) What parameter to use for categorisation of the population? (2) How to determine category boundaries? And, (3) how to quantify transition probabilities?

Concerning the parameter for classification (1), it is important that the parameter is a good proxy for the performance (growth, survival and reproduction) of individuals. Although often only one classification parameter will be available (e.g. stem diameter is often the only measurable parameter to determine size), sometimes several parameters may be used (e.g. number, form or size of leaves in seedlings). In that case, it is recommended to use the parameter that shows the strongest correlation with the demographic rates used in the model. In this thesis, seedling classification was based on height (*Bertholletia*), leaf number (*Geonoma*) or leaf length (*Euterpe*). Juveniles and adults were classified by stem diameter (*Bertholletia*) or stem height (other species).

The determination of category boundaries (2) can be done in two distinct ways: by using biological criteria or by using considerations of sample size. In both cases, the goal is to maximise differences in plant performance among categories and minimise its variation within a category. The second approach stems from the idea that two types of contrasting errors influence the reliability of transitions among categories: the sample error (which increases with smaller sample size and thus is high for narrow categories) and the distribution error due to variation in performance within a category (which increases with category width). Algorithms have been developed to determine category limits based on the minimisation of these errors (Vandermeer 1978, Moloney 1986), but these are rarely used in studies of woody plants (Chapter 7). More popular is the first type of classification, based on biological criteria. This was also used in this thesis. Using this technique, it is important to choose category limits such that differences in survival, growth and reproduction are maximised between successive categories. For instance, the category boundaries in the size-range were individuals become reproductive, should be chosen such that the difference in reproduction (e.g. the proportion of reproductive individuals or seed production) is maximised among categories. Furthermore, it should be kept in mind that very broad categories have the effect that individuals may stay for a very long time in one category, which may have a considerable and unrealistic influence on the output of the model (Chapter 7). Finally, despite these rules, the determination of boundaries and number of categories remains a highly subjective procedure.

The decision on how transitions are quantified (3) may also have important implications for model output. The most commonly used method to obtain transition probabilities among categories is to use observed frequencies of transitions from one to another category or permanence in the
same category (Chapter 7). Following this method, each individual is assigned to a category at time $t$, which is repeated at time $t+1$. Then the frequency of transitions to the larger, smaller or the same category are determined as the proportions of the initial number of individuals that is found in a larger, a smaller or the same category. In case the number of individuals in a category is small, if the category is wide, or if the growth rate is low, it can be difficult to adequately quantify transitions. In this case, also certain crucial transitions may not be observed at all.

Transition probabilities can also be calculated in a different way, by using demographic rates (so called vital rates: survival, growth and reproduction) that are underlying the probabilities in the transition matrix. This approach has been followed in the studies reported in this dissertation and in some other studies (e.g. Zagt 1997, Batista et al. 1998), and is more suitable for long-lived species (Chapter 7). The vital rates used for this method can be directly measured in the field (survival probability, growth rate and reproductive output). They are then related to the size of individuals to obtain size-dependent patterns of vital rates over the complete size-range of the species. This is done using regression techniques, or, in case no size-dependent pattern is found, by calculating an average value over several categories. Subsequently, for each category, an estimate of each vital rate can be obtained by filling in the midpoint of the category in the regression equation (or calculating an average value in case of no size-dependent pattern). The technical details of this method can be found in the methods sections of Chapters 2, 3 and 4.

The two parameterisation methods may be combined into one model (e.g. Chapters 3 and 4, Zagt 1997). This is useful when two different types of demography can be distinguished within a species, with seedling demography being characterised by high mortality, unpredictable and sometimes negative growth, and adult demography by low mortality and a continuous, deterministic growth. In this case (which is commonly found for tropical trees), seedling demography can be adequately described by using observed transition frequencies (especially when their sample size is large) and adult demography by using calculated transitions based on size-dependent patterns of vital rates.

In summary, different ways to construct and parameterise matrix models exist, resulting in different transition matrices. A careful choice of the method to determine the size and the contents of the transition matrix is important, as differences in methodology may have important implications for model output (Chapter 7).
Coping with variation in demographic rates

Matrix models assume that the performance of individuals (survival, growth and reproduction) in a certain size- (or age-) category is adequately described by an average value. Clearly, this assumption is not met when a certain demographic rate (growth, survival, reproduction) is highly variable. Such variation may be caused (1) by natural variation among the individuals in a category due to size-differences, age-differences, genetic variation, spatial variation and temporal variation; and (2) by uncertainty in parameter estimates. In the studies reported in this thesis, both sources of variation were of importance. The first type of variation was found to be large for seedling growth in all three species, and for juvenile growth in *Bertholletia* and *Euterpe*. This variation is partly related to the different light availability that these individuals experience. Adult trees, in contrast, are generally in a similar situation with regard to light availability. Large variation in seedling and juvenile growth has been commonly found for tropical tree species (e.g. Zagt 1997, Clark & Clark 1999). In the case of *Bertholletia*, the strong growth response to high light conditions increased the variability in this parameter. Another parameter that showed a high degree of variation is seed production in *Bertholletia*. In the other two species seed number was not recorded, but is likely to be highly variable among individuals and years (cf. Janzen 1978).

As for the second source of variation, in two of the three study species (*Bertholletia* and *Geonoma*), difficulties were encountered in estimating survival of adult individuals. This is a common problem: in a review of 37 matrix models for woody species (Chapter 7) problems with survival estimation were mentioned in >40% of the studies. In this review it was also shown that this uncertainty may have considerable influence on the output of matrix models (population growth, age estimates, sensitivity analysis), especially in case survival rates are very high.

In Chapter 6, a method is presented to take into account variation in demographic parameters in sensitivity analysis of matrix models. Regular types of sensitivity analysis (also called “perturbation analysis”) evaluate the importance of a certain demographic rate by applying a small absolute change (sensitivity, Caswell 1978) or a small change which is proportional to the demographic rate under consideration (elasticity, de Kroon et al. 1986). Thus, they do not take into account that certain demographic traits are (inherently) more variable than others, and that a given change in one parameter is more probable than the same change in another, less variable, parameter. The perturbation method used in Chapter 6 takes into account the variability of demographic rates and simulates the change in population growth rate resulting from ‘probable’ changes in demographic rates. It was applied to six plant species
to determine the influence of demographic variability on population growth rate. The results of the simulations show that demographic variation may influence population growth rate considerably. For instance, the large variation in juvenile growth rate for *Bertholletia* and *Euterpe* has a strong impact on the population growth rate.

**Coping with temporal variation**

In their basic form, matrix models are time-invariant, *i.e.* they assume that the conditions of the studied population will continue forever. In the studies reported in this thesis, demography was influenced by two types of temporal variation: variation in climatic conditions (rainfall; for all species) and the effect of harvest (in the case of *Geonoma*).

The climatic variation was caused by a strong reduction in rainfall from late '97 to mid '98, with average rainfall amounting to <100 mm per month over a year, whereas this normally is 143 mm. This year concurred with an El Niño Southern Oscillation episode, but no consistent pattern of low rainfall in El Niño years was found. Long-term rainfall records show that similar dry years occurred rather regularly in the region: on average one dry year in each eight years. Year-to-year variation in precipitation is also found elsewhere in the Neotropics (see *e.g.* Ropelewski & Halpert 1996). The drier year significantly affected demography of the three study species: recruitment of new seedlings was most strongly affected (reduced by 70-80% in all species), followed by seedling survival (0-20%) and growth (0-20%). Survival and growth of juveniles and adults was much less affected.

Temporal variation due to harvest may occur in case individuals gradually recover after exploitation, as *Geonoma* after leaf cutting (Chapter 5). This temporal variation may also result if a population's environment gradually changes after exploitation (*e.g.* Peña-Claros 1996, Zagt 1997), after a sudden environmental change (*e.g.* a hurricane, Pascarella & Horvitz 1999), or in the course of vegetation succession (*e.g.* tropical forest succession, Alvarez-Buylla 1994).

Several modifications to the basic model have been developed in order to cope with temporal variation in matrix population models. The resulting time-varying models can be classified into deterministic and stochastic models (Caswell 1989a). Deterministic models assume that different types of years follow a fixed sequence, *e.g.* always 1 dry year after 7 normal years. In contrast, in stochastic models the sequence of year-types is random, although their probability of occurrence is fixed, *e.g.* each year may be a dry year with a probability of 1/8.
Both deterministic and stochastic models have been applied in this thesis. In the study on *Geonoma* it was found that the sequence of dry and normal years — either deterministic or stochastic — had a very small impact on long-term population growth rate, probably due to the small difference in the most important demographic rates among years. For *Bertholletia* a stochastic model was applied to deal with climatic variation. For harvest simulations in *Geonoma* a deterministic model was used as the goal was to project population dynamics for various harvest regimes with a fixed harvest cycle (cutting leaves every 4, 8, or 16 yr). In that case, a fixed sequence of year-types was required, e.g. year with harvest, year after harvest, several years without harvest, etc. A related approach was applied for *Euterpe*. As it was assumed that cutting of adult individuals had no effect on the demography of the remaining population, the same matrix model was used for undisturbed and harvested populations. Extraction of palm heart was simulated by removing a certain percentage of adult individuals in the population structure at the start of each harvest cycle (see also Olmsted & Alvarez-Buylla 1995).

**Using matrix models to analyse plant demography**

Matrix models have been published for an estimated 140 plant species (M. Franco *personal communication*), of which at least 35 woody species (Chapter 7). Thus, they can be considered a popular tool for demographic analysis. Analyses of matrix models have been applied to assist in conservation of rare or endangered species (e.g. Silvertown *et al.* 1996, Heppell *et al.* 2000, Sæther & Bakke 2000), and to evaluate the impact and sustainability of extraction systems for plant species as is done in this thesis (Pinard & Putz 1992, Peters1996b).

Matrix models have been used more than any other type of model for the analysis of plant demography. Below a brief overview of strengths and weaknesses of matrix models is provided.

Strengths of matrix models include that they are relatively easy to construct, that they use a standard and simple model structure, that their output can be easily compared, that they can be constructed with limited data sets, that their methodology has been clearly described in textbooks, and that matrix models can be run using simple software (e.g. RAMAS-Stage, Applied Biomathematics, Setauket, New York) and even using spreadsheet programmes. Most other demographic models have more stringent data requirements, need more computing capacity and have a much more complex structure.

The simplicity of matrix models is also an important drawback as it requires certain important assumptions. Several of these assumptions may not
be realistic. Firstly, as mentioned before, standard matrix models assume population dynamics to be unchanged through time, which may not be true due to temporal variation in environmental conditions. Furthermore, matrix models assume that the performance of individuals in a category is adequately described by the average performance of these individuals. This may not be true for tree species that are gap-dependent and show a strong adaptive growth response (see also discussion section in Chapter 2). Also, it may not be realistic when variability in demographic rates is large. Thirdly, in matrix models, performance of individuals in a category is solely determined by their present status, i.e., they ‘forget their past’. This implies that an individual that passes rapidly through several size categories, may suddenly cease to do so and remain for a long time in one category. Also, individuals may remain for very long periods in a category with a low probability of outgrowth (Chapter 7). As past performance of an individual is often correlated with future performance in real-life demography, the assumption that demographic rates solely depend on the current size of an individual is often not realistic (e.g., Ehrlen 2000).

Given the above strengths and weaknesses, matrix models can still be considered as a very useful tool to analyse plant demography, especially when (1) data are scarce, (2) the researcher’s modelling skills are limited, (3) they are constructed bearing in mind their assumptions and their sensitivity to data constraints, and (4) when their model results are carefully interpreted. Concerning the latter point it should be taken into consideration that matrix model output is influenced by factors related to species’ life history and the environmental condition of the population on the one hand, but also by factors related to the methodology (Chapter 7).

Using matrix models to assess sustainability of extraction systems

Three methods have been used to evaluate the ecological sustainability of extraction systems of plants with matrix models (Figure 1). The main difference between these methods is which ‘type’ of dynamics is used: the first method uses the asymptotic dynamics, i.e., after a very long period of time. The two other methods use transient dynamics, i.e., over a short time interval. In this case, the matrix model projects changes in the size and structure of the population, starting from the initial population structure.

The first method, which has been used to evaluate sustainability of fruit and timber extraction, takes the asymptotic population growth rate (\(\lambda\)) as a criterion for sustainability. This is the stable growth rate of the population which is achieved as time goes to infinity. The reasoning behind this method is that the ‘surplus’ of individuals produced each year by a growing population...
can be harvested, without affecting the stability of the population. Sustainability is thus assured when a harvested population is stable or grows ($\lambda \geq 1$). In the case of seed extraction (Peters 1990a & b, Bernal 1998), the maximum sustainable yield is determined by increasing seed extraction in the model up to the level at which $\lambda = 1$ (indicating population stability). In the case of timber extraction, the maximum sustainable yield is found in a similar way, as the fraction of the population equalling ($\lambda - 1$) (Usher 1966, 1969) or by ($[\lambda - 1]/\lambda$) (Enright & Ogden 1979). An important disadvantage of this method is that it requires $\lambda$ to be larger than 1, otherwise no extraction is possible. A second disadvantage is that the method relies heavily on the value of $\lambda$, which is often uncertain. For instance, for population models which predict a growing population ($\lambda > 1$), the value of $\lambda$ often appears not to be significantly different from 1 (e.g. Alvarez-Buylla & Slatkin 1994). This implies that these populations may as well be stable or declining in size. This uncertainty is especially important since a large proportion of matrix models for trees and palms yield values of $\lambda$ close to one (65% of models for woody plants have $\lambda$ between 0.97 and 1.03, Chapter 7). Thirdly, the asymptotic population growth rate is calculated for a population in which the distribution of individuals over size categories is stable, i.e. does not change in time. Often in matrix studies, the observed population distribution deviates substantially from this stable stage distribution, which either implies that the transition matrix does not adequately reflect the species’ demography, or that the population structure is changing (e.g. due to vegetation succession).

Several of the above problems can be overcome by using one of the methods based on transient dynamics. The second method in Figure 1 uses the absolute changes in population size (or changes in size of a certain category of interest, e.g. adults) to evaluate sustainability. If this size does not drop below a certain level or below a certain proportion of its initial value (e.g. Olmsted & Alvarez-Buylla 1995, Zagt 1997), the extraction can be regarded as
sustainable. This method is more flexible than the previous, as various harvesting regimes with different extraction cycles and intensities can be used. This is impossible or difficult when using the previous approach. This method does not depend on the value of $\lambda$, but it still requires that the undisturbed population is growing (or stable) during the simulation period. When the population is declining, there is no scope for any harvest.

The third method in Figure 1 is similar to the second, with the difference that it does not stem from the assumption of a growing population. Rather, it considers the changes in the size of an extracted population (or size category) relative to its size in the undisturbed situation. If this proportion drops below a certain level, the extraction system can be considered unsustainable (e.g. Chapter 3, Peña-Claros 1996). This 'sustainability level' can be varied depending on the importance of a sustained production system and the risk for population decline that can be taken. As this approach does not require the population to grow over short or long periods, it is more flexible than the other methods.

In the study of *Bertholletia* actually a fourth method was used to assess sustainability of the extraction system in an indirect way. As it was not possible to study the demography of an undisturbed population, no comparison could be made between undisturbed and exploited populations. In this case, several indirect parameters were determined to assess sustainability: whether recruitment of new seedlings was found, whether the population was growing or stable, the age at first reproduction and the reproductive period of trees. Using these measures, also an assessment of the sustainability can be provided, in case no comparison with a control is possible.

In conclusion, matrix models have proven to be a useful tool to assess the sustainability of extraction systems. Besides, they provide insight into the species' demography that can be used to design silvicultural treatments aiming to increase harvest potential, or to provide information necessary for cultivating the species of interest.

**Can we derive rules of thumb to assess sustainability of extraction systems?**

Clearly, it is not possible to construct matrix population models for all species that are being exploited for non-timber forest products (NTFP). Therefore, the question is whether some rules of thumb can be obtained to assess the sustainability of extraction systems. Under what conditions is there scope for sustainable use and under what conditions not? Peters (1996b) assessed the management potential of non-timber products derived from tree species. Below a similar analysis is presented based on the results in this thesis.
The potential for sustainability of an extraction system depends on the interaction between the demography of the exploited species and the impact of the extraction on demography. To generate rules of thumb, therefore, information on these subjects should be generalised. Concerning demography, some generalisations can be derived from the comparison of the study species (Table 1) and the review of matrix model output for woody species (Chapter 7): population structures typically contain much more small than large individuals; survival is much more important than growth and reproduction for population growth and maintenance; reproductive categories contribute significantly to population growth; woody species are generally long-lived; and their populations are often stable in size.

As for the impact of extraction, this will depend on the plant part that is harvested and the harvest intensity and frequency. The ability of exploited individuals to recuperate after the harvest event and the time needed for recuperation are important. In case recuperation is not possible (when the individual is killed due to the extraction), there may still be scope for sustainable extraction, as long as the population can recover from the loss of exploited individuals. If killed individuals are crucial for population maintenance or their recuperation takes a long time, there is little scope for sustainability.

Combining the general patterns in demography of woody species and the impact of extraction, the prospects for sustainable use can be related to parameters dealing with demography and extraction (Figure 2). Three rather unambiguous relations can be established (left panels in Figure 2). A high harvest intensity limits the scope for sustainable extraction: overexploitation of non-timber products is well-documented. Concerning the extracted plant part, extracting the whole individual clearly decreases the scope for sustainable extraction, although this relation depends also on intensity and the importance of the killed individuals for population maintenance. The affected stage in the species’ life cycle is important, as a certain negative impact on performance of adults has much more effect on population maintenance than an equal impact on seedlings.

The other relations depicted in Figure 2 (right panels), are less clear as they depend on other factors. It is argued that high abundance of the exploited species provides more scope for management, as in rare species there is a higher probability of overexploitation (Boot 1997, Peters 1996b). However, there are several examples of severe resource depletion in forests dominated by one valuable species (e.g. Vasques & Gentry 1989). Clearly, the value of the product also plays a role as the risk of overexploitation is larger for a highly-valued product. Secondly, the scope for sustainable use has also been related to regeneration strategy of the species: shade tolerant trees were considered to
provide better opportunities as they may regenerate in an undisturbed forest (Peters 1996b). However, the high potential growth rates of gap-dependent species may offer good opportunities for silvicultural treatments that increase productivity. In addition, the long generally life spans of shade tolerant trees may make their exploitation unsustainable when individuals are severely damaged or killed due to extraction. Finally, there is no clear relation between life span and the scope for sustainable use. For instance, in long-lived species, the extraction of seeds may be sustained for long periods without causing the production to decline. However, seed extraction in short-lived plants is likely to have a much stronger impact as in these species population growth depends heavily on regeneration. In contrast, when complete individuals are killed, prospects are much better for short-lived species. Thus, no unique relation can be established in this case.

In conclusion, it remains difficult to generate rules of thumb to evaluate sustainability of extraction systems for non-timber products. Whether an extraction system is sustainable depends on the interaction of the species’ demography and the impact of extraction, and requires information on both subjects. A first rough evaluation of sustainability can be done, however, using limited information on the species’ life history, information on the impact of extraction, and the relations as provided in Figure 2.

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