Demography of exploited tree species in the Bolivian Amazon

Pieter A. Zuidema

PROMAB Scientific Series 2

The Programa Manejo de Bosques de la Amazonía Boliviana (PROMAB) is an international research, training and extension program advancing the sustainable exploitation and management of timberand non-timber forest resources in northern Bolivia. PROMAB is a joint effort of the Instituto para el Hombre, Agricultura y Ecología, Bolivia, the Universidad Técnica del Beni, Bolivia, and Utrecht University, the Netherlands.

PROMAB, Casilla 107, Riberalta, Beni, Bolivia (E-mail: promab@latinwide.com, Internet: www.bio.uu.nl/promab/promab), or: c/o Department of Plant Ecology, Utrecht University, PO Box 80084, 3508 TB Utrecht, the Netherlands (E-mail: pbc@bio.uu.nl).

P.A. Zuidema
Demography of exploited tree species in the Bolivian Amazon
PROMAB Scientific Series 2
PROMAB - Riberalta, Bolivia
ISBN: 90-393-2524-3
Keywords: population dynamics, tropical rain forest, non-timber forest products

Printed by:	Print Partners Ipskamp, Enschede
Cover:	Emy Franck
Layout:	Marjolein Kortbeek
Photos:	Pieter Zuidema

Demography of exploited tree species in the Bolivian Amazon

De demografie van geëxploiteerde boomsoorten in het Boliviaanse Amazonegebied

(met een samenvatting in het Nederlands)

La demografía de especies arboreas aprovechadas en la Amazonía Boliviana

(con un resumen ejecutivo en Español)

Proefschrift

ter verkrijging van de graad
van doctor aan de Universiteit Utrecht
op gezag van de Rector Magnificus,
Prof. Dr. H.O. Voorma,
ingevolge het besluit van het College voor promoties
in het openbaar te verdedigen
op woensdag 1 november 2000
des middags te 2.30 uur

door

Pieter Alle Zuidema

geboren op 16 april 1970 te Zuidelijke IJsselmeerpolders

Promotor: Prof. Dr. M.J.A. Werger
Co-promotor: Dr. R.G.A. Boot,
Verbonden aan de Faculteit Biologie
van de Universiteit Utrecht

PROMAB

Universiteit Utrecht

The studies reported in this thesis were carried out within the Programa Manejo de Bosques de la Amazonía Boliviana (PROMAB), Riberalta, Bolivia, and the Department of Plant Ecology, Utrecht University, the Netherlands. Financial support was obtained through grant BO 009701 from the Biodiversity program of the Netherlands Development Assistance (DGIS), Ministry of Foreign Affairs of the Netherlands.

To Lisa and Sara

Los árboles me dan un poco de miedo.
Son tan hermosos.

(Jorge Luis Borges)

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*Manupare river, Bolivian Amazon, with 'cusi' palms (*Attalea speciosa*).*

Chapter 1

General introduction

Amazonian forest use in historic context

Tropical forests in the Amazon region have been inhabited for thousands of years (Dufour 1990). Indigenous peoples used the forests to collect plant parts or hunt for subsistence (Dufour 1990, Colchester 1996). They made use of a large variety of tree species present in their forest environment (*e.g* Boom 1987), of which some were controlled in 'gardens' around their homesteads (Alcorn, 1990, Gomez-Pompa & Kaus 1990). A different type of forest use – large-scale commercial forest exploitation – was introduced in the region around 150 years ago. Demand for Amazonian products in Europe gave an economic value to several produces from the region, starting with the so called *drogas do sertão* in the mid 19th century, including quinine from the bark of the tree *Cinchona officinalis*. At a much larger scale, wild rubber from the tree *Hevea brasiliensis* was collected from 1850 onwards. The subsequent 'rubber boom' resulted in a 30yr period (1887–1917) during which rubber was a major Amazonian export product (Homma 1992). Numerous new settlements and cities were created throughout the area. In the second half of the 20th century, the higher international tropical timber demand, an extending road network and the availability of heavy machinery increased the opportunities for timber logging, which became a large-scale activity in the 1970s and 1980s (WRI 1988).

The history of forest use in Northern Bolivia – the study region of this dissertation – echoes that of Amazonia as a whole. Initially occupied by various indigenous tribes (*e.g.* Boom 1987), the area was gradually entered by colonists during the mid 19th century for the collection of quinine (Broekhoven 1996). The main colonisation of the area took place from the 1880s onwards for the extraction of rubber (Fifer 1970), which brought large amounts of revenues

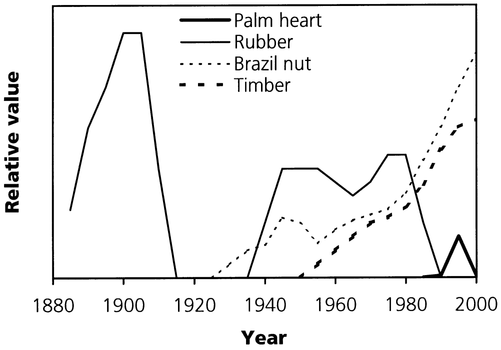


Figure 1
Schematic development of the export value of forest products from the Bolivian Amazon region in the period 1880-2000. Position along y-axis is only indicative for the value. Constructed by A. Bojanic, based on different sources.

to the region (Figure 1). Rubber was extracted in extensive *barracas* (forest estates) owned by a small number of rubber barons. Rubber tappers were subordinated to these *patrons* by a debt-peonage system (Assies 1997). From the 1920s onwards, a second forest product was harvested in the *barracas*: Brazil nuts from the tree *Bertholletia excelsa*. The economic importance of Brazil nuts was initially low, but foreign demand and market price increased from the 1980s onwards. From 1986 onwards -coinciding with a major drop in the price of natural rubber- Brazil nuts have been crucial for the regional economy of the Bolivian Amazon (Figure 1). Currently, the largest share of the world Brazil nut supply originates from Bolivia.

Commercial logging for timber has not been very intensive in the Bolivian Amazon due to the lack of roads in the area and the low prices for timber. In addition, during the so called "ecological pause" (*Pausa Ecologica Historica*) from 1990-1995, no new forest concessions were handed out. As a result, timber exploitation has focussed on high-valued species whose logs could be transported by river. Nowadays, there is a tendency to exploit more species for timber, as the road network is gradually expanding and improving. Furthermore, taxes for concessions that were handed over under the new forest law (since 1996) are paid on an area-basis, stimulating the extraction of timber from more species.

Another important forest product, palm heart from the (sub-)canopy *Euterpe precatoria* has been harvested at a commercial scale since 1991. After a rapid expansion of extraction activity and processing capacity, production declined over the past two years (Figure 1). Increased quality requirements from the main importer (Brazil) and low prices at the world market have strongly reduced the extraction of palm heart.

Sustainable forest management

In the 1970s and 1980s the rapid deforestation due to logging practices and recolonisation programmes was considered a serious threat to tropical forests and their biological diversity (Myers 1984, Wilson 1988). Gradually, it was recognised that tropical forests provide many potentially useful products, that they are the habitat for a vast number of plant and animal species, and that they have a regulating role for regional and global climate. This recognition culminated in the United Nations Conference on Environment and Development in Rio de Janeiro, 1992, where the Convention on Biological Diversity was signed.

At the same time, institutions related to forestry and conservation began to focus on sustainable forestry (*e.g.* FAO's Tropical Forest Action Plan). Several institutions have developed trials, guidelines and systems for sustainable timber management (*e.g.* ITTO 1990, 1993, Poore & Sayer 1991, IUCN 1992, see also Putz 1994, Heinrich 1995, Sist 2000). Although the issue of sustainable forestry has been put clearly on the (inter)national agenda, sustainable forest management is hardly practised to date. Only a fraction of the total tropical forest area is under certified sustainable management (Bowles *et al.* 1998). The main reason for this is probably that conventional logging is still more profitable (at the short term, Hammond *et al.* 2000) and that financial incentives to adopt sustainable management practices (*e.g.* certification) are still not sufficient (Pearce *et al.* 1999).

Non-timber forest products as a conservation and development strategy

The concern about tropical deforestation and biodiversity loss led to a recognition of the value of non-timber products from tropical forests (Myers 1984, de Beer & McDermott 1989, Peters *et al.* 1989b). These products were seen as a viable way to exploit the biological wealth of tropical forests without harming it, stimulating (rural) development at the same time (Prance 1990, Gentry & Blaney 1990, FAO 1991). It was argued that for non-timber forest products (NTFP), reconciling the use and conservation of tropical forests could be more easily achieved than for timber. Forest structure and functioning are not altered by extracting NTFP and in most cases extraction does not involve killing the individual plant (note that animals are not considered as NTFP here). Thus, the use of these products was introduced as a conservation and development strategy (Nepstad & Schwartzman 1992). A clear example of this strategy is the creation of extractive reserves in the Brazilian Amazon since 1985 (Fearnside 1989), which are protected areas were NTFP extraction (mainly rubber tapping) is allowed.

In recent years, the high expectations of NTFP to safeguard tropical forests have become more realistic (Browder 1992, Nepstad & Schwartzman 1992, Ruiz-Perez & Arnold 1996, Southgate *et al.* 1996, Assies 1997, FAO 1997a). Firstly, the methods used to derive NTFP values in two of the first valuation studies (Peters *et al.* 1989b, Myers 1984) have been criticised on methodolgy, leading to overoptimistic estimates (Southgate *et al.* 1996, Pearce *et al.* 1999). Secondly, sustainable use appears not to be guaranteed as there are many examples of overexploitation resulting from market demand (*e.g.* Vasques & Gentry 1989, Hall & Bawa 1993, Broekhoven 1996). Thirdly, apart from overexploitation, other factors may cause declines in NTFP extraction: a decreased market demand, an insecure market value, the cultivation of NTFP in plantations or their substitution by industrial products (Homma 1992, 1996, Assies 1997). In fact, the cultivation of rubber trees in South East Asia and the production of synthetic rubbers resulted in the bust of Amazonian rubber collection. A fourth factor relates to the abundance of NTFP: the high plant diversity in tropical forests (see *e.g.* Peters 1996a) inevitably leads to low average abundance of each species, and thus a low availability of the extracted product per hectare (Peters 1996a, Boot 1997). As a result, the productivity of collectors is generally low, and rural economies entirely based on extraction activities are not considered to be viable in the long run (Anderson 1992, Southgate *et al.*1996, Assies 1997). Finally, despite the presentation of NTFP as a strategy for sustainable forest exploitation, there are only few examples of large scale, commercial and sustainable extraction: an often mentioned example, the Brazil nut, is one of the focal species in this thesis (Chapter 2).

In spite of these unfulfilled expectations, it is evident that non-timber products are very important for millions of households in the developing world (FAO 1997a), and that they contribute substantially to local and regional economies (Homma 1992, FAO 1997a). Furthermore, a huge variety of products is used, some with actual international trade status (an estimated 150, FAO 1997a), and perhaps many with potential value.

It is useful to distinguish (potentially) commercial *vs.* non-commercial (subsistence) non-timber products. The latter group comprises the vast majority of products that are generally extracted on a relatively small scale and (therefore) in a sustainable manner. These products will not require much attention for forest management. The first group, however, are those that are extracted on a large scale which makes them susceptible to overexploitation. As for commercial timber extraction, for many commercial NTFP regulations are needed to prevent overharvesting and/or to ensure a proper distribution of revenues (FAO 1997a). Apart from regulations that limit the exploitation of a certain species, sustainable NTFP extraction may also be achieved by certification as an incentive for better management. To assess whether regulations are necessary or whether the extraction of a product may be certified, information on the impact of exploitation on future resource availability is required. Such information can be obtained in ecological studies of the type included in this dissertation.

Assessing sustainability of extraction of non-timber products

Before going into detail on the methods to evaluate ecological sustainability, it is useful to put this term in a broader context - that of sustainable development. Sustainable development is targeted at "the reduction of poverty by providing lasting and secure livelihoods that minimise resource depletion, environmental degradation, cultural disruption and social instability" (Barbier 1987). In this context, an exploitation system of NTFP is sustainable when it is ecologically sustainable, economically feasible and socially acceptable. In this thesis, the focus is on ecological sustainability.

The ecological sustainability can be evaluated at three levels: that of the individual, of the population and of the entire ecosystem (Ros-Tonen *et al.* 1995, Broekhoven 1996). At the individual level it makes a difference when extraction causes the death of the individual or when only some leaves of the plant are harvested. At the population level, extraction may be considered sustainable when the population does not become extinct as a result of exploitation, or when the productivity of the population (in terms of availability of the extracted product) does not decline. At the ecosystem level, sustainability is achieved when, broadly speaking, extraction does not alter the functioning of the ecosystem. This is very difficult to evaluate, as it requires insight in complex ecological relations of the exploited species with other species.

The focus of this dissertation is on the population level consequences of NTFP extraction, as at this level information can be obtained on how the production of the resource can be sustained for longer periods. This is important for both designing regulations on NTFP exploitation, and to obtain certification labels for these products.

Roughly, two ways can be distinguished to assess the impact and ecological sustainability of NTFP extraction at the population level. The first is to consider the population structure (*i.e.* the relative abundance of different-sized individuals in the population), *e.g.* by comparing that of an undisturbed with an exploited population (*e.g.* Peters 1996a). This approach may provide a first estimate of the impact of exploitation, especially when extraction involves removal of stems or complete individuals (*e.g.* for palm heart, Pollak *et al.* 1995, van Andel *et al.* 1998). In cases where extraction removes plant parts that do not leave clear signs (*e.g.* fruits, seeds, resins, leaves), this approach is more difficult and may result in wrong conclusions. Taking the abundance of new seedlings as an indication of the population's resilience to harvesting – a logical parameter in case seeds are harvested – may lead to different conclusions in different years as year-to-year variation in recruitment is large (see *e.g.* Chapters 2 & 3). Another problem is that the population structure or the abundance of seedlings are not necessarily an indication of the species' regeneration strategy or the population's performance (Condit *et al.* 1998). For instance, the abundance of seedlings of *Euterpe precatoria* in Brazil was considered a sign of high potential for palm heart management (Nepstad *et al.* 1992). However, an analysis based on population dynamics revealed that the species is long-lived and that replacement of the harvested adult individuals takes almost 100 yr (Chapter 3). Finally, considering population structures may also be misleading for species that require a different habitat for tree regeneration (*e.g.* mahogany –*Swietenia macrophylla*– regenerates in highly disturbed sites, Gullison *et al.* 1996).

The second method to assess sustainability is by using information on the population dynamics of the species (Hall & Bawa 1993, Peters 1996b). The extraction of NTFP inevitably influences the population dynamics: *e.g.* collecting fruits will reduce regeneration, harvesting leaves will reduce growth and tapping rubber will perhaps increase mortality. Therefore, by implicitly taking into account the dynamics of individuals and populations, it is possible to gain insight into how extraction affects the future performance of the population. To do so, two types of information are needed. First there should be an understanding of the undisturbed demography of the species, answering questions such as: what are rates of survival, growth and reproduction for different-sized individuals, what is the minimum reproductive size, which are the crucial life stages, etc. Secondly, information on how exploitation affects these demographic rates and life history characteristics is needed. This information can then be analysed using demographic models.

A large variety of demographic models are used in (forest) ecology (Vanclay 1995, Peng 2000). They can be grouped according to their unit of modelling: when this is the individual plant, they are called individual-based models (DeAngelis & Gross 1992) ; when this is a category of individuals based on age or size, they are called structured-population models (Tuljapurkar & Caswell 1997; although this is a somewhat wider term). The first type of model is more complete in the sense that population-level dynamics are based on the performance of all individuals, without lumping these into categories. As a consequence, these models are also more complicated to construct. Examples of individual-based models in forest ecology are gap-phase models and certain growth-yield models (*e.g.* Liu & Ashton 1995, Pacala *et al.* 1996). These models are especially useful when the environmental conditions of individuals change, *e.g.* as a result of climate change or logging for timber, and when these changes can be described at the individual level (Peng 2000).

The second type, structured-population models, categorise individuals and follow the distribution of individuals over categories in time, thus 'loosing track' of the individuals themselves. Matrix population models are the most popular and widely used type of structured-population models (Caswell 1989a). In these models it is assumed that the performance of individuals in a certain (age- or size-) category is adequately described by the average performance, and that the rates of survival, growth and reproduction do not change over time. Therefore, these models are less suitable to study the impact of timber extraction that causes considerable environmental changes (Boot & Gullison 1995, but see Zagt 1997). However, to evaluate the impact and sustainability of non-timber product extraction, matrix models are appropriate and widely used (see Chapters 2, 3 and 5, Pinard & Putz 1992). In this thesis, matrix population models have been used for this purpose.

As many different plant parts are collected as non-timber products, there are also many different ways in which extraction influences population dynamics. To analyse the impact of NTFP extraction, first an answer should be given to the following questions: (1) what size (or age) categories are affected by extraction?, and (2) which demographic rates (also called *vital rates*) are changed due to extraction? Answers to these questions are important to design a field study and construct the model. Figure 2 shows some examples of how NTFP extraction may influence population dynamics. As is seen in the figure, the extraction of seeds and palm heart (involving the death of the individual) has a direct effect on one or more arrows in the life cycle graph, whereas for leaves and latex this influence is indirect. In the first case, individuals, seeds or fruits are taken from the population, and the extraction can be readily translated into changes in transitions among categories (*e.g.* when 25% of the seeds are taken from the population, this results in a 25% reduction of the reproductive transitions), or changes in the population structure (*e.g.* cutting 50% of the adult palms results in a 50% reduction of their abundance in the population structure). However, when the impact of extraction cannot be directly translated into a numerical change in a size category or the value of a transition, harvest experiments are needed to establish this relationship. This can be done by applying one harvesting regime to part of the study population (Chapter 5), but different harvesting intensities

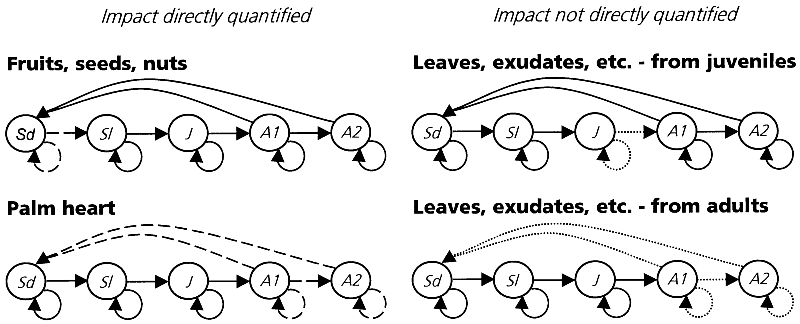


Figure 2
The influence of differences in extracted plant part on the population dynamics of an imaginary tree species. A generalised life cycle is shown, consisting of five categories: seeds (Sd), seedlings (Sl), juveniles (J), small adults (A1) and large adults (A2). Arrows indicate transitions among categories: arrows towards the right refer to growth, those that connect to the same category refer to persistence in the same category and those from adult to seed categories indicate reproduction. Drawn arrows are unchanged by extraction; broken arrows indicate transitions that are changed by extraction and can be directly quantified on the basis of harvest intensity; dotted arrows refer to transitions that may be influenced, but that can only be quantified in a harvest study. An assumption underlying this Figure is that there are no changes in demographic rates due to changes in environment resulting from extraction (*e.g.* increased light availability).

or frequencies may also be applied (*e.g.* Mendoza *et al.* 1987). The impact of extraction on population dynamics is then determined by combining the undisturbed and exploited population models (see *e.g.* Chapter 5, Zagt 1997).

Context of this study

This study was carried out in the Bolivian Amazon region, which occupies the northernmost department of Bolivia (Pando) and two provinces in other departments (Vaca Diez in Beni department and Iturralde in La Paz department; Figure 3). Some general and forest-related statistics on Bolivia and the study region can be found in Table 1. The climate in the region is characterised by an average rainfall of 1700-1850 mm, an average annual temperature of 26 °C and a pronounced dry season from May to September with <100 mm rain per month (Beekma *et al.* 1996, AASANA *unpublished data*). A considerable number of tree species is deciduous during the dry season. Soils in the non-flooded forests are generally xanthic to haplic ferrasols (DHV 1993). Non-flooded forests in the region have been classified as semi-evergreen tropical forests (DHV 1993), although other descriptors have also been used (*e.g.* Amazonian lowland moist forests; CDC - Bolivia). Forest cover in the region is very high (*c.* 95%), as timber logging and agriculture have not

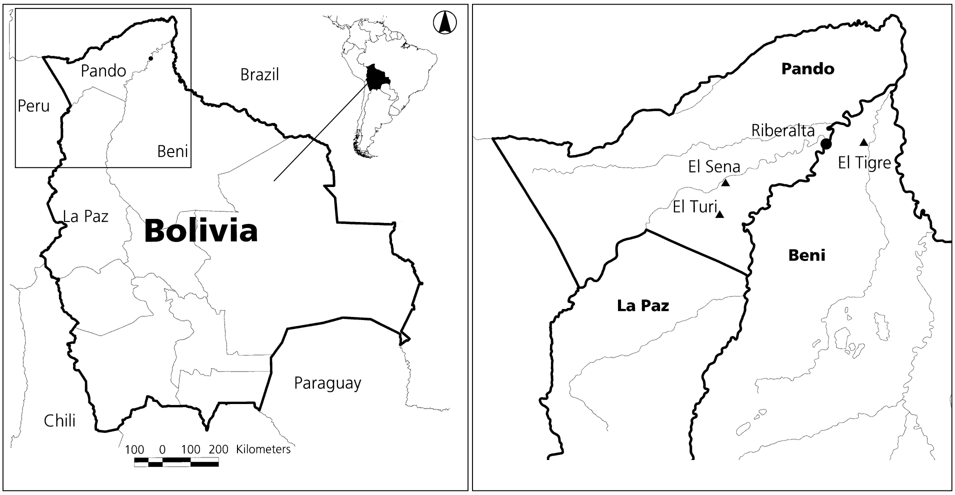


Figure 3
Map of Bolivia (left panel), indicating the Department boundaries, and of the Bolivian Amazon region (right panel), indicating the river system, the main town (dot) and three study sites where this research was carried out (triangles).

been practiced at a large scale (DHV 1993). Canopy height of forests in the region amounts to 25-35 m, with emergent trees attaining heights up to 45 m. Tree diversity (trees >10 cm diameter at breast height) in these forests amounts to 80 species per ha., which is relatively low compared to other Western Amazonian forests (Poorter *et al.* 2000). *Bertholletia excelsa*, the Brazil nut tree, is an important structural element in Northern Bolivian forests as it is an abundant emergent that often accounts for a large proportion of total basal area (DHV 1993).

The regional economy depends heavily on forest products (Table 1). The contribution of forest products to the total monetary influx in the Bolivian Amazon is over 60% (for 1998, A. Bojanic, *personal communication*). At the national level, on the other hand, participation of forest products in the GDP amounts to only 1.4% (INE 1996). The region is inhabited by 130.000 inhabitants of whom 80% live in the three larger towns (Riberalta, Guayaramerin and Cobija). Most inhabitants derive their income from forest products: mainly Brazil nuts, timber and palm hearts. The human development index for the region is low (0.50-0.55), reflecting that a large percentage of the population lives under the poverty line (UDAPSO/PNUD 1997). Other social indicators related to education and health also show low values for the region.

Table 1

General information on Bolivia and the Bolivian Amazon (Pando department, province of Vaca Diez in Beni department and part of province of Iturralde in La Paz department). Missing data are indicated by -.

General information		Bolivia	Bolivian Amazon	Source
Population (2000 projection)	x 1000	8,329	189	INE, Bolivia[1]
Population growth (1992)	[% yr^{-1}]	2.4	-	INE, Bolivia[1]
Life expectancy (1998)	[yr]	62	61	INE, Bolivia[1]
Area	[km^2]	1,098,581	104,561	INE, Bolivia[1]
Population density (2000 projection)	[km^{-2}]	0.008	0.002	INE, Bolivia[1]
Rural population (2000 projection)	[%]	33	33	INE, Bolivia[1]
GDP *per capita* (1995)	[US$]	830	950[2]	Ministerio de Hacienda, Bolivia
Economic growth (1997)	[% yr^{-1}]	4.2	-	Ministerio de Finanzas, Bolivia
Forest-related information				
Total tropical moist forest area (1995)	[km^2]	217,965[4]	98,287[5]	Iremonger *et al.* 1997
Deforestation rate (1986-1992)	[% yr^{-1}]	-0.3	-0.15	CUMAT 1992; DHV 1993
Forest area in national parks (1995)	[km^2]	52,110	0	Iremonger *et al.* 1997
Forest area under concession (1999)	[km^2]	56,000	15,000	Superintendencia Forestal, Bolivia
Forest area under certification (2000)	[km^2]	6,601	0	FSC, Mexico[3]
Forest area with Brazil nut (1993)	[km^2]	74,644	74,644	DHV 1993
Nr flowering plant species (1994)		16,500	-	WCMC 1994
Nr endemic higher plant species (1994)		4,000	-	WCMC 1994
Export earnings from timber (1998)	[mln US$]	78.3	16.0[2]	Cámara Forestal, Bolivia
Export earnings from NTFP				
- from Brazil nuts (1998)	[mln US$]	29.3	29.3	Cámara Forestal, Bolivia
- from palm heart (1998)	[mln US$]	12.0	7.0[2]	Cámara Forestal, Bolivia

[1] INE - Instituto Nacional de Estadistica, Bolivia: internet pages: www.ine.gov.bo viewed at 17 July 2000; [2] A.Bojanic *personal communication*; [3] Forest Stewardship Coucil internet pages: www.fscoax.org viewed at 17 July 2000; [4] Classified as 'lowland evergreen broadleaf forest' by source; [5] Estimated based on 94% of forest cover (DHV 1993).

Programa Manejo de Bosques de la Amazonía Boliviana (PROMAB)

This dissertation forms part of the Programa Manejo de Bosques de la Amazonía Boliviana (PROMAB), a research, extension and education programme of the Instituto para el Hombre, Agricultura y Ecologia (IPHAE, Riberalta, Bolivia), the Carrera de Ingenieria Forestal of the Universidad Técnica del Beni (CIF/UTB, Riberalta, Bolivia) and Utrecht University (The

Netherlands). Starting in 1995, PROMAB activities have included forest-ecological and socio-economic research, technical assistance and training of the region's forest users with emphasis on farmers and rural communities, training of forestry students and the dissemination of knowledge and information to forest users and governmental bodies responsible for the implementation of the forestry law. The programme's main goal is to improve the living conditions of forest depending people in Northern Bolivia through the sustainable use and conservation of their forests and forest resources.

This dissertation is the second publication in the PROMAB Scientific Series. The contents of existing and expected publications in this series are briefly outlined below:

1. Seedling growth of rain forest tree species (Poorter 1998). The influence of light and water availability on seedling growth is evaluated for a number of economically important rain forest tree species. Knowledge of the environmental requirements of tree species provides the ecological basis for the selection of species for silvicultural treatments, forest enrichment activities, tree plantations and agroforestry systems, as well as for the design of such activities.
2. Demography of exploited tree species in the Bolivian Amazon (this publication).
3. Mechanisms of secondary forest succession (Marielos Peña, expected early 2001). The last decade has seen an increased conversion of forest land into agricultural fields. When these fields are abandoned, natural forest regeneration follows. Processes which affect the course of this secondary succession, such as seed predation, germination, seedling establishment and growth, are studied in detail. Based on this knowledge, the secondary forests can be manipulated to increase the abundance of desired tree species, enhancing their economic value.
4. Economic dynamics of forest resources in the Bolivian Amazon (Alan Bojanic, expected early 2001). This study explores the tension between economic development and environmental impacts of commercial forest use in the northern Bolivian Amazon region. To obtain larger economic growth rates there is a need to intensify the extraction of forest products and hence to increase the degradation of natural resources. The study compares the potentials and limitations of different types of forest use.
5. Livelihood strategies of forest dwelling people in the northern Bolivian Amazon (Ariènne Henkemans, expected mid 2001). This study explores the potentials for sustainable forest livelihoods, based on the interest of former rubber tapping families and other forest residents living in two different forest settlement types. This study aims to improve our understanding of the overall importance of the forest within their past

and present livelihoods, and within their household strategies for future development.

Furthermore, the following publication of a study carried out in close cooperation with PROMAB is expected:

Variations and dynamics of extractive economies (Dietmar Stoian, University of Freiburg/CIFOR, expected early 2001). The importance of marketable NTFP in rural and peri-urban households is determined in the context of the historical evolution of extractive economies. The role of gathering, processing, and marketing of Brazil nuts and palm hearts is analysed from a livelihoods perspective, focussing on migratory patterns and trade-offs between extraction, agriculture, and wage labour.

Objectives of this study

The objectives of the present study are:

1. to analyse the demography of several tree species in the Bolivian Amazon, which are used for non-timber products;
2. to evaluate the impact and sustainability of non-timber product extraction from several tree species in the Bolivian Amazon; and
3. to assess the applicability of matrix population models for the analysis of tree demography and for the evaluation of ecological sustainability of extraction systems.

Outline of this thesis

This thesis addresses the demography and exploitation of three species used for non-timber products, two of which have a significant contribution to the regional economy (Brazil nuts from *Bertholletia excelsa* and palm heart from *Euterpe precatoria*) and one with economic potential for national and regional trade (palm leaves from *Geonoma deversa*). Results of a demographic field study on a fourth species, the canopy palm *Attalea butyracaea* ("palla") of which leaves are also used for roof thatching, will be published elsewhere. Field sites where demographic studies were conducted are indicated in Figure 3.

Following the four chapters that discuss the demography and exploitation of each of the study species, there are two chapters that deal with the application of matrix population models: one on how to cope with demographic variation and one that reviews the use of these models for long-lived woody plants. The contents of each of the chapters is briefly presented below:

Chapter 2 describes the demography of the Brazil nut tree (*Bertholletia excelsa*) at two sites where nuts are collected. The ecology of seeds and seedlings as well as the population dynamics of the species are described in relation to the extraction. Population matrix models are developed for both sites, and are used to obtain information on the impact of harvesting for future availability of Brazil nuts.

Chapter 3 analyses the demography of the asai palm (*Euterpe precatoria*) which is used for palm heart and assesses the impact of palm heart extraction for the population and the future availability of the product. A demographic field study is conducted in an undisturbed population. Subsequently, matrix population models are used to determine relative importance of different life stages, derive age estimates and simulate different harvest regimes.

Chapters 4 & 5 present the results of studies on the clonal understorey palm *Geonoma deversa* from which leaves are harvested for thatching. In Chapter 4, the clonal demography of the species is analysed and a new type of population model is presented in which the dynamics of ramets (stems) depend on the genet to which they belong. In Chapter 5, this model is extended to include the effect of leaf harvesting on population dynamics. The information on impact of leaf removal is obtained in a 2-yr field experiment in which leaves are harvested following common practice.

Chapter 6 presents a method to incorporate variability in demographic parameters (survival, growth and reproduction) into population matrix models. Using this 'perturbation method', insight can be obtained in the consequences of demographic variation or uncertainty in parameter estimates on the population growth rate, the main output parameter of matrix models. The method is applied to matrix models for a set of plant species, including all three species studied in this thesis.

Chapter 7 reviews the use of population matrix models for 35 woody species. The methodology used to construct these models, the problems encountered in model parameterisation and the output of the models are reviewed. Furthermore, the consequences of model construction, parameterisation and data constraints for the output of matrix models are analysed.

Acknowledgements

I thank Alan Bojanic for economic information on the Bolivian Amazon, and him, René Boot, Marielos Peña, Marinus Werger and Corien van Zweden for valuable comments on a draft version of this chapter. I am grateful to Hans ter Steege for preparing the maps for Figure 1.

In-shell Brazil nuts from Bertholletia excelsa.

Chapter 2

Demography of the Brazil nut tree (*Bertholletia excelsa*) in the Bolivian Amazon: impact of seed extraction on recruitment and population dynamics

Pieter A. Zuidema & René G.A. Boot

Summary

A demographic study was carried out on *Bertholletia excelsa*, the Brazil nut tree, in two primary forest sites in Northern Bolivia. At both study sites seeds ('Brazil nuts') of this emergent tropical forest tree have been harvested for several decades. In spite of the large proportion of seeds that are harvested (on average 93%), reasonable densities of recently emerged seedlings were found in both study populations. Seeds of *Bertholletia* are contained in woody fruits that are primarily opened by agoutis (caviomorph rodents). After fruit fall, most fruits are left untouched on the forest floor for 1-2 year before they are opened. This may be explained by the lower energetic costs of fruit opening in old fruits with a softened woody pericarp. However, the proportion of viable seeds is strongly reduced in old fruits. Growth in diameter at breast height (DBH) was low for treelets (<15 cm DBH) and adult trees (>100 cm DBH) and peaked for intermediate-sized trees (30-60 cm). These trees often attained an annual growth rate of > 1.5 cm yr^{-1}, which is high compared to other non-pioneer tropical trees. This, and the strong growth response to increased light availability found for seedlings and saplings, suggest that *Bertholletia* can be classified as a gap-dependent species. Matrix population models were constructed for both study populations, for normal and dry years separately. Population growth rates (λ) calculated for all models and a stochastic time-varying model were close to one, suggesting population stability. Population growth was most sensitive to stasis elements (persistence in one size category) in the transition matrix. Age estimates revealed that age at first reproduction (at DBH >60 cm) amounted to 126 and 141 yr in the two sites, and age in the last category (DBH >160 cm) 295 and 296 yr. Given the continuous rejuvenation of the population, the stable population size, the high age at maturity and the long reproductive period, it is concluded that current levels of Brazil nut extraction may be sustained at least for several decades and perhaps for even longer periods.

Introduction

The Brazil nut has received ample attention in the last decade as an example of an economically important non-timber forest product (NTFP) with high potential for sustainable use (*e.g.* Fearnside 1989, Prance 1990, Richards 1993, Clay 1997). The nut, produced by the emergent Amazonian tree *Bertholletia excelsa*, is predominantly collected from primary rain forest sites and its extraction has little impact on species composition and forest structure. Collection and processing of Brazil nuts is of major importance in local and regional economies in the Amazon regions of Bolivia, Brazil and Peru (Mori 1992, LaFleur 1992, Dominguez 1994, Broekhoven 1996), generating income for thousands of families (Clay 1997, Stoian *in press*). Although recent socio-economic studies suggest that the potential of Brazil nuts as a major pillar for sustainable forest management and regional development may not be as large as expected (Mori 1992, Homma 1996, Assies 1997, A. Bojanic *personal communication*), it remains an important example of how a 'minor' non-timber forest product may have a major influence on regional economy without large-scale forest alteration. Furthermore, exploitation of the Brazil nut tree in natural forest stands may be an adequate vehicle for conservation of its forest habitat, as efforts to grow *Bertholletia excelsa* in plantations have not been very successful, probably due to the lack of efficient pollinators (Mori & Prance 1990), the risk of inbreeding and the economics of establishing plantations. Certification of forests from which Brazil nuts are extracted may also serve the purpose of forest conservation (CFV 1999).

Despite the economic importance of the Brazil nut, its long extraction history (Mori & Prance 1990) and its example role for sustainable forest management, very little is known about the impact of extraction on the demography of the species and on the future availability of nuts. So far, studies on *Bertholletia excelsa* have mainly focussed on aspects of its cultivation: germination (Müller 1981, Kainer *et al.* 1999), seedling growth (Kainer *et al.* 1998, Poorter 1999, Zuidema *et al.* 1999), enrichment planting (Kainer *et al.* 1998, Oliveira 2000) and establishment of plantations (Müller 1981, Mori & Prance 1990 and references therein). Studies in natural populations have concentrated on population structures (Salomao 1991, Peres & Baider 1997, Viana *et al.* 1998), population genetics (Buckley *et al.* 1988, O'Malley *et al.* 1988), pollination mechanisms (Müller *et al.* 1980, Nelson *et al*. 1985) and dispersal ecology (Terborgh *et al.* 1993, Tabarelli & Mantovani 1996, Peres & Baider 1997, Peres *et al.* 1997). In spite of the considerable research attention paid to *Bertholletia* in biological literature, a quantitative analysis of the entire life cycle of the species is still lacking. Such analysis is crucial to determine the impact of large scale and intensive seed removal from natural populations on the maintenance of populations and the future availability of Brazil nuts.

In this paper we present results of a study on the demography of *Bertholletia excelsa* in two Bolivian primary forest sites where Brazil nuts have been collected for several decades. The first goal of this study is to determine whether recruitment of new seedlings still occurs in exploited populations. Extraction of Brazil nuts from natural populations interferes with the complex dispersal strategy of *Bertholletia excelsa*. Seed dispersal in this species strongly depends on caviomorph rodents (agoutis, *Dasyprocta* sp.) that are able to gnaw open the woody pods and subsequently disperse part of the seeds by scatterhoarding. In forests where Brazil nuts are collected, a large number of seeds is taken away. This is likely to alter seed handling of the agoutis, as they tend to consume (*i.e.* destroy) more and scatterhoard less seeds when food availability is low (Forget 1996, Bouwman & van Dijk 1999). We will determine the proportion of seeds extracted by Brazil nut collectors and the proportion of the remaining fruits that is opened by agoutis. As the woody fruits can remain intact on the forest floor for some time, we will relate seed condition to time since fruit fall. Furthermore, we study fruit and seedling distribution patterns to evaluate the consequences of seed dispersal, seed predation and germination on the spatial distribution of seedlings.

The second goal is to analyse population dynamics of the species under primary forest conditions, with the final purpose to determine the consequences of seed removal for population dynamics. To this end, we investigate size-dependent patterns of survival, growth and reproduction and assess the regeneration strategy of the species by relating growth to light availability. The effect of climatic variation on vital rates is also investigated as one of the two measurement years coincided with a particularly dry (El Niño) year. Dry years occur regularly in northern Bolivia and may be common throughout the distribution area of *Bertholletia excelsa* as it typically occurs in areas with two to seven dry months (< 60 mm precipitation, Müller 1981). We will construct population matrix models to obtain insight in the importance of different life stages and processes for population maintenance and growth. Furthermore, we derive age estimates for different size categories. Such estimates can be used to determine at what time scale Brazil nut extraction may influence future availability of the resource. Finally, we use the information on recruitment and population dynamics to assess the consequences of nut extraction for population maintenance and sustained seed production.

Study Species

Bertholletia excelsa H.B.K. is a large emergent Neotropical forest tree that may attain a total height of up to 50 m and a diameter at breast height (DBH) of up to 300 cm (exceptionally 400-500 cm, Salomao 1991). The species is distributed throughout Amazonian forests in non-flooded (*terra firme*) forests (Mori & Prance 1990). Peres & Baider (1997) reported clumped distribution of *Bertholletia* at landscape level, but random distribution of individuals within stands. In the northern Bolivian Amazon region, densities of individuals >30 cm DBH vary between <1 to >9 trees per ha, with the predominant density being 1-5 adult trees per ha (DHV 1993). Due to its large adult stature, *Bertholletia* often accounts for a large proportion of total basal area in the forests where it occurs (Salomao 1991, DHV 1993).

Bertholletia has a complex dispersal ecology that almost completely depends on the scatterhoarding activity of agoutis (Peres & Baider 1997). Seeds of the species are contained in a large capsular woody fruit (diameter > 10 cm; hereafter 'pod'). Primary dispersal is by gravity (barochoric): pods drop to the forest floor, but are not damaged by the impact of the fall and remain closed. As pods do not possess an opening sufficiently large for the large seeds (*c.* 20 × 50 mm) to leave the fruit without assistance, seeds can only be released by active opening. This is predominantly done by the diurnal agoutis which are capable to efficiently gnaw open the thick and tough woody pericarp of the pod (Peres & Baider 1997). Agoutis typically eat part of the seeds after opening the pod, and scatterhoard the remaining seeds for later consumption. Seeds are scatterhoarded in caches of usually one seed at distances of generally <10 m (Peres & Baider 1997, Bouwman & van Dijk 1999). Cached seeds are predated upon by agoutis or other rodents (Peres & Baider 1997), among others by tracking the scent of the seeds (Murie 1977). Those cached seeds that for whatever reason are not consumed within 12-18 months - the germination period of *Bertholletia* (Müller 1981) - may germinate. Germination success seems to be dependent on moist storage conditions (Kainer *et al.* 1999), and seeds may remain viable for several years (Watson 1901).

On rare occasions seeds may also be found germinating within an intact pod on the forest floor (Peres & Baider 1997, P.A. Zuidema, *personal observation*). Also clumps of seedlings may be found surrounded by the remainders of a pod (P.A. Zuidema, *personal observation*), probably indicating that seeds have germinated after the woody pericarp has completely disintegrated.

Brazil nut collection is carried out in the wet season during or after the main peak in pod fall (primary dispersal). During collection, pods are searched below the tree crown, taken to a central location below or just outside the tree crown and opened with a machete. The seeds are then taken out of the pods and transported in large bags to a nearby house or settlement from where they are further transported to processing plants. During harvest practices, Brazil nut collectors may actually serve as seed dispersers when they unintentionally leave seeds at the location where they open the pods, or drop seeds from their bags while walking along forest trails.

Currently, the largest share of the world supply of shelled Brazil nuts originates from Bolivia (Man-Producten 1998). The Brazilian production is slightly lower and has decreased over the last years due to increased labour costs and high deforestation rates.

Methods

Study sites

This study was carried out in two primary moist tropical forest sites in the northern Bolivian Amazon which are about 140 km apart. The first site, forest reserve El Tigre (Beni department, 10°59'S, 65°43'W) is a 830-ha research site of the Programa Manejo de Bosques de la Amazonia Boliviana located at 50 km from the town of Riberalta. Annual precipitation in Riberalta amounts to about 1703 mm (average over 1948-1998) with a pronounced dry season from May to September (< 100 mm rain per month). The reserve is largely covered with primary forest but also contains patches of secondary forests in different successional stages. Reproductive *Bertholletia* trees are heterogeneously distributed over the reserve. The second research site is located close to the community El Sena (Pando department, 11°30'S, 67°15'W), in a forest area with similar forest structure and species composition. The abundance of adult *Bertholletia* trees is comparable between the sites. No precipitation data are available for El Sena, but total annual precipitation is comparable between sites (Beekma *et al.* 1996), although seasons are slightly shifted to later dates in El Sena (compare Peruvian Amazon, Terborgh 1990). Related to this, the *Bertholletia* fruiting season also starts later: in El Sena pods fall from November till February (peaking in January) compared to October till January (peak in December) in El Tigre.

In both sites Brazil nuts were collected during the study period, by people from nearby communities. Nut extraction has been carried out for several decades in both areas, as El Tigre is in the vicinity of the town where most Brazil nuts are processed and El Sena has been an important settlement for a long period (Fifer 1970). Agoutis are commonly hunted in El Sena for their meat; in the forest reserve El Tigre hunting has been forbidden since 1994, but has probably not ceased completely.

During the second measurement year rainfall in Riberalta was strongly reduced: during the wet season (Dec '97-Mar '98) precipitation amounted to 874 mm compared to an average value of 1037 mm (SD=234 mm for '48-'98 data), during the subsequent dry season (May '98 - Sep '98) this was 94 mm compared to an average of 203 (SD=73 mm). The subsequent occurrence of two drier-than-normal seasons caused the 12-mo moving average precipitation to drop below 100 mm mo^{-1} which is considerably lower than average (143 mm mo^{-1}). Moving average values below 100 mm mo^{-1} were also observed in other years with very low rainfall in both wet and dry season (1956, '63, '69, '83 and '85), occurring at a frequency of 0.12 (=6/50) during the period 1948-1998. Three out of these six considerably drier years concurred with El Niño Southern Oscillation episodes (ENSO), but significant anomalies in monthly precipitation during ENSO episodes were not found (results not shown; *cf.* Ropelewski & Halpert 1996).

Study design

In each of the study sites measurements on *Bertholletia* individuals of all sizes were carried out in a permanent plot. In El Tigre a 12-ha (400 × 300 m) plot was established to search and study all *Bertholletia* individuals >5 cm DBH (diameter at breast height). Individuals <5 cm DBH and seedlings were searched and measured in six randomly chosen 25 × 25 m subplots per ha (total searched area equalled 4.5 ha). In two of these subplots per ha, seedlings of all sizes (with minimally one fully expanded leaf) were searched at initial measurement, and these plots were used to quantify seedling recruitment after one and two years. In the remaining four subplots per ha, larger seedlings (> 50 cm height) and treelets were searched for at initial field evaluation. In El Sena a similar method was used, but with a 6-ha plot and using a 20 × 20 m grid. Seedlings of all sizes and treelets <5 cm DBH were searched and measured in six randomly chosen subplots per ha (total area: 1.4 ha). In both sites, seedlings and treelets encountered outside the selected subplots or just outside the plots were also included to increase sample size.

Narrow trails used by Brazil nut collectors dissected the study plots in both sites, but these do not significantly influence the prevailing understorey light regime. Brazil nut collection was generally carried out without removing the understorey vegetation.

Additional *Bertholletia* trees in primary forest outside the study plots were measured to increase the sample size. Individuals of >4 cm DBH that were encountered along trails used by Brazil nut collectors within *c.* 2 km distance from the study plots were searched and measured (El Tigre: *n*=135; El Sena: *n*=138).

Field measurements

Bertholletia individuals included in the study were measured annually. Trees >1 cm DBH were generally measured at the end of the dry season (in Oct-Nov) during 1996-98. An additional measurement was conducted for trees outside the study plots in Dec 1999 (El Sena) and Jan 2000 (El Tigre) to obtain growth data over 3 yr. In El Sena, part of the individuals >1 cm DBH included in the study had been marked and measured in 1992 (van Rijsoort *et al.* 1993), which made it possible to verify the DBH growth rates obtained over the 2-yr study period. Individuals <1 cm DBH were generally measured at the end of the wet season (Feb-Mar) during 1997-'99.

Individuals of >1 cm DBH were tagged with an aluminium label. At each field evaluation DBH (at 1.3 m height) was measured (to nearest mm, using pi-graduated tape) and the reproductive status was assessed. The number of pods opened by Brazil nut collectors was counted for all reproductive trees with non-overlapping crown-shadows within the plots and a random selection of individuals outside the plots (El Tigre: n=33; El Sena: n=41). At initial measurement, the location of the diameter tape was carefully marked with paint on at least three positions around the tree bole. In El Tigre, use was made of data on pod production of 42 trees that were studied simultaneously with the present study (Leigue Gómez & Boot *in press*). Total height and height up to first branch of each individual >1 cm DBH were estimated once during the study period.

Individuals of <1 cm DBH were tagged with an aluminium label and marked with a coloured plastic string around their base and by attaching a large piece of coloured plastic foil on a tree or branch above them. Each year the following measurements were conducted: plant height (to nearest cm, following the stem), diameter at 0.1 m height and if possible at 1.3 m (to nearest 0.1 mm, using calliper), number of green leaves (marking the newest leaf at every branch to determine leaf production).

All measured individuals were assigned a score of the modified Dawkins illumination index (Dawkins & Field 1978, Clark & Clark 1992) to characterise light climate. The scores were 1 (no direct lateral or overhead light), 2L (little direct lateral light, no overhead light), 2M (some direct lateral light, no overhead light), 2H (substantial direct lateral light, no overhead light), 3 (some overhead direct light), 4 (full overhead direct light; in canopy) and 5 (full overhead and lateral direct light; emergent). All studied individuals inside the plots were mapped to the nearest meter.

The density of pods which were not removed by the Brazil nut collectors was assessed in the recruitment subplots in March-April 1998 and February-March 1999. The following parameters were determined for pods that were encountered: location to the nearest meter, whether opened by agoutis and the time since the pod fell to the forest floor. The latter was assessed by experienced Brazil nut collectors, based on the two criteria: (1) whether the pod still possessed an outer shell around the woody pericarp; and (2) the toughness of the woody pericarp. The outer shell that is present at the time of pod fall typically disintegrates within one year; the woody pericarp is known to disintegrate in three years. A 1-yr old pod is therefore notably harder than a 2-yr old pod.

To determine the viability of seeds in pods of different age, 50 pods aged 0, 1 and 2 yr (ageing method as above) were selected outside the study plots in both sites in March 1999. The total number of seeds per pod was counted and each seed was dissected to assess whether it was still intact.

Data analysis

As demographic information was collected during two years with different precipitation (normal and dry year), data on survival, growth and fruit production were first tested for differences between years. This was done for each site separately. In the case of no difference, data of the two measurement years were pooled for further analyses. Subsequently, differences between sites were investigated, mostly in combination with the analysis of size-dependent patterns in the demographic parameter under consideration. This was carried out using linear, non-linear or logistic regression models. In addition, the influence of light level on vital rates was assessed by adding Dawkins illumination scores to these regression models as dummy variables.

Analysis of growth in DBH was confined to those individuals for which no measurement problems were recorded. Commonly occurring measurement problems, especially in large adult trees, were infestation of the bark by termites, a peeling bark and local irregularities in the tree bole. The removal of individuals with light to serious measurement problems reduced the number of individuals for DBH growth analysis by 15 and 17% for El Tigre and El Sena respectively. Annual DBH growth was calculated by linear regression of DBH against time (over 2-3 yr; 6 yr for some trees in El Sena). Tree diameter growth is typically non-linearly related to initial diameter, with low values for both small and large-sized individuals and high growth rates at intermediate sizes. To describe this pattern, the Hossfeld IV equation (Zeide 1993) was fitted through the DBH growth data, using a non-linear regression procedure with a least-squares loss function. The Hossfeld IV equation is of the form:

$$\Delta\,\mathrm{DBH} = \frac{b \times c \times \mathrm{DBH}^{(c-1)}}{\left[b + (\mathrm{DBH}^{c}/a)\right]^{2}} \qquad (1)$$

where (DBH is the annual DBH growth rate (cm yr^{-1}) and a, b and c are fitted parameters.

Spatial distribution of pods and seedlings relative to adults trees was assessed following the methodology of Hamill & Wright (1986). This analysis was performed only for the study site El Tigre due to the irregular plot form in El Sena. Using this method it is possible to determine whether pods or seedlings have a clumped, random or over-dispersed spatial distribution relative to adult trees. The method uses a null distribution which assumes a random distribution of seedlings relative to adult trees, *i.e.* that each location in a plot is equally likely to contain a seedling (formulae in Hamill & Wright 1986). By comparing the relative dispersion of pods left by Brazil nut collectors, pods opened by agoutis, newly emerged seedlings and older small seedlings, insight is gained in the spatial pattern of the processes of seed dispersal, germination and early seedling survival.

Transition matrix construction

The study populations were divided into 17 size categories: the four smallest based on plant height and the remaining on DBH (Table 1). Categorisation was based on biological criteria that maximise differences in vital rates among categories. For example, the first size category was chosen such that it included all newly emerged seedlings. Similarly, the first reproductive category was established as to maximise the contrast in fecundity between categories. Furthermore, limits for the first seven categories were chosen such that the height range of each successive category was doubled (Table 1).

Stage-based population matrix models (Lefkovitch 1965, Caswell 1989a) were used to project population size and structure for the two study populations. These models have a convenient standardised form, have relatively low data requirements for model parameterisation and are a useful tool to examine consequences of demographic disturbances that may result from extraction of plant parts (Boot and Gullison 1995). Matrix models use the equation $\mathbf{n}(t+1)=\mathbf{A}\mathbf{n}(t)$ where $\mathbf{n}(t)$ and $\mathbf{n}(t+1)$ are column vectors containing the population structure at time t and $t+1$, respectively, and $\mathbf{A}$ is a square matrix containing transition probabilities among categories during one time-step. The growth rate of the population is the dominant eigen value (λ) of matrix $\mathbf{A}$, and the stable stage structure of the population can be shown to be the right eigenvector w of matrix $\mathbf{A}$ (Caswell 1989a).

Elements a_{ij} of $\mathbf{A}$ can be grouped according to their position in the matrix: growth elements (G) represent an individual's probability to grow from one category to the next (elements in the sub-diagonal of the matrix); stasis

Table 1

Classification criteria and characteristics for 17 size categories of *Bertholletia excelsa*. Categories *1-4* are based on plant height, *5-17* on diameter at breast height (DBH). Shown are estimates for total height and height to lowest branch (mean ± 1 SD), proportion of individuals per Dawkins illumination score, percentage of reproductive individuals (Repro), survival percentage (σ; normal-year data for categories *1-4*; sites and years combined for *5-17*), and initial sample size (*n*).

	Diameter	Height		Dawkins illumination score							Repro	σ		*n*	
		total	branch	1	2L	2M	2H	3	4	5		Tigre	Sena	Tigre	Sena
	[cm]	[m]	[m]				[%]				[%]	[% yr^{-1}]			
1		<0.35		58	37	4	2	-	-	-		61	49	*100*	*51*
2		0.35-0.7		32	46	8	5	8	-	-		89	72	*17*	*18*
3		0.7-1.4		11	53	32	-	5	-	-		100	100	*18*	*4*
4		1.4-2.3		13	50	19	19	-	-	-		91	100	*28*	*6*
5	1-4	3.8 (1.6)	3.0 (1.3)	3	32	32	26	16	-	-	0	99		*33*	*5*
6	4-9	8.6 (2.4)	7.0 (2.3)	-	19	10	48	19	5	-	0	100		*16*	*4*
7	9-20	16.4 (3.2)	12.9 (3.5)	-	6	-	-	56	38	-	0	100		*7*	*9*
8	20-30	-	19.1 (2.4)	-	-	-	-	27	73	-	0	100		*1*	*10*
9	30-40	29.0 (3.6)	21.0 (4.1)	-	-	-	-	-	40	60	50	100		*4*	*2*
10	40-50	31.7 (1.5)	21.0 (2.4)	-	-	-	-	-	57	43	100	100		*3*	*3*
11	50-60	31.3 (3.0)	23.1 (1.7)	-	-	-	-	-	29	71	86	100		*7*	*1*
12	60-80	30.9 (2.9)	21.7 (2.5)	-	-	-	-	-	7	93	100	100		*14*	*14*
13	80-100	33.5 (3.4)	23.1 (3.4)	-	-	-	-	-	-	100	100	100		*34*	*12*
14	100-120	35.0 (3.0)	23.0 (3.0)	-	-	-	-	-	-	100	97	100		*31*	*30*
15	120-140	35.3 (3.5)	23.0 (3.4)	-	-	-	-	-	-	100	100	100		*31*	*27*
16	140-160	36.3 (3.2)	23.3 (2.9)	-	-	-	-	-	-	100	100	98		*18*	*30*
17	>160	36.2 (1.3)	23.7 (2.2)	-	-	-	-	-	-	100	100	98		*5*	*23*

elements (P) represent the probability of remaining in the same category (diagonal) and fecundity elements (F) represent the number of offspring produced by an individual in a certain category (elements in the upper row, except for the top-left element).

Matrix elements were parameterised using the underlying vital rates: survival, growth and reproductive output (Caswell 1989a). The value of growth elements (G) of category i was calculated as $G_i = \sigma_i \times g_i \times c_i^{-1}$, where σ_i is the survival probability in that category, g_i the growth rate (cm yr^{-1}) and c_i the category width (cm). Stasis elements (P) were then determined as $P_i = \sigma_i - G_i$. Fecundity (F) elements were calculated as $F_i = \sigma_i \times Pr\{f\}_i \times f_i$, where $Pr\{f\}_i$ is the probability that an individual in category i is reproductive and f_i the number of offspring produced by a reproductive individual in category i. The value of f_i was determined as the category-specific pod production, multiplied by the number of seedlings that emerged per pod produced during the previous year. A time-lag of one year between pod production and appearance of new seedlings is too short for most seedlings given that the majority of pods is not opened directly after pod fall (see Results), and the reported time to germination is 12-18 months (Müller 1981). However, not sufficient data on fruit production were available from preceding years to use a longer time-lag. As fruit production at the population level remains rather constant over years (Leigue Gómez & Boot *in press*), the influence of this calculation on model output is presumably very small. The number of newly emerged seedlings was counted in subplots. Total pod production for the study plots was determined by counting all pods harvested by Brazil nut collectors and adding the number of pods that remained after harvest which was based on counts in subplots.

Four transition matrices were constructed: one for each combination of study site and year-type. The matrices were parameterised with different values for a vital rate (growth, survival or reproduction) when this was found to be significantly different between sites and/or years. Otherwise the data for sites and/or years were pooled to determine the value for that vital rate.

Population matrix analyses

Both time-invariant and time-varying matrix models were applied to simulate population dynamics of *Bertholletia* in the two study sites. For the time-invariant models - standard matrix models that assume demography to be constant in time - population growth rates (λ) were calculated. Furthermore, elasticity analysis (de Kroon *et al.* 1986) was carried out to determine the contribution of different matrix elements to the value λ of the normal year model for both sites. Age estimates for categories of the normal-year matrix models were determined using algorithms for determining ages in stage-based matrix models (Cochran and Ellner 1992): age conditional at entering a category (τ) and age of residence in a category (S) were calculated.

Time-varying models were applied to describe long-term population dynamics for sequences of normal and dry years. As dry years are not assumed to occur in a deterministic cyclic pattern in time, a time-homogeneous stochastic model was applied (*sensu* Caswell 1989a). This model is based on the fixed probabilities of transitions between normal and dry years, denoted by q (the probability that a normal year is followed by a dry year) and p (probability of the reverse).

Time-homogeneous models have the property that the probability distribution of stage structures eventually converges to a stationary distribution (Caswell 1989a), so that final stage distributions are independent from initial population structures. Long-term population growth can be approximated numerically, by using population growth at each time step (Silva *et al.* 1991):

$$\log\lambda(t) = \log N(t+1) - \log N(t) \tag{2}$$

where N is the population size and $\log\lambda(t)$ is the instantaneous growth rate (*not* the dominant eigenvalue of a matrix). These instantaneous estimates can then be averaged over a long time interval (T yr; Silva *et al.* 1991):

$$\overline{\log \lambda_s} = \frac{1}{T-1} \sum_{t=1}^{T-1} \log \lambda(t) . \tag{3}$$

In stochastic matrix models, autocorrelation (ρ) among year-types may play an important role (Tuljapurkar 1989). It is defined as $\rho = 1 - p - q$ (Silva *et al.* 1991), with positive values ($0<\rho<1$) when years of the same type tend to appear in a row, and negative values ($-1<\rho<0$) when year-types tend to alternate. The frequency of dry years (π) is related to the degree of autocorrelation as $\pi = q / (1-\rho)$.

Stochastic population models were performed using the frequency of dry years as obtained from the meteorological records ($\pi=0.12$), without allowing the occurrence of two consecutive dry years ($p=1$; thus $\rho=-q=0.136$), as this is rather unlikely. Average stochastic population growth rates (λ_s) and mean population structures were then calculated over a period of 3000 simulation years ($T=3000$), after an initial period of 1000 years.

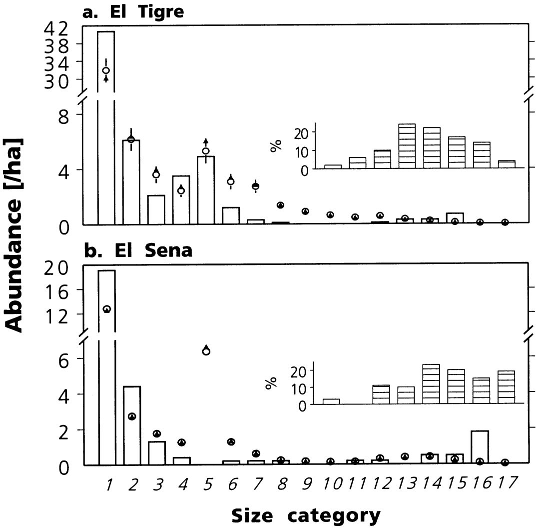


Figure 1
Population structures of *Bertholletia excelsa* in two sites in the Bolivian Amazon where Brazil nuts are extracted: El Tigre (a) and El Sena (b). Shown are observed population structure from study plot data (bars) and stable stage structures resulting from a time-invariant matrix model for a normal year (triangles) and a stochastic time-varying model for normal and dry years (dots; error is 1 SD of 3000 structures). The hatched bars in the inset denote the proportion of individuals measured outside the study plots in categories *10-17* (*n*=127 for El Tigre and 120 for El Sena).

Results

Size distribution, tree allometry and reproductive status

Bertholletia population structures in the study sites showed a declining abundance from small seedlings to large adult trees (Figure 1), with a slightly higher abundance of large trees (60-160 cm DBH; categories *12-16*) compared to trees of 10-60 cm DBH (*7-11*). This was more clearly observed in the larger sample of trees measured outside the plots (inset in Figure 1). In El Sena no individuals of 1-4 cm DBH were found inside the subplots that were searched, although some individuals of that size were found and measured outside these subplots. The largest individual was found in El Sena measuring 267 cm DBH; in El Tigre the maximum DBH was 190 cm. The 'hump' of large reproductive individuals in El Sena was located at higher DBH values: the average DBH for reproductive individuals there was 126.9 (SD=38.2) compared to 107.5 cm (SD=30.8) in El Tigre (T-test: t_{263}=-4.66; $p<0.001$).

Tree height steeply increased in individuals up to 40 cm DBH, after which height increment per unit DBH increment levelled (Table 1; *cf.* Salomao 1991). Reproductive trees were 26 to 42 m tall (total height). Height up to first branch of adult trees ranged from 15 to 30 m, the latter not being different between sites (T-test: t_{280}=-1.21; $p>0.05$; overall mean=22.6 m). Height to first branch was linearly related to the ln-transformed DBH (Height[m]=-0.68 + 5.0 × Ln(DBH[cm]), R^2=0.80, n=341, $p<0.001$), also indicating the larger height increment per cm of DBH increment for small individuals. This allometric relation was not different between sites (no effect of adding site to linear regression).

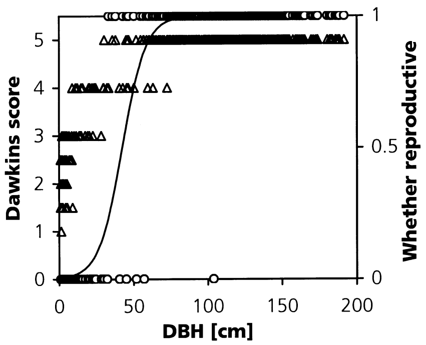


Figure 2
Relation between tree crown position, reproductive status and DBH in *Bertholletia excelsa*. Modified scores for the Dawkins crown illumination index (triangles, left axis) and reproductive status (dots, right axis; whether tree has produced fruits once: 0=no, 1=yes) and a logistic regression for reproductive status (line, right axis; Constant = -5.4056, Regression coefficient = 0.1272, R^2 = 0.93 [Nagelkerke 1991]) are shown in relation to DBH. Two individuals larger than 200 cm DBH are not shown.

Reproductive status was strongly related to tree size (Figure 2): 98% of the individuals with DBH >40 cm were reproductive (n=84), whereas this was only 3.5% for those 1-40 cm DBH (n=280). Due to the strong correlation of crown position (Dawkins score) and DBH, the former was also highly associated with reproductive status: almost all (270 out of 278) reproductive trees included in the study were emergent (Dawkins score 5), and very few emergent trees were not reproductive (6 out of 276).

Seed and seedling ecology

Of the total production of pods in the study plots, on average 93% was harvested by Brazil nut collectors (data of three fruiting periods; El Tigre: 92-99%; El Sena: 91-97%). Not all pods left by the collectors were opened by agoutis. The proportion of opened pods increased with time since pod fall (Figure 3): from 3% in freshly fallen pods (<4 months on forest floor), to 21% in 1-yr old pods and 52% in 2-yr old pods (averaged over two sites and two data collection years).

Mean seed number per pod equalled 18.5 (SD=3.3, range: 8-26, n=300), which is comparable to the values obtained in other areas (Moritz 1984 [17.5-18.8], Peres & Baider 1997 [17.1], Viana *et al.* [18.0], Leigue Gómez & Boot *In press* [18.0]). Seed number in El Sena was somewhat higher than in El Tigre (18.8 compared to 18.1; ANOVA: $F_{1,294}$=12.6, p<0.001) but did not differ between three years ($F_{2,294}$=0.52, p>0.05). The proportion of intact seeds decreased with time since pod fall (Figure 4): from approximately 95 % in freshly fallen pods to almost none in pods that are present on the forest floor for two year (*c.* 24-28 months). The number of intact seeds was influenced by pod age in both sites (ANOVA: $F_{2,147}$=666.0, p<0.001 [El Tigre], $F_{2,147}$=523.9, p<0.001 [El Sena]), but sites differed considerably in the number of intact seeds of 1-yr old pods (Figure 4; 0.24 in El Tigre and 13.3 in El Sena). This may be due to the difference in pod fall period between the sites: in El Tigre the major portion of pods falls early in the wet season (November) whereas in El Sena this is in the mid wet season (January). The 1-yr old pods in El

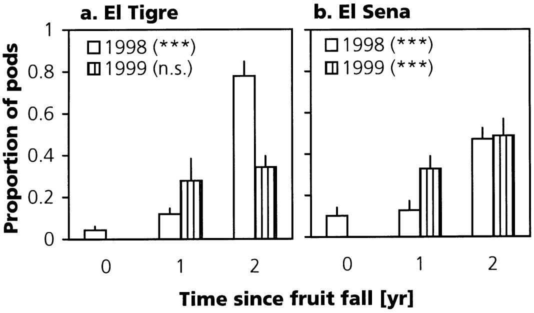


Figure 3
Proportion of pods of *Bertholletia excelsa* opened by agoutis (*Dasyprocta* sp.) in relation to time since fruit fall, in two sites in the Bolivian Amazon where Brazil nuts are collected: El Tigre (a) and El Sena (b). Different bar types refer to data collected in different years. Significance indications (ns: not significant; ***: $p<0.001$) in the legend are from χ^2 tests for differences in the proportion of opened pods among ages (test results [χ^2 ; n]: Tigre 1998 [117.4; 317], 1999 [4.5; 106] Sena 1998 [31.8;199], 1999 [31.9; 152]). Counts only included pods not collected by Brazil nut collectors.

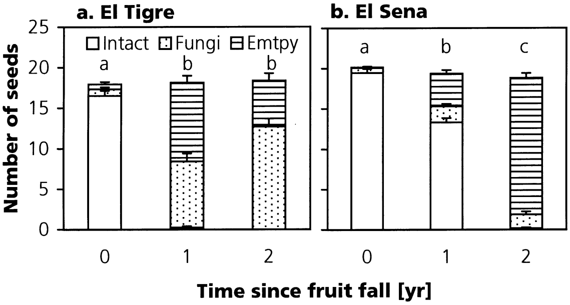


Figure 4
Seed quality in relation to time since fruit fall for *Bertholletia excelsa* in two sites in the Bolivian Amazon: El Tigre (a) and El Sena (b). Seeds were classified as empty (seed shell is empty; seed has completely rotten), infected by fungi and intact (no signs of damage). Different letters above bars indicate significant ($p<0.05$; Tukey's HSD) differences in the number of intact seeds between years.

Tigre therefore have experienced wet conditions for two months longer than those in El Sena. Of the seeds that were not intact, a substantial to large part had completely rotten after 1-2 yr.

Using the densities of pods opened by agoutis and that of new seedlings, the number of new seedlings per pod was calculated. Per 2-yr old pod opened by agoutis an estimated 3.0 new seedlings appeared in El Tigre and 0.82 in El Sena (using 2-yr old pods to account for the time lag for seed dispersal and germination). After the dry year, the El Tigre value dropped to 0.47 whereas that in El Sena remained constant at 0.80 seedling per opened pod. New seedlings appeared predominantly under dark forest understorey conditions: 97% of the newly emerging seedlings was assigned Dawkins score 1 or 2L (n=133).

Pods encountered in the study plots were highly clumped relative to adult trees (Figure 5a & b), although the degree of clumping was different for unopened and opened pods (Kolmogorov-Smirnov test: Z=3.48, $p<0.001$). Unopened pods were predominantly found below crowns of adult trees (90%

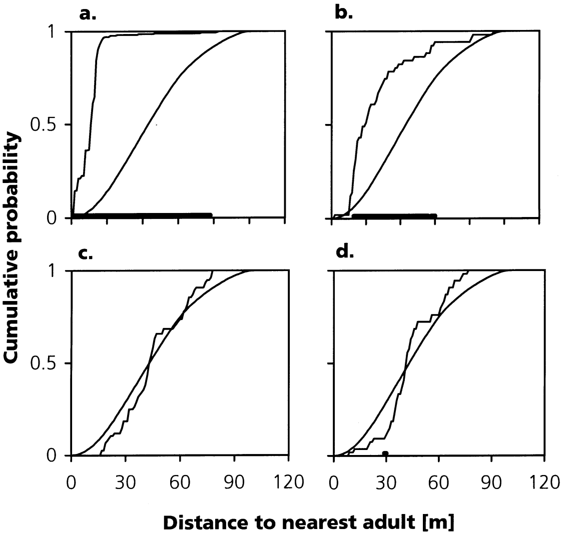


Figure 5

Spatial distribution of pods (a & b) and seedlings (c & d) relative to adult trees of *Bertholletia excelsa* in study site El Tigre in the Bolivian Amazon. Observed cumulative probability of distances from pods or seedlings to adult trees (step function, 1998 data) is compared to a theoretical distribution which assumes random distribution (smooth curve, identical for all graphs). Shown are observed distributions for pods not opened by agoutis (a; *n*=266), those opened by agoutis (b; *n*=51); newly emerged seedlings all in size category *1* (c; *n*=76) and existing seedlings of at least one yr, in size categories *1-3* (d; *n*=54). Clumping occurs when the observed probability is higher than the theoretical, over-dispersion when it is lower. For each distance the observed and theoretical distribution were compared by a Kolmogorov-Smirnov test: distances for which significant (*p*<0.05) differences were found are marked with the thick line along the x-axis.

within 15 m from trunk) whereas pods opened by agoutis were much less clumped with respect to adult trees, and a substantial part of these pods was found far from adult trees (22% at more than 35 m). In contrast to pods, seedlings were in general randomly distributed relative to adult trees, with a tendency for overdispersion (lower than expected abundance) at short distance from adults (Figure 5c & d). Distribution of newly recruited and existing (larger) seedlings were similar (KS test: Z=0.65, $p>0.05$). In accordance with the difference in spatial distribution of pods and seedlings is the finding that new seedlings do not appear more often in subplots with opened pods than in those without (El Tigre: $\chi^2=1.73$, $n=24$, $p>0.05$; El Sena: $\chi^2=0.03$, $n=36$, $p>0.05$). Both results suggest that new seedlings appear at some distance from the pods from which their seeds originated.

Size- and light dependent survival, growth and reproduction

Survival probability steeply increased with plant size from around 50% for small seedlings (category *1*), to almost 100% in categories *3-17* (Table 1). A positive relation between seedling height on survival was found for individuals in categories *1-4*, but light level did not influence survival probability (Table 2).

Table 2

Effect of size, study site and light level on vital rates of *Bertholletia excelsa* for individuals classified by height (categories *1-4*) and DBH (*5-17*). Multiple linear regressions were applied for growth (cm yr^{-1}) and pod production; multiple logistic regression for survival (with R^2 *sensu* Nagelkerke 1991). Shown are coefficients of determination for the complete regression model, that for the model without Dawkins scores (in parentheses), the value of the constant in the equation and values of partial regression coefficients for parameters included in the equation. Site and Dawkins scores were entered as dummy variables, with El Tigre as reference value for Site, and Dawkins score 4 (for pod production) and 1 and 2L combined (remaining parameters) for light level. Dawkins scores 4 and 5 were combined for all analyses except for that of pod production. Growth rates are in cm yr^{-1}. Significance indications are: -: not tested, ns: $p \geq 0.05$, *: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$.

Cat	Parameter	Period	R^2	Constant	Size	Site	Dawkins illumination score				*n*
							2M	2H	3	4&5	
1-4	Survival	'97-'98	0.19 (0.19)	-0.33 ns	0.026 ***	ns	ns	ns	ns	ns	220
		'98-'99	0.22 (0.20)	-0.74 **	0.020 ***	1.16 ***	1.2 *	ns	ns	-	303
	Height growth	'97-'98	0.20 (0.10)	2.72 ns	0.040 *	ns	10.9 ***	ns	20.4 ***	-	137
		'98-'99	0.26 (0.06)	0.13 ns	ns	ns	ns	10.4 *	30.8 ***	-	186
5-17	Survival	'96-'98	ns								
	DBH growth[1]	'96-'98	0.59 (0.47)	0.02 ns	0.016 *	0.27 *	-	ns	ns	0.36 *	76
	Ln(#pods)	'96-'99	0.08 (0.08)	3.90 ***	0.007 **	-0.21 *	-	-	-	ns	100

[1] **Only for individuals 1-40 cm DBH**

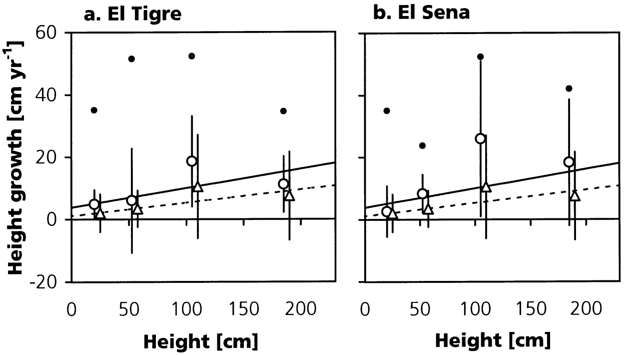


Figure 6
Size-dependent pattern in seedling height growth in *Bertholletia excelsa* in two sites in the Bolivian Amazon: El Tigre (a) and El Sena (b). Shown are mean growth (± 1 SD) for categories *1-4* in a normal (open dots) and a dry year (triangles), linear regressions for normal (drawn line; Growth = 3.77 + 0.062 × Height, R^2=0.10) and dry year (broken line; Growth = 1.04+0.042 × Height, R^2=0.06) and maximum growth rate observed per category for both years together (closed dots). Regression lines are not different between sites.

Almost no mortality was observed for individuals with DBH >1 cm: of the 374 trees studied, only four individuals died in two years. Differences between sites and size-dependent patterns could therefore not be determined. However, those individuals that died were either small (1.4 cm DBH) or fairly large (140 and 214 cm DBH). A higher mortality risk for small (<10 cm DBH) compared to larger (>10 cm DBH) trees has been found for a considerable number of tree species in Panama (Condit *et al.* 1995); this could be due to high damage risk or to low light availability. Large *Bertholletia* trees, on the other hand, may be more vulnerable to mortality as they gradually senesce. Signs of senescence were observed in trees of >80 cm DBH: 6.7% of these trees (*n*=239) had lost one or more of their main branches (typically 2-4 for full-grown trees). To account for the presumably higher mortality risk in small (1-9 cm DBH; categories *5*-7) and large (>120 cm DBH, *12-17*) trees in the transition matrices, we applied a slightly lower survival rate for these size ranges. The survival probabilities used for matrix parameterisation were the midpoints of the binomial 95% -confidence intervals (CI95%) of the survival rate for small (categories *5*-7), medium-sized (*8-14*) and large (*15-17*) trees (CI95%: 0.969-1.000; 0.990-1.000 and 0.970-0.998, respectively).

Seedling height growth was highly variable within size categories (Figure 6), as indicated by high coefficients of variation (CV) ranging from 75-322 (mean=164). Maximum growth rates were very high, often amounting to more than 40 cm yr^{-1}, being one order of magnitude higher than the average for some categories. The high variation in growth rates concurred with high

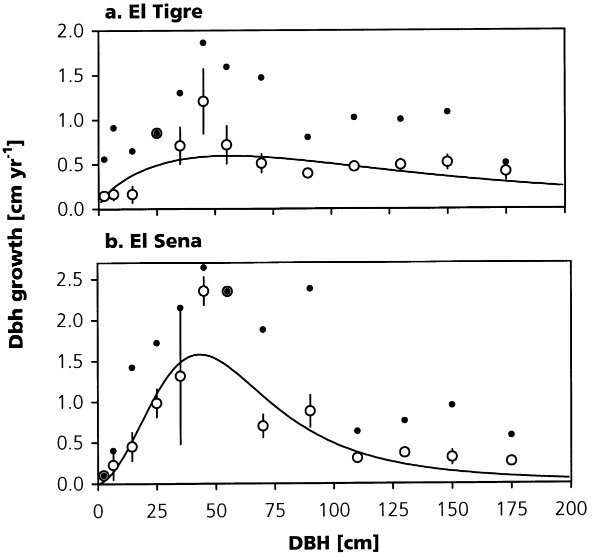


Figure 7
Size-dependent pattern in DBH growth in *Bertholletia excelsa* in two sites in the Bolivian Amazon: El Tigre (a) and El Sena (b). Shown are fitted Hossfeld IV equations (lines), observed average (± 1 SD) growth rate (open dots; for categories *5-17*) and observed maximum growth rate (closed dots). Fitted parameters *a*, *b* and *c* (eq. 1) equaled 133.7, 20.8 and 1.61, respectively, for the El Tigre (R^2=0.23, *n*=167) and 119.1, 422.5 and 2.67 for El Sena (R^2=0.41, *n*=130).

variation in light level received by seedlings (Table 1). Light level had a large influence on seedling growth in regression models: adding Dawkins illumination scores to a model with plant size alone substantially increased the proportion of variation explained (Table 2).

Part of the large seedlings experienced severe height loss due to damage (herbivory, fallen debris), often followed by rapid reiteration. Both large height reductions due to damage and very high growth rates during reiteration were not used in growth analyses as they strongly influenced average growth rates and represented only a small portion of the total seedling population (*c.* 5%).

Growth in DBH also showed considerable variation, both among and within size categories (Figure 7). Growth rate increased up to *c.* 60 cm DBH and then gradually declined. In the size range with high growth rate (30-60 cm DBH), annual DBH increments of >1.5 cm were often observed. The peak in the growth curve was wider and more pronounced in El Sena than in El Tigre, and observed maximum growth rates were higher in the former site (2.64 compared to 1.86 cm yr^{-1}). The reason for a less pronounced peak for El Tigre is probably that high growth values were restricted to a narrow DBH range and were therefore not detected by the Hossfeld growth curve that has a limited flexibility (Zeide 1993).

Between-site differences in DBH growth pattern were assessed by comparing the residual variation of the site-specific Hossfeld models as presented in Figure 7 with that of a model in which data for both sites were combined. The site-specific models accounted for significantly more variation

($F_{3,291} = 7.2$; $p<0.001$), indicating that equations differed between sites. A site effect on DBH growth was also obtained in a linear regression using only trees in the increasing leg of the growth-size curve (1-40 cm DBH; Table 2), with the El Sena growth rate being higher.

Light levels received by *Bertholletia* trees shifted from being generally low and highly variable for pole-sized trees (categories *5-6*) to very high and restricted to one Dawkins score for large emergent trees (*12-17*; Table 1). For example, pole-sized trees were assigned to as many as five Dawkins illumination scores. Variation in light availability for small trees (1-40 cm DBH) explained part of the observed variation in DBH growth (Table 2).

Production of pods was highly variable among individuals (averaged over three years: geometric mean=102; CI95%: 21.5-474.4; n=102; maximum=1032 by tree of 125 cm DBH) and within individuals over the three measurement years (average CV=71.4, n=102; extreme example of production of 31 pods followed by 1003 pods). But pod production at population level was much less variable (*cf*. Leigue Gómez & Boot *in press*). In each of the measurement years, a certain proportion of the reproductive individuals (mostly different individuals each year) did not produce any pods: this proportion did not differ among years (Cochran Test: Q=0.55, $p>0.05$) and averaged 7.5%. After excluding these zero-producing trees, pod production was related to tree size in a regression analysis: DBH and site differences explained only a small part of the large variation in pod production (Table 2). For this analysis and for matrix parameterisation, trees 40-60 cm DBH were excluded as they sporadically produced pods, and if so, only produced few (1-6) pods.

Differences between years

Seedling demography was strongly affected by the dry year. Seedling growth was on average 4.7 (El Tigre) and 3.0 cm yr^{-1}(El Sena) lower during the dry measurement year (Wilcoxon matched pairs test: Z=-2.01, n=68, $p<0.05$; and Z=-2.95, n=35, $p<0.01$, respectively). Seedling survival was only different between years for El Tigre ($\sigma_{normal}=0.73$, $\sigma_{dry}=0.57$; $\chi^2=9.55$, n=355, $p<0.01$), but not for El Sena ($\sigma_{normal}=0.64$, $\sigma_{dry}=0.76$; $\chi^2=3.05$, n=202, $p>0.05$). The most severe effect was in abundance of newly recruited seedlings, which was much lower after the dry year: in El Tigre by 80% (5.3 ha^{-1} compared to 25.8 ha^{-1}); in El Sena by 56% (7.0 ha^{-1} compared to 16.0 ha^{-1}).

Differences in tree growth were less clear: in El Tigre dry-year DBH growth was slightly reduced (difference=0.11 cm; Wilcoxon: Z=-4.23, n=184, $p<0.001$) whereas in El Sena it was somewhat higher (difference=0.14; Z=-3.92, n=149, $p<0.001$). Variation between sites in rainfall distribution over the year and severity of the dry year may in part have been responsible for this finding, making the interpretation of these growth differences difficult. Since

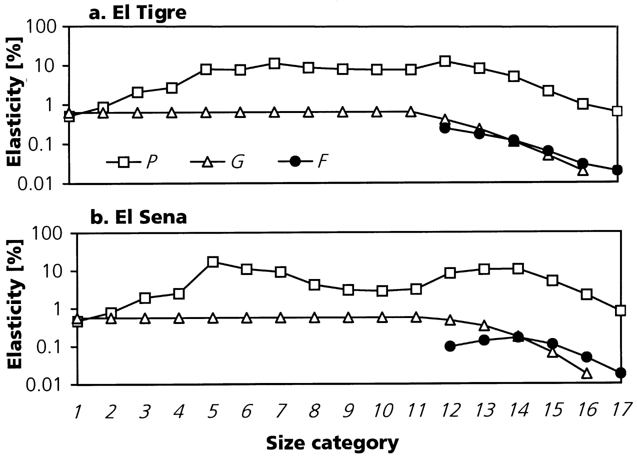


Figure 8
Elasticity values for population matrix models of *Bertholletia excelsa* in two sites in the Bolivian Amazon: El Tigre (a) and El Sena (b).
Shown are elasticity values for probability of stasis (P), growth (P) and fecundity transition (F) for normal-year population transition matrices.

observed differences are relatively small compared to measurement errors and as the reliability of DBH increment data is considerably improved when calculated over several years, growth data of different years were combined.

Matrix model output

Four transition matrices were constructed (Table 3): per site one for a normal (N) and for a dry year (D). Year-type matrices differed in seedling growth and survival (categories *1-4*), and for recruitment of new seedlings. Matrices of the two study sites differed in all vital rates except for tree survival (categories *5-17*) and seedling height growth (*1-4*).

Population growth rates (λ) of the four time-invariant matrix models were all close to one ($\lambda_{\text{Tigre,N}} = 1.0165$; $\lambda_{\text{Tigre,D}} = 0.995$; $\lambda_{\text{Sena,N}} = 1.0071$; $\lambda_{\text{Sena,D}} = 1.0041$). Population growth rate in El Tigre fluctuated more with year-type, in accordance with the stronger changes in seedling demography there during the dry year. Elasticity analysis for the normal-year matrices showed that permanence elements in the transition matrices contributed most to population growth (Figure 8). Growth and fecundity elements had much lower contributions to λ, growth being more important in the early reproductive categories and fecundity more in late reproductive classes. Low contributions of fecundity elements for λ may indicate that Brazil nut harvesting has a low impact on population growth. Elasticity patterns were similar for both study sites.

Age calculations based on the normal-year matrix models revealed that estimated age at entering the first reproductive category (*12*) equalled 141 (±47, 1 SD) yr for El Tigre and 126 (±51) yr for El Sena (Figure 9). Mean age in the last size category was estimated to be 295 (±83) and 296 (±94) yr, respectively. It should be noted that the standard deviations given for age estimates are based on the variation in the number of time steps needed to

Table 3

Population transition matrices for *Bertholletia excelsa* in two sites in the Bolivian Amazon where Brazil nuts are extracted: El Tigre (a) and El Sena (b), for a normal (N) and a dry (D) year. Columns are category at time *t*; rows at time *t*+1.

a. El Tigre

N	*t*:	*1*	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*	*11*	*12*	*13*	*14*	*15*	*16*	*17*
t+1:	*1*	0.455	0	0	0	0	0	0	0	0	0	0	12.3	14.6	16.9	19.3	22.3	26.6
	2	0.091	0.587	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	3	0	0.147	0.780	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	4	0	0	0.134	0.821	0	0	0	0	0	0	0	0	0	0	0	0	0
	5	0	0	0	0.167	0.941	0	0	0	0	0	0	0	0	0	0	0	0
	6	0	0	0	0	0.044	0.938	0	0	0	0	0	0	0	0	0	0	0
	7	0	0	0	0	0	0.047	0.961	0	0	0	0	0	0	0	0	0	0
	8	0	0	0	0	0	0	0.034	0.946	0	0	0	0	0	0	0	0	0
	9	0	0	0	0	0	0	0	0.049	0.940	0	0	0	0	0	0	0	0
	10	0	0	0	0	0	0	0	0	0.055	0.937	0	0	0	0	0	0	0
	11	0	0	0	0	0	0	0	0	0	0.058	0.936	0	0	0	0	0	0
	12	0	0	0	0	0	0	0	0	0	0	0.059	0.966	0	0	0	0	0
	13	0	0	0	0	0	0	0	0	0	0	0	0.029	0.968	0	0	0	0
	14	0	0	0	0	0	0	0	0	0	0	0	0	0.027	0.971	0	0	0
	15	0	0	0	0	0	0	0	0	0	0	0	0	0	0.024	0.965	0	0
	16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.020	0.967	0
	17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.018	0.985
D	*t*:	*1*	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*	*11*	*12*	*13*	*14*	*15*	*16*	*17*
t+1:	*1*	0.411	0	0	0	0	0	0	0	0	0	0	3.2	3.8	4.4	5.0	5.8	6.9
	2	0.028	0.560	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	3	0	0.057	0.772	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	4	0	0	0.065	0.873	0	0	0	0	0	0	0	0	0	0	0	0	0
	5	0	0	0	0.095	0.941	0	0	0	0	0	0	0	0	0	0	0	0
	6	0	0	0	0	0.044	0.938	0	0	0	0	0	0	0	0	0	0	0
	7	0	0	0	0	0	0.047	0.961	0	0	0	0	0	0	0	0	0	0
	8	0	0	0	0	0	0	0.034	0.946	0	0	0	0	0	0	0	0	0
	9	0	0	0	0	0	0	0	0.049	0.940	0	0	0	0	0	0	0	0
	10	0	0	0	0	0	0	0	0	0.055	0.937	0	0	0	0	0	0	0
	11	0	0	0	0	0	0	0	0	0	0.058	0.936	0	0	0	0	0	0
	12	0	0	0	0	0	0	0	0	0	0	0.059	0.966	0	0	0	0	0
	13	0	0	0	0	0	0	0	0	0	0	0	0.029	0.968	0	0	0	0
	14	0	0	0	0	0	0	0	0	0	0	0	0	0.027	0.971	0	0	0
	15	0	0	0	0	0	0	0	0	0	0	0	0	0	0.024	0.965	0	0
	16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.020	0.967	0
	17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.018	0.985

b. El Sena

N	*t*:	*1*	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*	*11*	*12*	*13*	*14*	*15*	*16*	*17*
t+1:	*1*	0.455	0	0	0	0	0	0	0	0	0	0	3.6	4.3	5.0	5.7	6.6	7.9
	2	0.091	0.587	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	3	0	0.147	0.780	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	4	0	0	0.134	0.821	0	0	0	0	0	0	0	0	0	0	0	0	0
	5	0	0	0	0.167	0.975	0	0	0	0	0	0	0	0	0	0	0	0
	6	0	0	0	0	0.010	0.957	0	0	0	0	0	0	0	0	0	0	0
	7	0	0	0	0	0	0.028	0.948	0	0	0	0	0	0	0	0	0	0
	8	0	0	0	0	0	0	0.047	0.886	0	0	0	0	0	0	0	0	0
	9	0	0	0	0	0	0	0	0.109	0.848	0	0	0	0	0	0	0	0
	10	0	0	0	0	0	0	0	0	0.147	0.838	0	0	0	0	0	0	0
	11	0	0	0	0	0	0	0	0	0	0.157	0.852	0	0	0	0	0	0
	12	0	0	0	0	0	0	0	0	0	0	0.143	0.942	0	0	0	0	0
	13	0	0	0	0	0	0	0	0	0	0	0	0.053	0.963	0	0	0	0
	14	0	0	0	0	0	0	0	0	0	0	0	0	0.032	0.976	0	0	0
	15	0	0	0	0	0	0	0	0	0	0	0	0	0	0.019	0.974	0	0
	16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.011	0.978	0
	17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.007	0.985
D	*t*:	*1*	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*	*11*	*12*	*13*	*14*	*15*	*16*	*17*
t+1:	*1*	0.660	0	0	0	0	0	0	0	0	0	0	1.7	2.0	2.3	2.6	3.0	3.6
	2	0.044	0.753	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	3	0	0.077	0.867	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	4	0	0	0.073	0.892	0	0	0	0	0	0	0	0	0	0	0	0	0
	5	0	0	0	0.097	0.975	0	0	0	0	0	0	0	0	0	0	0	0
	6	0	0	0	0	0.010	0.957	0	0	0	0	0	0	0	0	0	0	0
	7	0	0	0	0	0	0.028	0.948	0	0	0	0	0	0	0	0	0	0
	8	0	0	0	0	0	0	0.047	0.886	0	0	0	0	0	0	0	0	0
	9	0	0	0	0	0	0	0	0.109	0.848	0	0	0	0	0	0	0	0
	10	0	0	0	0	0	0	0	0	0.147	0.838	0	0	0	0	0	0	0
	11	0	0	0	0	0	0	0	0	0	0.157	0.852	0	0	0	0	0	0
	12	0	0	0	0	0	0	0	0	0	0	0.143	0.942	0	0	0	0	0
	13	0	0	0	0	0	0	0	0	0	0	0	0.053	0.963	0	0	0	0
	14	0	0	0	0	0	0	0	0	0	0	0	0	0.032	0.976	0	0	0
	15	0	0	0	0	0	0	0	0	0	0	0	0	0	0.019	0.974	0	0
	16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.011	0.978	0
	17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.007	0.985

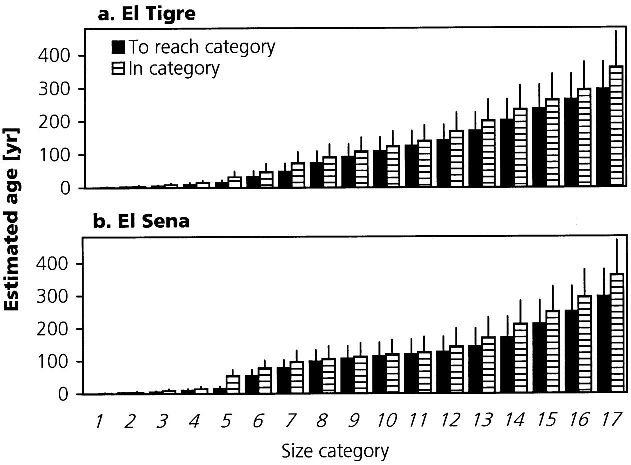


Figure 9
Ages estimates based on matrix population models of *Bertholletia excelsa* in two sites in the Bolivian Amazon: El Tigre (a) and El Sena (b).
Shown are the mean (± 1 SD) age conditional on reaching a category and the mean age of residence (± 1 SD) in a category (τ and *S*, respectively, in Cochran & Ellner 1992).

reach a certain category, and do not include among-individuals variation in vital rates (Cochran & Ellner 1992).

Time-varying stochastic matrix models yielded mean population growth rates (log(λ_s)) intermediary between log-transformed population growth rates (λ) for normal and dry year matrix models: 0.0141 (SD=0.1381) for El Tigre and 0.0064 (SD=0.0206) for El Sena. Population growth varied considerably, especially for El Tigre where demography was more strongly affected in the dry year. For both study sites, the value zero was included in the interval mean ±1 SD of the stochastic growth rates, indicating that, given a dry-year frequency (π) of 0.12 and when considered over a long period, population sizes are likely to be stable.

Stable stage distributions generated by matrix models resembled the observed population structure in the study plots well, though not very closely (Figure 1). The 'hump' in the size distribution, *i.e.* the higher density of trees in categories *12-16* compared to those in *7-11*, was also obtained in the stable stage distributions, being more pronounced for El Sena than for El Tigre. Differences between stable stage distributions resulting from standard matrix models and from stochastic time-varying models were generally small and more pronounced in seedling categories that were most affected by the dry year.

Discussion

Regeneration in exploited populations

A very high proportion (on average 93%) of the total seed production is collected from the two exploited *Bertholletia* populations under investigation.

Although this value may vary with total pod production, price paid to collectors and number of collectors working in the area, it was rather constant over three years and two sites. Of the pods left by Brazil nut collectors, almost half are not opened by agoutis at all, and only a small fraction is opened shortly after pod fall (Figure 4). The majority of pods that are gnawed open by agoutis are 1-2 yr old. Agoutis may leave pods on the forest floor in order to reduce energetic costs to open the pods, since the pod's woody pericarp gradually softens. However, the risk of this 'waiting attitude' is that a large proportion of seeds in 1-2 yr old pods are infected by fungi or have completely rotten. Thus, a trade-off may exist for agouti's between the costs to release seeds and seed quality, resulting in a time-window for seed release and dispersal, perhaps around one year after seed fall. Clearly, additional studies on seed dispersal are needed to confirm this hypothesis.

The difference in spatial distribution of pods opened by agoutis and those not opened (Figure 5) suggests that agoutis may transport part of the pods before opening them and scatterhoarding the seeds. This behaviour is confirmed by seed dispersal studies in Peru (Ortiz 1995). In seed predation experiments, agoutis scatterhoard *Bertholletia* seeds at a maximum distance of 20-40 m from seed deposits (Peres & Baider 1997, Peres *et al.* 1997, Bouwman & van Dijk 1999), although the majority is found at much shorter distances.

Pods left by Brazil nut collectors and new seedlings differed greatly in their spatial distribution, the former being highly clumped around parent trees and the latter randomly dispersed. The more diffuse dispersion pattern in seedlings may be the result of primary (and secondary) dispersal (*cf.* Hamill & Wright 1986, Peres & Baider 1997), a higher removal rate of cached seeds close to adult trees (*cf.* Howe & Smallwood 1982, Peres *et al.* 1997), more cotyledon predation of recently emerged seedlings at high density or close to adult trees (as cotyledons become part of the stem, cotyledon predation fills the individual; *cf.* Howe & Smallwood 1982, Oliveira 2000), and spatial variation in light conditions. 'Seeding' of *Bertholletia* by Brazil nut collectors may also have contributed to the observed difference in spatial distribution of pods and seedlings. Seeding activity has been suggested as an important contribution to tree regeneration (Ortiz 1995), but field evidence has not been obtained from this and other studies.

Bertholletia seedling dynamics were characterised by high rates of recruitment and mortality. For example, in '98 new seedlings accounted for 68% of the seedlings in category *1* in El Tigre, but 65% of these seedlings died within one (dry) year. High turnover rate in seedlings and strong influence of climatic circumstances cause seedling abundance to vary greatly in time, implying that seedling abundance alone is an unreliable indicator for

Bertholletia regeneration potential, although this is sometimes taken as such (Mostacedo & Fredericksen 1999).

Bertholletia demography

The demography of *Bertholletia* is characterised by a highly variable growth rate for seedlings to medium-sized (DBH <50 cm) trees. The variability in growth is partly explained by variation in light availability, which is high for saplings and medium-sized trees (Table 1, Viana *et al.* 1998). Maximum seedling and sapling height growth observed in this study often exceeded 40 cm yr^{-1} and is comparable to values obtained for *Bertholletia* seedling under experimental high light conditions (Poorter 1999) and in abandoned agricultural fields (Kainer *et al.* 1998, M.Peña-Claros *personal communication*). The maximum DBH growth rates found here (>2 cm yr^{-1} in El Sena; >1.5 cm yr^{-1} in El Tigre) are remarkably high compared to other neotropical non-pioneer tree species (Lieberman *et al.* 1985, Korning & Balslev 1994, Clark & Clark 1999). Plasticity in growth and a high maximum growth rate are important traits for an adequate response to increased light availability, necessary to compete with neighbouring plants when a treefall gap is formed (Denslow 1987). These demographic characteristics place *Bertholletia* in the least shade-tolerant portion of the continuum of climax (non-pioneer) tree species (Whitmore 1989), and support its classification as a gap-dependent (Mori & Prance 1990) or light-demanding (Salomao 1991, Kainer *et al.* 1999) species. Results from a gap inventory in one of the study sites (El Tigre) confirm *Bertholletia*'s gap-dependence: Myers *et al.* (2000) found that sapling (height >130 cm) density increased with gap area and light availability whereas seedling abundance was indifferent to these factors.

Bertholletia demography is furthermore characterised by a long life span: large trees (>160 cm DBH) may age over three centuries and age at entering the first reproductive category (60-80 cm DBH) is more than 120 yr, according to the estimates based on our transition matrices (Figure 9). Trees in the most abundant adult size categories in the study sites averaged an estimated 200 yr. These ages are much higher than those reported for fully reproductive *Bertholletia* trees in plantations, which range from 11 (grafted) to 30 yr (Mori & Prance 1990 and references therein). The matrix-based age estimates (Figure 9) used here should be interpreted with some care as they use two simplifying characteristics intrinsic to matrix models. Firstly, they use average values for vital rates (survival, growth and reproduction) and cannot cope with variation in these parameters. This simplification may generate somewhat higher age estimates in case population maintenance is dependent on individuals with above-average growth to reach the canopy. Secondly, in matrix models individuals 'forget their past', *i.e.* performance of an individual is not autocorrelated in time, causing slow-growing individuals to be able to abruptly speed up and jump to successive categories in short time. Similarly, matrix models also allow individuals to have biologically impossible life histories, *e.g.* completing their entire life cycle in as few time steps as there are categories or to stay in one category for 100 yr (when stasis probability equals 0.95, about $(0.95)^{100} \cong 0.5\%$ of individuals stay for 100 yr in that category). These unrealistic life histories increase the variation in age estimates (Zagt 1997) and are especially important for categories with high stasis probability (Boucher 1997). Nonetheless, *Bertholletia* life span is undoubtedly very long, as adult stature is large and adult growth rate is typically low (≤ 0.5 cm yr^{-1}). Our age estimates are supported by the only ^{14}C-dated *Bertholletia* individual (Camargo *et al.* 1994). This tree of 225 cm DBH was estimated to be 440 ± 60 yr (mean ± 1 SD), suggesting a life-long DBH growth of 0.6 cm yr^{-1} for this trees. When applying this rate to the midpoints of size categories with reproductive trees, comparable ages are found (117 and 292 yr for trees of 70 and 170 cm DBH, respectively). Clearly, many more individuals should be ^{14}C-dated to determine age distributions of different-sized *Bertholletia* trees. Furthermore, to obtain insight in the influence of growth rates on age of adult trees, individual-based growth simulations may be applied (Lieberman & Lieberman 1985, Lieberman *et al.* 1985, Zagt 1997, Martinez-Ramos & Alvarez-Buylla 1998). However, such growth simulations require larger sample sizes than available here to yield reliable results, especially in the low-abundant size categories which show the largest growth plasticity and are most responsive to increased light availability.

The commonly observed higher abundance of certain adult classes in size distributions of *Bertholletia* populations, has been interpreted as the result of past Amerindian cultivation of the species (Clay 1997) or of large-scale disturbances necessary for regeneration (Mori & Prance 1990, Peres & Baider 1997). The low abundance categories typically found in *Bertholletia* populations (Pires 1984, DHV 1993, van Rijsoort *et al.* 1993, Salomao 1991, Peres & Baider 1997, Viana *et al.* 1998, Figure 1), coincide with the peak in DBH growth for trees of 30-60 cm DBH (Figure 7). Similarly, the typical 'hump' of adult trees in *Bertholletia* size distributions (references as above) matches with the decreasing growth rate at increasing size for trees >60 cm DBH. Thus, by rapidly growing through certain categories and slowly through others, respectively low and high densities are obtained. The stable stage distributions from our matrix models (Figure 1) show that the typical *Bertholletia* population structure can be generated by size-dependent growth patterns (Caswell 1989a, p.105). The weaker 'hump' in the stable stage distribution for El Tigre is probably the result of the less-pronounced DBH growth curve for this population (Figure 7).

Impact of extraction on future nut production

The impact of nut extraction on future availability of Brazil nuts from natural populations is not easily quantified, as seed removal is not the only effect of exploitation. Apart from extracting nuts, Brazil nut collectors also commonly hunt agoutis and they may act as 'seeders' when dropping harvested Brazil nuts (Ortiz 1995). The latter activity increases possibilities for recruitment, but the extent to which this contributes to *Bertholletia* regeneration is unclear and probably small. Also the effect of lower agouti density on *Bertholletia* regeneration is not known. Furthermore, the reduction in *Bertholletia* seed availability may change seed handling by agoutis (*cf*. Forget 1996). In a seed removal experiment in El Tigre, the proportion of scatterhoarded seeds to consumed seeds (a measure for agouti dispersal activity) decreased with the density at which *Bertholletia* seeds were offered (Bouwman & van Dijk 1999). This implies that the number of scatterhoarded seeds – those that have prospects for germination – is diminished first by the collection of Brazil nuts, and probably furthermore by changes in agouti seed handling.

The complex changes in exploited *Bertholletia* populations make it difficult to carry out simple numeric manipulations of seed production in matrix models to determine demographic consequences of exploitation, as has been conducted for several NTFP products (Peters 1990a & b, Bernal 1998). However, using the demographic information collected in the two exploited *Bertholletia* population studied and the matrix model analyses, the impact of exploitation can be assessed indirectly.

Firstly, elasticity analysis shows that population growth rate in the exploited population is rather insensitive to changes in fecundity in the transition matrix and very sensitive to changes in permanence in size categories (Figure 8). This is typical in long-lives species (Silvertown *et al.* 1993), and would therefore also have been found for an unharvested study population. Due to the low sensitivity for fecundity, simulations of heavy seed harvests resulted in only small reductions in population growth rate (λ) for several tropical tree species (Peters 1990 a&b, Bernal 1998). However, results of such simulations should be interpreted with great care as population growth in these cases strongly depends on the survival probability in the last categories, which is typically high in long-lived trees and therefore is partly responsible for the low reduction in population growth (Zagt 1997).

Secondly, age estimates presented here indicate that *Bertholletia* trees may age over a century before producing a considerable amount of pods (at 60–80 cm DBH), and that the period during which trees are reproductive is long, often amounting to over 150 yr (Figure 9). This implies that it will take very long before changes in production of pods as a result of exploitation can be detected in the number of pods produced.

Thirdly, in exploited populations, recruitment does take place: there is input of new seedlings and individuals of all size categories can be found in exploited populations. Furthermore, matrix models for exploited populations do not predict shifts in population structure over time (Figure 1), as was found for simulations of fruit harvests in other tree species (Peters 1996). We therefore expect that current extraction practices do not lead to future changes in size distribution.

In conclusion, the results of this study suggest that high levels of Brazil nut extraction may be sustained at least for several decades without reducing production potential and that there are good prospects for continued regeneration of exploited populations, which would safeguard productivity for even longer periods.

Acknowledgements

We are very grateful to all members of the fieldwork team: Luis Apaza, Rene Aramayo, Miguel Cuadiay, Nico Divico, James Joffrey, Alejandro Hayashida, Nazareno Martinez, Jeannette van Rijsoort, Thomas Stockman, Saida Ugueto, Corien van Zweden and others. Furthermore we thank Jhon Leigue Gómez for sharing data on pod production in El Tigre and Roderick Zagt for script files to derive age estimates. Wim Dijkman, Marinus Werger and Roderick Zagt gave valuable comments on a draft version of this paper. This study was partly funded by grant BO 009701 from the Netherlands Development Assistance.

*Processed palm hearts from the 'asai' palm (*Euterpe precatoria*).*

Chapter 3

Demographic constraints to sustainable palm heart extraction from a sub-canopy palm in Bolivia

Pieter A. Zuidema & René G.A. Boot

Abstract

Reproductive individuals of the sub-canopy palm *Euterpe precatoria* are cut for the extraction of palm heart. As this harvest practice causes the death of a large individual, exploitation has a potentially large impact on population dynamics and future availability of palm heart. To assess this impact, a two-year demographic study was carried out in an undisturbed population located in a Bolivian non-flooded moist forest. Vital rates (survival, growth and reproduction) were recorded and transition matrix models were constructed. Survival steeply increased from seedlings (50-70%) to small juveniles (>95%). Seedling growth rate was very low and was not related to plant size or seedling light availability. Height growth of stemmed individuals was slow in both small and large individuals, and peaked in intermediate-sized, pre-reproductive individuals. The probability of being reproductive sharply increased with size and amounted to 90% for palms >15 m height. Low mortality risk and slow growth of reproductive palms resulted in a high probability of stasis in the transition matrix. As a result, population growth strongly depended on the survival of reproductive individuals (high elasticity). Precisely these individuals are cut for palm heart. Age estimates showed that reproductive individuals are old, at least more than 70 yr, and on average probably more than 90 yr. Long periods are therefore needed for replacement of exploited individuals from seeds. Both population size and abundance of reproductive individuals were severely reduced in simulations with heavy harvest intensities (75-100%) and short harvesting cycles (4-8 yr). But also the mildest of the 16 simulated harvest regimes (cutting 25% of the reproductive stems every 32 yr) caused the availability of palm heart to decrease continuously when compared to an undisturbed situation. Therefore, it is concluded that the demographic characteristics of the species (single-stemmed, long-lived and slow-growing) probably severely limit the species' potential for sustained commercial exploitation.

Introduction

Non-timber forest products (NTFP) have been presented as an important source of income from tropical forests with a higher potential for sustainable use than timber extraction (Nepstad & Schwartzman 1992, Richards 1993). Whether these products can be repeatedly harvested without depleting the future stock is determined by the impact of extraction on the individual plant and the population, and furthermore by the harvesting intensity. At the level of the individual plant, it is important to consider which plant part is harvested, as this largely determines the impact on individual plant performance. On the one hand, collection of fruits does not damage the individual (*e.g.* Peters *et al.* 1989a, Mori & Prance 1990, Velasquez Runk 1998). The other extreme, felling of complete individuals to collect apical meristems (Peña-Claros & Zuidema 1999) or stem tissue (Olmsted & Alvarez-Buylla 1995, Pinard 1993), causes the death of the individual. Extraction of other plant parts such as leaves (*e.g.* from palms, FAO 1997b), exudates (*e.g.* rubber, Dijkman 1951) or bark may have intermediate impact on plant performance (survival, growth and reproduction), depending on the function of the plant part, the extraction intensity and the harvest frequency. Of further importance is the method of NTFP extraction: intensive cutting of adult individuals of the canopy palm *Mauritia flexuosa* to collect fruits have severely depleted populations and future harvest potential in parts of the Peruvian Amazon (Vasques & Gentry 1989).

Apart from the impact of extraction on individuals, the effect on populations also determines whether NTFP extraction can be sustained in exploitation systems with repeated harvests. Exploitation can be sustained when populations have the ability and opportunity to recover after each harvest, *i.e.* if harvested populations are still viable and if they are left undisturbed for sufficient time to regain pre-harvest size and structure. However, in many instances overharvesting and short recovery periods have depleted populations exploited for NTFP (Vasques & Gentry 1989, Nepstad *et al.* 1992, Hall & Bawa 1993). Economic pressure, unclear responsibility for resource management and overoptimistic judgments on the recovery potential of exploited populations are important causes of resource depletion. But, equally important is the lack of biological information to base guidelines for sound NTFP exploitation. Information on the demography of exploited species and how this is affected by exploitation is essential for assessing the impact on future resource availability (Hall & Bawa 1993), and to determine whether current (or alternative) harvest regimes may be sustained for longer periods.

This chapter reports on a demographic study of the Neotropical sub-canopy palm *Euterpe precatoria*, which is exploited for palm heart - the apical meristem of the palm which is sold as a delicacy. Palm heart extraction involves cutting of reproductive individuals of the species and removing their apical meristems. In contrast to clonal palms exploited for palm heart (*e.g. Euterpe oleracea* and *Bactris gasipaes*; Anderson 1988, Tabora *et al.* 1993, Pollak *et al.* 1995), extracting palm heart from *Euterpe precatoria* causes the death of the genetic individual. Usually about 90% of reproductive individuals are cut. As a consequence, there is a strong impact of exploitation on population dynamics (Peña-Claros 1996). Palm heart extraction from wild *Euterpe* stands in Bolivia has rapidly increased since 1992 (CNF 1999) and there are indications that current extraction practices are limiting the species' regeneration and deplete the future stock (Peña-Claros 1996, Mostacedo & Fredericksen 1999, Peña-Claros & Zuidema 1999). Severe overharvesting has caused local extinction of the single-stemmed sub-canopy palm *Euterpe edulis* in Brazil, a species with similar life history (Galetti & Fernandez 1998).

To assess the impact of palm heart extraction on the demography of *Euterpe precatoria* and the future availability of the resource, we analyze the undisturbed life history of the species in a 2-yr demographic study and simulate the effect of palm heart extraction. First, size-dependent patterns in survival, growth and reproduction are assessed. These vital rates are also related to light availability, as this provides information on the regeneration strategy of the species and may be used to assess the possibility of silvicultural measures. Subsequently, dynamics of an undisturbed population are evaluated using population matrix models (Caswell 1989a). Matrix models are applied as they are a relatively simple and straightforward tool to analyse life history (Silvertown *et al.* 1993), and examine consequences of demographic changes resulting from NTFP extraction (Pinard & Putz 1992, Boot & Gullison 1995). Two population transition matrices are constructed: for a normal and a dry year. Dry years occur frequently in the study region, which is located at the south-western border of the Amazon lowland forest belt, and certain demographic parameters respond strongly to this climatic variation. For a long-lived species as *Euterpe*, coping with such climatic variation in a way that minimises risks for population maintenance is essential. Age estimates of reproductive individuals cut for palm heart are derived as to indicate the period required for replacement of felled individuals from seeds. Finally, transition matrices are used to perform harvest simulations that project the consequences of different harvest regimes on total population size and abundance of exploited (reproductive) individuals.

Study species

Euterpe precatoria Mart. is a Neotropical (sub-)canopy palm species that may attain heights up to 30 m. The species is distributed from Belize and Guatemala in the north to the Bolivian Amazon region in the south (Henderson *et al.* 1995). In Bolivia the species (further referred to by its generic name only) is found in seasonally flooded forests, forest islands in savanna areas and *terra firme* forest (Moraes 1996, Peña-Claros & Zuidema 1999). The density of reproductive individuals varies widely between habitat types: high densities are typically found in inundated forests and forest islands in savanna areas (*e.g.* 260 ha^{-1}, Peña-Claros & Zuidema 1999), whereas individuals in *terra firme* forests occur at lower densities (*e.g.* 23 ha^{-1} in this study).

Recently germinated *Euterpe* seedlings possess pinnate leaves with typically 6-8 leaflets. As individuals become larger, the number of leaflets increases gradually to over 100 for palms of >4 m height to leaf tip. Stems develop in the soil before emerging, and become visible aboveground in individuals with leaf length of more than approximately 1.5 m. In contrast to most palm species, *Euterpe* stems have secondary growth: DBH (diameter at breast height, at 1.3 m) gradually increases from 2 cm for individuals of 1.5 m stem height to 12-18 cm DBH in for individuals over 12 m tall. Most palms at the research site become reproductive when they attain a height of over 17 m, but this value depends on forest canopy height (Peña-Claros & Zuidema 1999).

Euterpe fruits are produced during the dry season (April-June) and may therefore be an important food source during a period of lower fruit and seed availability. Fruits are reported to be consumed and dispersed by mammals (monkeys) and birds (Kahn & de Granville 1992; more species mentioned by Galetti and Aleixo [1998] for the related *E. edulis*), but detailed information on dispersal agents is lacking. As adult individuals of *Euterpe precatoria* have a slender stem and a small crown, felling of these palms does not change forest structure and light level of the remaining individuals.

Palm hearts are collected from natural *Euterpe* stands by collectors who may harvest up to 60 palm hearts per day (Stoian *In press*). Harvested palm hearts are sold (price per palm heart: US$ 0.20-0.50) to processing plants in the region where they are canned and exported. In 1997, an estimated 7.3 million *Euterpe* palm hearts were processed in Northern Bolivia (Stoian, *In press*). At the national level, the export value of palm hearts amounted to US$ 12 million in 1997 and 1998 (CNF 1999), which makes palm hearts the second most important non-timber forest product in Bolivia, after Brazil nuts (from *Bertholletia excelsa*). Recently, trading of palm heart collected from natural stands was reduced due to low price level at the world market.

Methodology

Study area

This study was carried out in the forest reserve El Tigre (Beni department, 10°59'S, 65°43'W), located in the northern part of the Bolivian Amazon region. The 830-ha reserve, research and training site of the Programa Manejo de Bosques de la Amazonia Boliviana, is largely covered with primary forest but also contains patches of secondary forests in different successional stages. *Euterpe* occurs throughout the primary forest area at similar densities.

Forests in the study region can be classified as (semi)evergreen tropical lowland moist forests (DHV 1993). Mean annual precipitation amounts to 1703 mm in Riberalta (average over period 1948-1998), 40 km west of the forest reserve. Rainfall is unevenly distributed over the year, with a dry period from May to September with <100 mm rain per month (total dry period rain ± 1 SD: 203 ± 73 mm) and a wet season from December to March with precipitation exceeding 240 mm mo^{-1} (1037 ± 234 mm).

During the study period, rainfall in the second measurement year was very low during both wet (Dec '97 - Mar '98: 874 mm) and dry (May '98 - Sep '98: 94 mm) season. The subsequent occurrence of two drier-than-normal seasons caused the 12-mo moving average precipitation to drop below 100 mm mo^{-1} which is considerably lower than the average value over the period 1948-1998 (143 mm mo^{-1}). Moving average values below 100 mm mo^{-1} were also observed in other years with very low rainfall in both wet and dry season (1956, '63, '69, '83 and '85). The frequency of dry years during the period 1948-1998 therefore amounted to 0.12 (=6/50). Three out of these six drier years coincided with El Niño Southern Oscillation episodes (ENSO; warm episodes), but no overall difference in monthly precipitation was found during ENSO episodes (results not shown; *cf*. Ropelewski and Halpert 1996).

Study design

The study site was located in an area where no *Euterpe* palm heart extraction had occurred (no signs of cut adult palms). One 6-ha plot was used for the study, located on flat terrain, in *terra firme* forest with a canopy height of 25-30 m. At initial field evaluation, all individuals of which the youngest unfolded leaf had a leaf length (*i.e.* distance from soil surface to leaf tip) of >2 m were located relative to a grid of 25 × 25 m, measured and tagged. Smaller individuals were measured and tagged with colored plastic strings in subplots (25 × 25 m): all individuals with leaf length of <2 m in two randomly selected subplots per ha, and individuals of 0.25-2 m leaf length in two additional subplots per ha.

Field measurements

Euterpe individuals included in the study were measured in the period January-March in 1997, 1998 and 1999. Depending on the size of the individual, different measurements were carried out. For stemmed individuals <14 m (stem height), stem height (up to base of youngest leaf) was measured to the nearest 0.1 m, using a telescopic fiberglass rod. Above 14 m, stem height was visually estimated to the nearest m. For small individuals (<4 m stem height) the following parameters were determined for the youngest completely expanded leaf: leaf length (from forest floor to leaf tip) and leaf blade length (both to the nearest cm).

Leaf number was counted for individuals of all sizes. Leaf production was calculated in two ways: by direct observations and by indirect calculation. Direct counts of leaf production were carried out for individuals up to 10 m stem height, by painting the petiole of the youngest leaf at each field evaluation. Indirect estimation of leaf production was done for individuals >10 m for which leaves could not be marked. All living and dead leaves on the palm or stuck in the canopy were counted and all leaves on the forest floor were marked with paint. After one yr, these counts were repeated and the number of new fallen leaves on the forest floor was counted as well. The number of leaves produced was then determined as the difference in total leaf number (dead or alive) between the first and second evaluation plus the number of new fallen leaves on the forest floor. These calculations were only carried out for reproductive individuals, as their leaves possess a thick petiole base that does not disintegrate within one year.

The light environment of all measured individuals was characterized at initial measurement using a modified Dawkins illumination score (Dawkins & Field 1978, Clark & Clark 1992, Zagt 1997). The scores were: 1 (no direct lateral or overhead light), 2L (little direct lateral light, no overhead light), 2M (some direct lateral light, no overhead light), 2H (substantial direct lateral light, no overhead light), 3 (some overhead direct light), 4 (full overhead direct light; in canopy) and 5 (full overhead and lateral direct light; emergent). Although subjective, this parameter has successfully explained patterns of growth and survival for several tropical tree species (Clark & Clark 1992, Zagt 1997). Dawkins scores used for the analysis were always estimated by the first author.

Reproduction of *Euterpe* individuals was assessed from the way in which leaves are positioned: leaves of a reproductive individual are positioned close to each others along the stem (with overlapping petiole bases), whereas those of juvenile palms are located at some distance of each others. Racemes bearing fruits were counted at initial measurement. The number of new seedlings in the population was recorded at second and third field measurement in two subplots per ha that were also used for seedling inventories.

For individuals of which stem height could not be measured (>14 m), height growth was calculated by multiplying annual leaf production rate and internode length. As it is not possible to climb the slender *Euterpe* stems, data on internode length were obtained from individuals that had been cut or had died naturally. Internode lengths were measured on stems of 32 adult individuals (with a total height ranging from 14 to 22 m) in climax forest similar to that of the study plots. Length of all internodes from a height of 2 m till the base of the lowest leaf were measured and averaged per 1-m interval over all individuals.

Data analysis

As climatic conditions differed between the first and second measurement year, vital rates (survival, growth and reproduction) were first tested for differences between years. When significant differences were found between years (this was the case for height growth), year-based values were used in further testing and construction of transition matrices; when no difference was found (for leaf blade growth and survival), average values over two years were used. Size-dependent patterns in vital rates were evaluated using regression analysis. To determine whether, in addition to size, light level also had an influence on vital rates, Dawkins illumination scores were entered as dummy variables into these regression models.

Stem height growth was non-linearly related to height, with lower values for short and tall individuals and higher height growth at intermediate sizes. To describe this pattern, the Hossfeld IV function was fitted through the data, using non-linear regression with a least-squares loss function (Zeide 1993):

$$g(h) = \frac{b + c + h^{(c-1)}}{\left[b + (h^{c}/a)\right]^{2}} \tag{1}$$

where $g(h)$ is the annual growth rate (m yr^{-1}) for an individual of stem height h (m) and a, b and c are fitted parameters. For $g(h)$ only height growth rate measured (for individuals <14 m) and calculated using leaf production rate were included.

Size-dependent survival of stemmed individuals was assessed using the product of two logistic regression equations, which allows higher mortality for both small and large individuals (Model V in Huisman *et al.* 1993):

$$\sigma(h) = \frac{1}{1 + e^{a+bh}} \times \frac{1}{1 + e^{c+dh}}, \tag{2}$$

where $\sigma(h)$ is the annual survival probability of an individual of height h (m); and a, b, c and d are parameters to be estimated with b and d having opposite signs.

Determining size categories

Eleven size categories were identified, based on a combination of biological criteria that maximize differences in vital rates among categories and considerations of sample size (*cf.* Vandermeer 1978, Moloney 1986; Table 1). Furthermore, category limits were chosen in a way that doubled the height range of each successive category (up to 10 m).

Category limits for small stemless individuals (categories *1-4*) were determined by leaf length, doubling the height for each successive category. Transition probabilities for these categories were not based on this parameter, though, as no correlation was found between growth in leaf length and initial leaf length. Such a correlation, though not strong, was found for leaf blade length (growth in two yr and initial size: Spearman's r=0.17, p<0.01, n=248). Category limits based on leaf length were therefore converted to leaf blade length, and individuals in categories *1-4* were classified by leaf blade length.

For stemmed individuals (categories *5-11*), stem height was used as classifying parameter, using categories with doubling height up to 10 m and 5-m categories for larger individuals. Almost all reproductive individuals were contained in the two last categories (*10* and *11*).

Transition matrix construction

Stage-based population matrix models (Lefkovitch 1965) were used to project population size and structure for an undisturbed population and to simulate different harvest regimes. These models use the equation:

$$\mathbf{n}(t + 1) = \mathbf{A}\ \mathbf{n}(t) \tag{3}$$

where $\mathbf{n}(t)$ and $\mathbf{n}(t+1)$ are column vectors containing the population structure at time t and $t+1$, respectively, and $\mathbf{A}$ is a square matrix containing transition probabilities among categories during one time-step. The asymptotic growth rate of the population is given by the dominant eigenvalue (λ) of matrix $\mathbf{A}$, and the stable stage structure of the population can be shown to be the right eigenvector w of matrix $\mathbf{A}$ (Caswell 1989a). Elements a_{ij} of the $\mathbf{A}$ can be grouped according to their position in the matrix: stasis elements (P) represent the probability of remaining in the same category (elements in diagonal of matrix); growth elements (G) represent an individual's probability to pass from one category to the next (sub-diagonal); retrogression elements (R) represent the probability of returning to the previous category (above diagonal) and fecundity elements (F) represent the number of offspring produced by an individual in a certain category (elements in upper row, only for categories containing reproductive individuals).

As several vital rates were considerably lower in the dry second measurement year (see *Results*: *Differences between years*), two annual transition matrices were constructed, one for a normal year (**N**) and one for a dry year (**D**). Transition matrices only differed for those vital rates that were significantly different between years; otherwise the 2-yr average was used.

Transition probabilities were calculated using the different vital rates (survival, growth and reproduction), except for the first two categories. For these categories observed transition frequencies were used. In the first category, growth in leaf blade length could not be determined accurately due to the small size of the individuals. In the second category, observed frequencies were used because many plants (36% in first yr and 48% in second yr) had a negative growth rate; individuals in this category could thus either continue to the third or retrogress to the first category. Using the average value for growth rate does not allow to include both progression and retrogression in the transition matrix.

For categories *3-11* calculated transition probabilities were preferred as these depend less on the number and distribution of individuals within a category than observed transitions. Furthermore, they can be based on regression equations that relate a vital rate to plant size over a wide size range. In case no size-dependent relation was found, the average value was used over all categories involved. The value for the growth transition (G) of category i was calculated as $G_i = \sigma_i \times g_i \times c_{\mathrm{i-1}}$, where σ_i is the survival probability in that category, g_i the growth rate and c_i the category width. The values of the latter two variables were based on leaf blade length for categories *3-4*, and on stem height for *5-10*. The size midpoint of a category was used to determine the value of g_i from a linear regression or from the Hossfeld IV equation (Eq. 1). Stasis elements (P) were then determined as $P_i = \sigma_i - G_i$. Fecundity (F) elements were calculated as $F_i = \sigma_i \times Pr\{\mathrm{rep}\}_i \times f$, where $Pr\{\mathrm{rep}\}_i$ is the probability that an individual in category i is reproductive and f the number of offspring produced by one reproductive individual. As *Euterpe* seeds germinate within one year, f is expressed as the number of newly emerged seedlings at the end of the measurement year per reproductive individual. The value of f was determined as the quotient of the density of newly recruited seedlings and reproductive individuals, thus without knowledge on which adult tree has produced which seedling.

Population matrix analyses

The transition matrices for a normal and a dry year were combined in a time-varying matrix model to obtain projections of population size over sequences of normal and dry years. A periodic matrix model was used for this purpose (Caswell 1989a), using a fixed sequence of normal and dry years with the frequency of dry years equaling 1/8 (based on long-term precipitation records; see *Methodology*: *Study area*). The periodic model used is of the form:

$$\mathbf{n}(t+8) = \mathbf{D}\ \mathbf{N}^7\ \mathbf{n}(t) \tag{4}$$

where $\mathbf{n}(t)$ and $\mathbf{n}(t+8)$ are population structure at time t and $t+8$, and $\mathbf{N}$ and $\mathbf{D}$ are the transition matrices for a normal and a dry year, respectively.

Population growth rates (λ) were calculated for both year-based and periodic models. The observed population structure was compared with the stable stage structure for the normal year matrix only, as in periodic matrix models the right eigenvector of the product matrix is cyclic (Caswell 1989a). Elasticity analysis (de Kroon *et al.* 1986) was carried out for the normal year model to determine the contribution of different size categories and different types of matrix elements to the population growth. In addition, elasticities were calculated for the vital rates (survival, growth and reproduction), *i.e.* parameters underlying the matrix elements, using the approach of Caswell (1989a, p. 135). Third, elasticity analysis was carried out for the periodic model in Eq. 4, to determine the effect on long-term population growth of changes in demographic rates during the periodic cycle of year-types. Using the approach of Caswell and Trevisan (1994), elasticities were calculated for each of the eight matrices included in Eq. 4.

Harvest simulations were carried out with different harvest intensities (cutting 25, 50, 75 and 100% of the reproductive individuals) and different harvest cycle length (allowing recuperation for 32, 16, 8 and 4 yr). Palm heart harvests were simulated by reducing the number of reproductive individuals in the population vector, according to the harvest intensity and the proportion of reproductive individuals in the category. It was assumed that cutting of adult palms does not alter the dynamics of the remaining population. As *Euterpe* individuals possess a small crown and a slender stem, and adult densities are relatively low (around 25 ha^{-1}), an increase light conditions (due to the creation of canopy gaps) or mortality of smaller individuals (due to felling damage) is not expected.

Harvest simulations were only applied to categories *10* and *11* as the proportion of reproductive individuals in category *9* is very low. The reduction in density was applied to the population vector before that vector was multiplied with the transition matrix:

$$\mathbf{n}(t+1) = \mathbf{N}\ [\ \mathbf{n}(t) - q\mathbf{r}\ ] \tag{5}$$

where q is the harvest intensity and $\mathbf{r}$ is a vector containing the proportion of reproductive individuals for all categories (0 for categories *1-9* , 0.69 for *10* and 1.00 for *11*). Harvest regimes were applied to the sequence of normal and dry years in Eq. 4. Simulations always started with a harvest, which was then repeated every 4, 8, 16 or 32 yr, for a period of 240 yr. Dry year transition matrices (**D**) were used at yr 8,16, 24, etc. The impact of harvest regimes was assessed both for total population size and for the abundance of reproductive individuals.

Results

Size-dependent patterns in vital rates

Survival, growth, and reproduction varied widely over the whole size range of individuals included in the study (Table 1). Survival steeply increased from category *1* to *3*, and remained rather stable over the remaining size range. Growth rates were highly variable in categories *2-4* without showing a clear pattern. In larger individuals, on the other hand, growth initially increased with size up to category *9* and then diminished sharply to very low values in the main reproductive categories (*10* and *11*). Leaf production increased over the complete size range of the species: for '97-'98 it varied from 1.0 leaves yr^{-1} in category *1* to a maximum of 2.4 in category *8* for directly determined leaf production and 3.1 in category *11* for indirectly determined production. The proportion of reproductive individuals steeply increased with stem height, amounting to 3% in category *9*, 79% in *10* and 98% in *11*.

Regression analysis revealed strong size dependence of some vital rates and absence of size-effects in others (Table 2). In small individuals that were categorized by leaf blade length (*1-4*), plant size expressed as leaf blade length positively influenced survival probability, whereas growth rate was not influenced by size.

In larger individuals (categories *5-11*), measured height growth, leaf production rate and probability of being reproductive increased with palm height (Table 2). For directly observed leaf production, palm height explained a substantial part of the variation, but for indirectly calculated leaf production rates, variation was large and the influence of height was very small or absent. The probability of reproduction increased steeply with stem height starting at a height of approximately 10 m. In contrast, the number of fruiting racemes was not related to plant size.

Table 1
Classification criteria and category characteristics for a population of *Euterpeprecatoria*. Symbols used: σ is survival, *g* is growth (and SD; growth in leaf blade length for categories *1-4* and in stem height for *5-11*), *Pr*{rep} is proportion of individuals that is reproductive, and *n* denotes initial

Cat.	Blade length [cm]	Stem height [m]	Dawkins illumination score 1	2L	2M	2H [%]	3	4	5
1	≤ 2		72	24	4	1	-	-	-
2	≤ 19		36	56	8	-	-	-	-
3	≤ 44		28	66	6	-	-	-	-
4	≤ 94		15	70	13	3	-	-	-
5	> 94	≤ 1.25	5	50	33	12	-	-	
6		≤ 2.5	3	20	57	20	-	-	-
7		≤ 5	-	21	53	19	6	-	-
8		≤ 10	-	1	11	39	47	2	-
9		≤ 15	-	-	3	9	64	22	2
10		≤ 20	-	-	-	-	25	69	6
11		> 20	-	-	-	-	2	89	8

Table 2
Effect of plant size and light availability on several vital rates of *Euterpe precatoria* for individuals classified by leaf blade length (categories *1-4*; in cm) and stem height (*5-11*; in m). Multiple linear regression analysis was used for growth and leaf production, logistic regression for survival (categories *1-4*) and reproduction (with R^2 *sensu* Nagelkerke [1991]), and a double logistic equation (Eq. 2) for survival in categories *5-11*. Shown are the coefficient of determination (between parentheses the value for the regression model without Dawkins scores); value of the constant; regression coefficients and significance indications (-: not tested, ns: *p*(0.05, *: *p*<0.05, **: *p*<0.01, *: *p*<0.001) for plant size and Dawkins score; and sample size. The influence of light availability**

Cat.	Parameter		Period	R^2		Constant	Size	
1-4	Survival	[yr^{-1}]	'97-98	0.15	(0.12)	0.96	0.05	*
			'98-99	0.12	(0.12)	0.89	0.04	**
	Leaf blade growth	[cm yr^{-1}]	'97-99	ns	(ns)			
	Leaf production - direct	[yr^{-1}]	'97-98	0.08	(ns)	0.99	ns	
			'98-99	ns	(ns)	179		
5-11	Survival	[yr^{-1}]	'97-99	ns	(ns)			
	Stem height growth[1]	[m yr^{-1}]	'97-98	0.51	(0.42)	0.02	0.04	***
			'98-99	0.29	(0.26)	0.01	0.02	**
	Leaf production - direct	[yr^{-1}]	'97-98	0.47	(0.33)	1.04	0.08	**
			'98-99	0.38	(0.37)	1.03	0.11	***
	Leaf production - indirect	[yr^{-1}]	'97-98	0.08	(0.06)	-0.78	0.16	*
			'98-99	ns	(ns)			
	Reproductive status		'97	0.85	(0.79)	-15.4	0.84	***
	# Racemes with fruits		'97	0.04	(ns)	0.6	ns	

[1] Only includes measured stem height growth.

Table 1 (continued)

sample size (sample sizes used to determine growth rates may be lower). Note that vital rates are category means and are in most cases not used for construction of transition matrices.

Cat.	σ	*g*		*Pr*{rep}	*n*
	'97-99	'97-'98	'98-'99	'97	
	[yr^{-1}]	[cm yr^{-1}]	[cm yr^{-1}]		
1	0.722^1				*158*
2	0.906	0.9 (2.8)^2			*50*
3	0.968	2.4 (3.9)^2			*32*
4	0.962	0.4 (6.1)^2			*40*
5	0.959	8 (8)	5 (6)	0.00	*87*
6	0.913	23 (17)	11 (12)	0.00	*30*
7	0.968	32 (23)	20 (15)	0.00	*47*
8	0.950	53 (35)	29 (30)	0.00	*102*
9	0.991	64 (42)	38 (39)	0.03	*58*
10	0.956	8 (12)	16 (13)	0.79	*81*
11	0.951	5 (5)	7 (5)	0.98	*83*

^{1} this is the '97-'98 value; 0.489 for '98-'99; ^{2} these are values for '97-'99

Table 2 (continued)

was tested by adding each Dawkins illumination score (except for a reference score) as a dummy variables to the regression model. The reference Dawkins scores were 1 for parameters in categories *1-4*; 3 for reproductive status, number of reproductive structures and indirect leaf production; and 2L for the remaining parameters in categories *5-11*. Although Dawkins score and palm height are correlated, there was no problem of collinearity in the regression models in which both variables were use. Regressions for variables related to reproduction only includes individuals >10 m stem height; that of the number of racemes, only reproductive individuals.

Cat.	Parameter		Dawkins illumination score '97						*n*
			2L	2M	2H	3	4	5	
1-4	Survival	[yr^{-1}]	0.8 *	ns	-	-	-	-	*269*
			ns	ns	-	-	-	-	*228*
	Leaf blade growth	[cm yr^{-1}]							*248*
	Leaf production - direct	[yr^{-1}]	0.2 *	0.6 ***	-	-	-	-	*219*
									179
5-11	Survival	[yr^{-1}]							*505*
	Stem height growth		-	0.1 *	ns	0.4 ***	0.4 **	-	*233*
			-	ns	ns	0.3 **	0.4 *	-	*225*
	Leaf production - direct	[yr^{-1}]	-	ns	0.5 **	1.5 ***	ns	-	*213*
			-	ns	ns	ns	ns	-	*220*
	Leaf production - indirect	[yr^{-1}]	-	-	-	-	ns	2.5 *	*106*
									104
	Reproductive status		-	-	-	-	2.3 ***	ns	*219*
	# Racemes with fruits		-	-	-	-	0.8 *	0.8 **	*141*

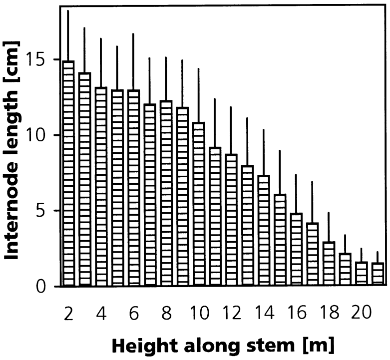


Figure 1
Relation between internode length (average and 1 SD) and height along stems (lower boundary of 1-m interval) in individuals of *Euterpe precatoria*. Sample size is 32 individuals for 2-14 m height, and 31, 30, 25, 21, 16, 12, 6 and 3 for subsequent 1-m intervals.

Internode length decreased strongly with height along the stem (Figure 1; Pearson correlation of height and mean internode length: r=-0.987; p<0.001; n=20): mean internode length was 14.9 cm at 2-3 m height and only 1.4 cm at 21-22 m. Combined, the size-dependent patterns of leaf production rate (generally increasing) and internode length (generally decreasing) resulted in the size-dependent growth pattern with highest rates at intermediate size (Figure 2). This pattern was conveniently described using the Hossfeld IV relation (Eq. 1).

Effect of light level

Dawkins illumination scores increased with size category (non-parametric correlation: Gamma statistic = 0.93, p<0.001, n=746), but variation in light condition was substantial as in all size categories, individuals were assigned at least three Dawkins scores (Table 1). Reproduction was strongly associated with Dawkins illumination score (correlation: Gamma=0.99, p<0.001, n=469): all reproductive individuals were assigned a score of 3 or higher. Also, a higher light level increased the probability of being reproductive in equal-sized palms, and the number of fruiting racemes (Table 2).

Furthermore, light availability explained part of the variation in growth that was not accounted for by size (Table 2). An increase in Dawkins score for a stemmed individual of a certain size led to elevated rates of height growth and leaf production (Table 2). In smaller individuals (categories *1-4*), the influence of light level on vital rates was less clear as only for the '97-'98 data on leaf production and survival there was an effect of Dawkins score. For these individuals, regression models explained only a small portion of the observed variation in vital rates. The highly variable leaf blade growth was not related to either light or size in regression analysis.

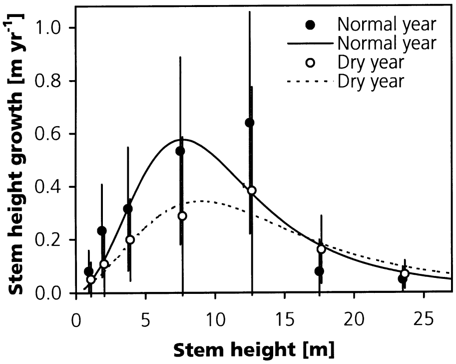


Figure 2
Size-dependent patterns in stem height growth of *Euterpe precatoria*. Shown are fitted Hossfeld IV equations (lines; Eq. 1) and observed growth rates per size category (average and 1 SD; categories *6-11*). Fitted parameters *a*, *b* and *c* equaled 7.52, 73.38 and 2.72, respectively, for the normal year (R^2=0.44, *n*=346) and 6.12, 81.83 and 2.43, respectively, for the dry year (R^2=0.23, *n*=340). Category values for the dry year are slightly shifted for the sake of clarity. The high observed averages for category *9* (at stem height 12.5 m) compared to the fitted line are due to the low sample size for growth rates in this category (above the limit to measure height growth and below reproductive size that allows for indirect determination of leaf production) and the bias towards small individuals with typically higher growth rate.

Differences between years

A number of vital rates differed between measurement years (Table 3). Measured height growth, and directly observed leaf production rate were lower during the dry year ('98-'99). No inter-annual differences were found for growth in leaf blade length, survival probability of individuals in categories *2-11* and size of newly recruited individuals. The largest difference between years was the number of recruits per reproductive individual which decreased

Table 3
Difference in vital rates of *Euterpe precatoria* in a normal ('97-'98) and a dry ('98-'99) measurement year. Averages (SD; geometric mean for recruitment), between-year difference (Dif.) and test results (test value and significance; -: not tested, ns: $p \geq 0.05$, *: $p<0.05$, **: $p<0.01$, ***: $p<0.001$) are shown. Paired t-tests were carried out for continuous parameters and χ^2 test for survival. Survival probability of categories *2-11* was not different between years when tested per category.

Parameter		Average (SD)				Dif.	*t* or χ^2		*n*	
		Normal year		Dry year		[%]			Normal	Dry
Leaf blade growth	[cm yr^{-1}]	1.05	(5.98)	0.99	(6.00)		0.01	ns	*189*	*189*
Stem height growth	[m yr^{-1}]	0.30	(0.32)	0.19	(0.29)	-37	5.55	***	*243*	*243*
Leaf production - direct	[yr^{-1}]	1.47	(0.81)	1.22	(0.66)	-17	6.85	***	*381*	*381*
Leaf production - indirect	[yr^{-1}]	3.09	(3.17)	5.00	(3.61)	+62	-3.51	**	*99*	*99*
Leaf length of recruits	[m]	0.12	(0.04)	0.12	(0.04)		-0.04	ns	*107*	*21*
Survival - category *1*	[yr^{-1}]	0.722		0.489		-32	20.5	***	*158*	*219*
Survival - categories *2-11*	[yr^{-1}]	0.964		0.943			3.59	ns	*610*	*594*
# Recruitment	[adult^{-1}]	5.9		1.2		-80				

Table 4

Transition matrices for a normal (N, '97-'98) and a dry (D, '98-'99) year for a population of *Euterpe precatoria* in forest reserve El Tigre, Beni, Bolivia.

N

Category at *t*:		*1*	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*	*11*
Category	*1*	0.677	0.125	0	0	0	0	0	0	0.15	3.88	5.65
at *t*+1:	*2*	0.044	0.724	0	0	0	0	0	0	0	0	0
	3	0	0.093	0.896	0	0	0	0	0	0	0	0
	4	0	0	0.044	0.919	0	0	0	0	0	0	0
	5	0	0	0	0.022	0.909	0	0	0	0	0	0
	6	0	0	0	0	0.048	0.875	0	0	0	0	0
	7	0	0	0	0	0	0.082	0.836	0	0	0	0
	8	0	0	0	0	0	0	0.121	0.847	0	0	0
	9	0	0	0	0	0	0	0	0.110	0.885	0	0
	10	0	0	0	0	0	0	0	0	0.073	0.923	0
	11	0	0	0	0	0	0	0	0	0	0.034	0.957

D

Category at *t*:		*1*	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*	*11*
Category	*1*	0.475	0.125	0	0	0	0	0	0	0.03	0.79	1.15
at *t*+1:	*2*	0.014	0.724	0	0	0	0	0	0	0	0	0
	3	0	0.093	0.896	0	0	0	0	0	0	0	0
	4	0	0	0.044	0.919	0	0	0	0	0	0	0
	5	0	0	0	0.022	0.918	0	0	0	0	0	0
	6	0	0	0	0	0.039	0.902	0	0	0	0	0
	7	0	0	0	0	0	0.055	0.889	0	0	0	0
	8	0	0	0	0	0	0	0.068	0.894	0	0	0
	9	0	0	0	0	0	0	0	0.063	0.900	0	0
	10	0	0	0	0	0	0	0	0	0.057	0.921	0
	11	0	0	0	0	0	0	0	0	0	0.036	0.957

by a factor five. As there were no replicates of the study plots, the difference in recruitment could not be tested, but was considered large enough to justify the use of year-specific values for the transition matrices of the two years.

The leaf production rate determined indirectly was higher during the dry year, in spite of its high variability (Table 3). This contra-intuitive finding may reflect practical difficulties of using this indirect method to determine leaf production. Fortunately, the influence on the size-dependent pattern in height growth rate was not large (Figure 2).

As measured height growth and leaf production rates differed between years, Hossfeld functions (Eq. 1) were fitted for both measurement years separately (Figure 2). The normal-year fit yielded higher growth rates for individuals up to 17 m height and similar values for larger individuals. Between-year differences in growth were largest (>0.2 m yr^{-1}) for individuals of 5-9 m height.

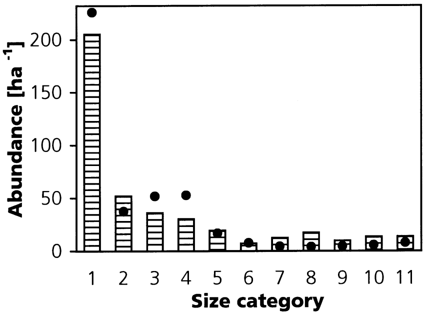


Figure 3
Population structure of a *Euterpe precatoria* population in a 6-ha plot located in forest reserve El Tigre, Beni, Bolivia. Category definitions and sample sizes are in Table 1. Bars denote observed population structure, filled circles denote the stable stage distribution of the normal-year matrix model, scaled to the same total abundance.

Results of annual matrix models

Based on the results of the statistical analysis, two annual transition matrices were constructed (Table 4). For category *1*, annual observed transitions were used. For categories *2-4* the values for leaf blade growth and survival were based on two years and were combined for the three categories. For categories *5-11*, survival was also based on two years and individuals in all categories were combined to calculate the overall survival probability. Growth rates for these categories were based on the year-specific fitted Hossfeld equations (Figure 2) and reproduction on a logistic regression for the probability of being reproductive (as in Table 2, but with only size as independent variable; R^2=0.78, Constant=-14.6, Regression coeffient=0.88) and the year-based number of recruits per reproductive individual. Dawkins illumination scores were not included in the transition matrices.

Population growth rate (λ) for the normal year (**N**) was 0.977, and for the dry year (**D**) somewhat lower: 0.960. The difference between these values can be explained by the lower growth rates in categories *5-11* during the dry year (Table 3, Figure 2) and to the greatly reduced recruitment and survival following the dry year (Table 3). Stable stage structure resulting from the normal-year matrix resembled the observed population structure reasonably well (Figure 3).

Two types of elasticity analysis were carried out: based on matrix elements (providing the proportional change in population growth resulting from a proportional change in a matrix element), and based on vital rates (providing this change for a proportional change in a vital rate: *i.e.* survival, growth or reproduction). Elasticity analyses for matrix elements (Figure 4a) showed that by far the largest proportion of total elasticity was confined in stasis elements (0.92) and that categories *10* and *11* (containing reproductive individuals exploited for palm heart) accounted for almost half of the total elasticity. Elasticity analysis based on vital rates showed that survival probability was the most important vital rate in determining λ, followed by growth and

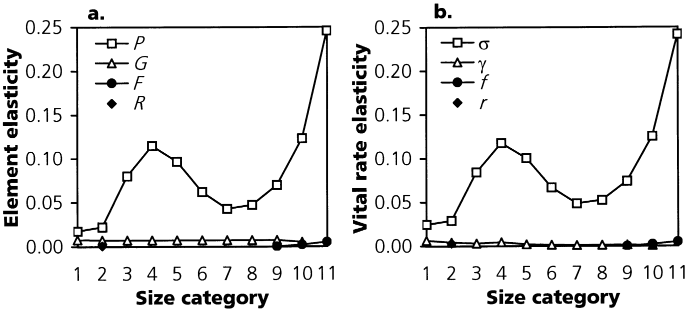


Figure 4

Elasticity values for matrix elements (a) and for vital rates (b) of a matrix model of *Euterpe precatoria* for a normal year (N). Elasticities are shown per category and per type of matrix element (*P*: stasis, *G*: growth, *F*: fecundity, *R*: retrogression) or per type of vital rate (σ: survival probability, γ: transition probability of a surviving individual [=growth rate/class width], *f*: number of offspring of a surviving individual, *r*: retrogression probability of a surviving individual). Vital rate elasticities are scaled to sum to unity for the sake of comparison, but cannot be interpreted as contributions to the population growth rate.

reproduction (Figure 4b). Using this type of elasticity analysis, the largest values were also obtained in the last categories. For the dry-year matrix (**D**), patterns of both types of elasticities were similar, but with somewhat higher values for stasis elements and survival probabilities (results not shown).

There was a close resemblance of the two types of elasticities (Figs 4a and b), when comparing elasticities for survival probability (σ) with stasis elements (*P*), growth rate (*g*) with growth transition elements (G), and number of offspring (*f*) with fecundity (*F*). This close relation is probably due to the high values for survival probability that were used, and the small differences in these values over the size categories (σ=0.941 for *2-4*, σ=0.957 for *5-11*; see formulae in Caswell 1989a, p 135).

Age estimates for categories of the normal-year matrix (**N**) were determined using the algorithms presented by Cochran and Ellner (1992) (Figure 5). Calculated ages showed that reproductive individuals which are cut for palm heart are old: individuals entered the first category with a high probability of reproduction (*10*) at an estimated age of 70 ± 20 yr (average ± SD of τ, conditional age), and mean age (S; mean age of residence) in the high-reproductive categories *10* and *11* amounted to 82 ± 26 yr and 106 ± 35 yr, respectively. Similarly, the mean age at which individuals become reproductive (μ; generation time) was long: 94 ± 33 yr. The estimates of mean age in a size category were rather sensitive to changes in survival in the last size categories, although a 0.01 change in survival probability did not alter age estimates drastically (Figure 5).

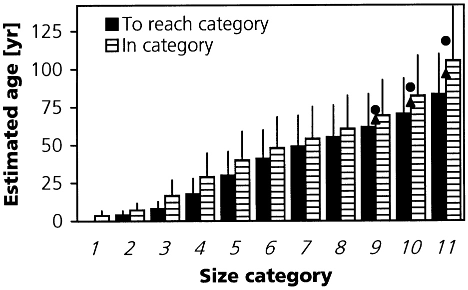


Figure 5

Age estimated for size categories of *Euterpe precatoria* using equations of Cochran and Ellner (1992). Black bars represent the age at first reaching a category (τ), hatched bars the mean age of palms in a category (S; mean age of residence). Error bars denote 1 SD, derived from equations for variance of age estimates presented by Cochran and Ellner (1992). Circles and triangles shown for the last three categories are values of S using a matrix with survival probability of categories *5-11* increased, respectively, decreased by 0.01.

Results of periodic matrix model

As for the two annual matrix models, the periodic matrix model (Eq. 4) projected a declining population size with the asymptotic growth rate being intermediary between those of the annual models (λ_{ND}=0.974). Elasticity analysis for the periodic matrix showed very similar patterns as that for the normal-year matrix (results not shown), both when considering total elasticity per type of matrix element (stasis, progression, retrogression, fecundity) and per size category. This implies that in spite of the considerable among-years differences in some vital rates, the relative importance of different life history components for long-term population growth is hardly changed.

Using the sequence of normal and dry years without palm heart extraction, projections were made of the development of the whole population size and that of the density of reproductive individuals. Population size fluctuated periodically due to the occurrence of dry years and declined in time when considered over several climatic cycles (solid lines in Figure 6). This is in accordance with a population growth rate smaller than one. Similarly, the abundance of reproductive individuals declined gradually for the undisturbed population (solid lines in Figure 7). However, in contrast to the whole-population size, adult abundance was hardly influenced by the sequence of normal and dry years. This can be attributed to the fact that survival and growth rates for the high-reproductive categories (*10-11*) were equal or similar in the normal- and dry-year matrix (Figure 2, Table 3).

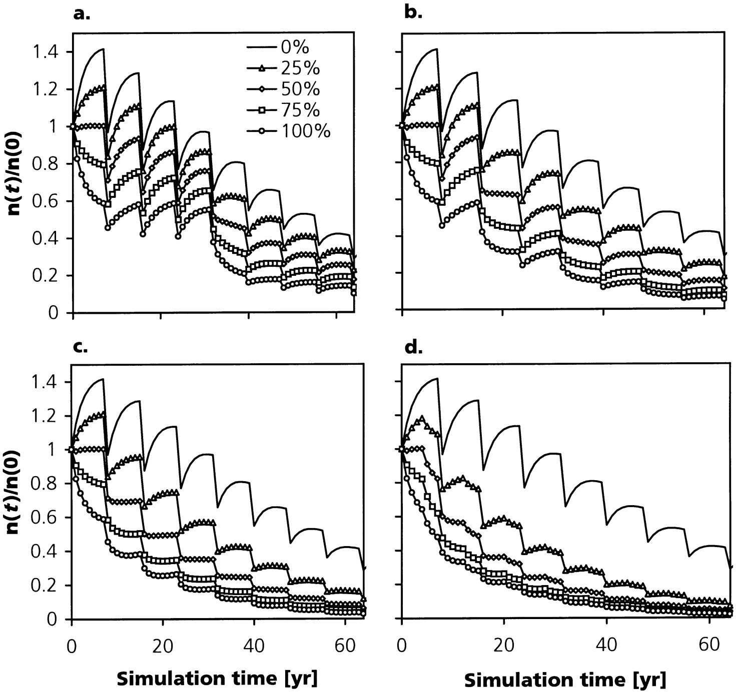


Figure 6
Simulated changes in population size relative to the initial size for populations of *Euterpe precatoria* in response to year-to-year climatic variation and different harvest regimes. Simulations were carried out for harvests every 32 (a), 16 (b), 8 (c) and 4 years (d) at different intensities (25-100%). The projection of population size for an undisturbed population is included in each graph for comparison. For clarity, projections are shown for 64 yr, but the patterns remained the same after this period.

Harvest simulations

Simulations of different harvest intensities and cycle lengths were carried for total population size (Figure 6) and abundance of reproductive individuals (Figure 7). In both cases, simulation results were expressed relative to the initial abundance, *i.e.* to the observed abundance in the field. Due to the inherent decline of population size ($\lambda<1$), harvested populations did not recuperate to their initial size in absolute terms. Therefore, the impact of extraction regimes was assessed relative to the situation for an undisturbed population.

Higher extraction intensities and shorter harvesting cycles caused trajectories of exploited populations to deviate more from that of an undisturbed population, indicating population decline relative to the undisturbed situation (Figure 6). Very strong reductions were found when harvests were repeated every four or eight years, and these results appeared to be relatively insensitive to the extraction intensity applied. For light extraction and long recuperation periods between harvests, the occurrence of dry years

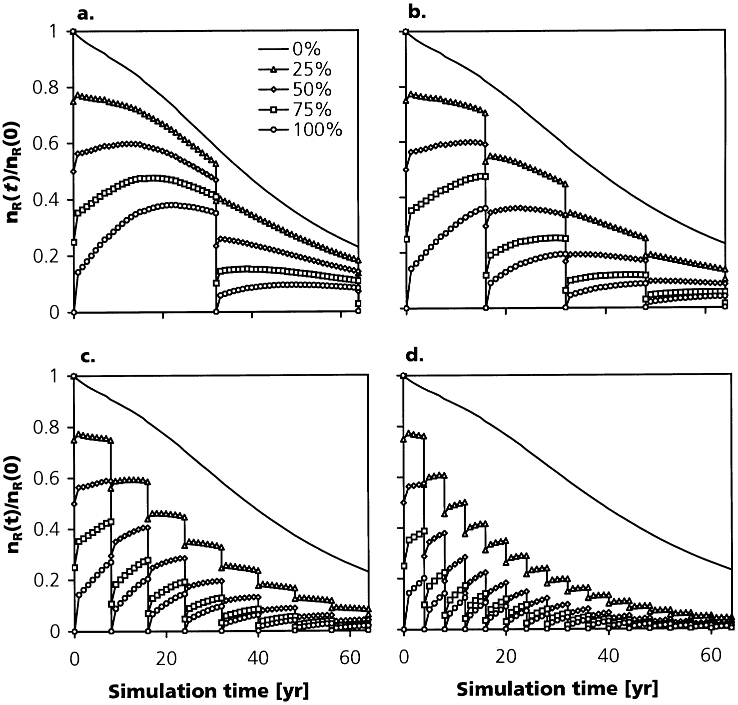


Figure 7
As Figure 6, but for changes in abundance of reproductive individuals (n_R).

had a larger impact on population size than extraction, probably due to the severely reduced recruitment in dry years and the fact that small seedlings constitute the largest portion of the population structure (category *1* contains almost 50% of all individuals).

As for the simulations of total population size, the abundance of reproductive individuals was severely declined when simulating high extraction levels (75-100%), in both short and long cycles (Figure 7). The reverse situation, short cycles (4-8 yr) in combination with both severe and light extraction, yielded similar results.

For the interpretation of the simulation results, it is necessary to know whether populations are able to fully recover their pre-harvest size after a single extraction. This appeared not to be the case for both total populations and reproductive individuals. When effects of a single extraction are simulated, total size of harvested populations and density of reproductive individuals never reached 100% of that for an undisturbed population after the same simulation period. The maximal proportion of the undisturbed population size that is recuperated decreased with harvest intensity and amounted to 93, 85, 78 and 71% for extraction intensities of 25, 50, 75 and 100%, respectively. In all cases this maximum recuperation was reached after 75-80 yr. The incomplete

Table 5

Effect of cycle length and extraction intensity on availability of reproductive individuals of *Euterpe precatoria* for palm heart extraction. Shown is the number of harvests after which the simulated abundance of reproductive individuals no longer reaches 50% of the abundance of an undisturbed population after the same number of simulated years. The value between parentheses is the relative abundance of reproductive individuals that is reached after the indicated number of harvests.

	Extraction intensity			
Cycle length	25%	50%	75%	100%
32 yr	8 (46%)	4 (43%)	2 (47%)	2 (36%)
16 yr	6 (44%)	3 (45%)	2 (43%)	1 (44%)
8 yr	5 (49%)	2 (49%)	1 (47%)	1 (30%)
4 yr	4 (45%)	2 (42%)	1 (41%)	1 (21%)

recovery of populations after a single harvest is due to the fact that the size of exploited populations lags behind that of an undisturbed population, and that exploited populations are not able to reduce this difference as their intrinsic growth rate (λ) is the same as that for the undisturbed population – the same transition matrix is used.

To compare the availability of palm heart for the 16 simulated extraction regimes, we determined after how many harvests the abundance of reproductive individuals did not recuperate to 50% of the abundance of an undisturbed population (Table 5). The value of 50% seems a conservative goal if sustainable extraction is envisaged, but it may not given the inability of simulated populations to recover completely after a single harvest. As expected, the combination of high extraction intensity and short cycle length led to rapid depletion of the stock of reproductive individuals. Projections for harvest intensities of 75–100% and a cycle length of 4–8 years show a very strong and rapid decrease in abundance of exploitable individuals, as already after one harvesting cycle, abundance of reproductive individuals fails to reach 50% of that for an undisturbed population. In the severest of the 16 extraction regimes, four years of recuperation leads to a recuperation of only 21% of the reproductive individuals that would be available without harvesting. But also the mildest extraction regime (cutting 25% every 32 yr) caused simulated adult abundance to drop below 50% of the undisturbed availability after some time (eight cycles).

Discussion

Patterns in individual vital rates

Plant size was strongly related to vital rates, explaining a moderate to substantial part of the variation in vital rates, especially for the larger, stemmed individuals (Table 2). Size-dependent patterns for survival, leaf production, height growth, internode length and reproduction found in this study (Figures 1 and 2, Table 1) were very similar to those observed for *Euterpe precatoria* populations in seasonally flooded forests (Peña-Claros 1996, Peña-Claros & Zuidema 1999).

The strong size-dependent increase in survival probability of small individuals observed for the study species is typically found in tropical forest palms (Enright & Watson 1992, Olmsted & Alvarez-Buylla 1995, Svenning & Balslev 1997, Silva Matos *et al.* 1999). Low survival in seedlings can be attributed to low understory light levels (Chazdon & Fetcher 1984, Zagt 1997, Nicotra *et al.* 1999), damage due to falling debris (Clark & Clark 1989), high herbivore pressure (Howe & Smallwood 1982) and (other) sources of density-dependent mortality. The latter two factors were found to considerably influence the seedling performance in the congeneric *Euterpe edulis* (Carvalho *et al.* 1999, Silva Matos *et al.* 1999).

Height growth rate of *Euterpe* individuals was highest for intermediate-sized individuals (Figure 2). Similar size-dependent patterns in growth were found for other palms (Bannister 1972, Enright & Watson 1992, Olmsted & Alvarez-Buylla 1995). Low growth rates in small individuals were mostly due to light limitations whereas the reduced growth in (large) reproductive individuals can mainly be attributed to high construction costs for reproductive structures (*cf.* Piñero et al 1982, Peña-Claros 1996).

Light availability was highly correlated with plant size; nevertheless it explained an additional part of the variation in vital rates (Table 2). A positive effect of light level on height growth of equal-sized individuals, as found in this study, was also observed for a population of the study species in seasonally flooded forest (Peña-Claros 1996). Furthermore, the probability of being reproductive and the number of reproductive structures increased with light level for palms of a certain size (*cf.* Enright 1992).

For small, stemless individuals, plant size nor light availability was related to growth (Table 2). Under experimental conditions and using a broader light range, growth of *Euterpe* seedlings did respond to light availability (Poorter 1999): biomass and height growth strongly increased in the range of 3 to 25% of full daylight. Although methodological constraints (narrow range of light availability, broad categories for light availability, small sample size, low measurement precision) may in part be responsible for the lack of a clear relation, stochastic factors (competitive position and density in the seedling stand, Zagt 1997, Silva Matos *et al.* 1999; damage by falling debris, Clark & Clark 1989; herbivory, Carvalho *et al.* 1999) are also likely to have influenced seedling performance, thus obscuring simple size- and light-dependent patterns.

Population dynamics

Population growth rates and patterns of elasticity found for the study species are similar to those found for other long-lived palms (Piñero *et al.* 1984, Enright & Watson 1992, Pinard 1993, Olmsted & Alvarez-Buylla 1995, Svenning & Balslev 1997, Silva Matos *et al.* 1999) and for long-lived species in general (Silvertown *et al.* 1993), with population growth rates relatively close to one, large contributions to population growth of stasis elements and of (pre-)reproductive categories, and low contributions of fecundity. Population growth rates found in this study are below one for both the normal and dry year and for the time-varying model, suggesting that populations are declining in size. However, the (high) variability of certain vital rates and the difficulty to estimate vital rate values induces uncertainty in the estimate of the population growth rate. For instance, survival of large individuals is very important for population growth (Figure 4b), but it is difficult to obtain a reliable estimate of survival probability for these size categories as very few individuals died during the study. Confidence intervals for λ were not determined using the analytical formulae derived by Alvarez-Buylla and Slatkin (1991), as coefficients of variation for growth rates in all size categories are higher than 50% (range: 66-379, Table 1) and are therefore too large to yield reliable estimates for confidence intervals (Alvarez-Buylla & Slatkin 1994). However, given the life history of the species (long-lived and non-pioneer) and the successional status of the studied forest (primary forest) we assume the *Euterpe* population to be stable, at least over the period of interest when assessing sustainability of current extraction practices.

Transition matrices are typically constructed using average values of vital rates. This assumes that the performance of all individuals in a category is conveniently characterized by that of an individual with average performance. This approach has two important implications that should be kept in mind when interpreting model output. First, in their standard form, matrix models do not cope with the variability and uncertainty in vital rates that are used to construct the transition matrix. When variation in vital rates is large, as was found for the study species, a substantial part of the information that characterises the species' life history cannot be incorporated into the model. As a consequence, the output of the model is perhaps better considered as an approximation of a species' life history, instead of an exhaustive representation of all aspects of its life history.

Second, the use of average values implies that dynamics of the entire population depend on the average performance of individuals. This assumption may not be met in case individuals with above-average growth rates have a much higher probability of becoming reproductive. In that case, only the fast growing individuals assure the influx of reproductive individuals that maintains the population. This may be the case in gap-dependent tropical forest species that need high light conditions to reach the canopy (Denslow 1987). The few individuals that encounter a canopy gap have a much higher probability to become adult and contribute to population growth than those that remain in understorey conditions. Although *Euterpe precatoria* cannot be characterized as a strongly gap-dependent species, there are indications that slow- and fast-growing individuals have distinct survival probabilities. In small-sized palms (categories *1-4*), growth of individuals that died during the following year was lower than that of surviving individuals (leaf blade length : 0.14 and 0.67 cm yr^{-1}, respectively; t=-0.82, p<0.001 , n=210); and the same was found for larger individuals (categories *5-11*; stem height growth: 0.17 and 0.30 cm yr-1, respectively; t=-2.3, p<0.05 , n=263). Growth and survival are thus somehow interrelated, and slower growing individuals have a higher probability of dying. However, as death may be a process that lasts for more than one year, part of these individuals may already be in the process of dying. Incorporating such interrelations in matrix models is complicated by the fact that individuals in matrix models "forget their past", *i.e.* transition probabilities are only based on an individual's current status and not on their past. A high mortality for slow-growing individuals probably implies that stasis elements in the transition matrices presented here may be somewhat too high as individuals that remain a long time in one category (*i.e.* grow slowly) in reality experience an extra high mortality risk. This bias may have caused somewhat higher elasticity values for stasis elements (*cf.* Enright *et al.* 1995) and consequently higher age estimates (*cf.* Boucher 1997).

In spite of the above considerations, it is unlikely that given the closed-canopy forest conditions in the study area, *Euterpe* individuals may become reproductive in a much shorter time than indicated by the age estimates provided in Figure 5. For comparison, if only the 10% fastest growing individuals per size category are taken into account and stage durations are calculated (Caswell 1989a, p. 84) for these individuals, the sum of stage durations in the pre-reproductive categories (*1-9*) still amounts 60 yr. Similarly, long periods to reach reproductive size were also calculated for *Euterpe precatoria* in flooded forests (96 ± 48 yr; Peña-Claros & Zuidema 1999) and for *Iriartea deltoidea* in upland forests (57 yr, based on different method; Svenning & Balslev 1997).

Year-to-year variation in precipitation and the occurrence of dry years, which regularly occur in Northern Bolivia and elsewhere in the distribution area of the species, is not likely to have a large impact on population maintenance and growth over longer periods, as is shown by the small differences in population growth for a normal and a dry year. The strong dependence of population growth on adult survival and the finding that this trait is probably not affected by year-to-year variation is responsible for this long-term stability. Over short periods, however, the size of the population may vary greatly due to the strong influence of dry years on seedling recruitment and survival (Figure 6), causing strong temporal variation in seedling density.

Constraints for sustainable extraction

Palm heart extraction has a strongly negative impact on the demography of *Euterpe precatoria*, as population growth is highly sensitive to changes in survival probability in the last categories (Figure 4). Also, individuals exploited for palm heart are old (Figure 5), implying that their replacement from seeds takes many years. Simulations of population size (Figure 6) and abundance of reproductive individuals (Figure 7) show that high extraction intensity and short extraction cycles are expected to strongly diminish population size and rapidly deplete the stock of exploitable individuals. The time to recover seems to be the main limiting factor in all simulated harvest regimes, as maximal recuperation after a single harvest is only reached after 75-80 yr. Even the mildest extraction regime (cutting 25% of all reproductive individuals every 32 years) leads to a continuous decrease in the abundance of reproductive individuals relative to that for an undisturbed population. Long harvest cycles (16 or 32 yr) in combination with low extraction intensities (cutting 25 or 50% of the adults) may be an option for management of *Euterpe* populations for a certain period of time, but regulations imposing low-intensity extraction may be hard to implement given the current extraction practice (cutting 90% and short cycles), the low revenues per palm heart, and the high costs for exploitation control. One way to increase productivity of *Euterpe* populations would be to apply silvicultural measures that increase light availability in order to accelerate growth for pre-reproductive palms which strongly respond to increased light (Table 2; Peña-Claros 1996). However, the low revenues from palm heart extraction severely limit the economic viability of applying such interventions.

The results of this study are based on an analysis of the population dynamics of the species. The use of static measures such as the population structure or the quotient of seedling and adult densities, may in this case have been misleading. Seedlings of the species are rather abundant, suggesting a strong potential for sustainable management (Nepstad *et al.* 1992). However, static measures do not take into account that recuperation may take very long, thus reducing the potential for sustainable use. Such information can only be derived when data on vital rates are available.

In this study the impact of extraction was assessed by comparing projections of population size and abundance of reproductive individuals for exploited populations with those for an undisturbed population. The declining size of the undisturbed population (λ<1) did not allow us to use the absolute norm of a positive population growth rate as an indicator of "sustainable exploitation", as has been applied in simulations of fruit harvests (using asymptotic growth rate [λ>1]; Peters 1990a and b, Bernal 1998) and palm extraction (using transient dynamics: Olmsted & Alvarez-Buylla 1995). Instead, we used a method that is not dependent on the value and "sign" (>1 or <1) of the projected population growth rate. The advantage of this method is that it does not take the projected population growth rate as a fact, as is implicitly done in the other approaches. This is of importance as it is increasingly becoming clear from population matrix studies that the value of λ is highly sensitive to uncertainties in parameter estimation (*e.g.* Wisdom *et al.* 2000, Bierzychudek 1999), natural variation in vital rates (*e.g.* Sarukhan *et al.* 1982, Alvarez-Buylla & Slatkin 1994) and differences among populations or observation periods (*e.g.* Piñero *et al.* 1984, Horvitz & Schemske 1995). As long as there is no indication of a strong decline in population size and population growth does not deviate largely from unity, a certain stability of population size may be assumed, thus allowing for the use of relative measures for population size of abundance, as was done here.

Our harvest simulations are based on the study of a particular population in a particular period, and should be interpreted carefully when applied to other sites, forest types or periods. However, a comparison of preliminary results from the present study with those from a demographic study on *Euterpe precatoria* in seasonally flooded forests elsewhere in Bolivia, showed close resemblance of demographic parameters and matrix model output (Peña-Claros & Zuidema 1999). This is remarkable in view of the large differences between the two research sites in environmental conditions (canopy height, seasonal flooding) and in density of the species, which was a factor 13 higher in the flooded forest. This similarity probably shows that certain life history traits specific for *Euterpe precatoria* (single-stemmed, long-lived, slow growing) determine the negative impact of palm heart extraction and severely constrain sustainable exploitation of the species. It therefore seems justified to state that the intensive extraction of palm heart from *Euterpe precatoria* as currently practiced is incompatible with the species' life history.

Acknowledgements

We are grateful to Luis Apaza, Rene Aramayo, Miguel Cuadiay, Nico Divico, Alejandro Hayashida, Santiago Mamani, Marielos Peña, Corien van Zweden and others for their indispensable help with field work. We thank Marielos Peña for advice on the study setup and for organising field work in 1998. Roderick Zagt kindly provided a MATLAB m-file for the calculation of ages, and Dietmar Stoian gave us some necessary figures related to palm heart economics. Alan Bojanic, Marielos Peña, Lourens Poorter, Marinus Werger and Roderick Zagt are acknowledged for helpful comments on a draft version of this paper. Part of this study was financed by grant BO009701 from the Netherlands Development Assistance.

Leaf arrangement in the clonal 'jatata' palm Geonoma deversa .

Chapter 4

Life history of a clustered understorey palm: an integrated analysis of genet and ramet demography using population matrix models

Pieter A. Zuidema & Marinus J.A. Werger

Summary

A two-year demographic field study was carried out on the forest understorey palm *Geonoma deversa* in the Bolivian Amazon. The goal was to analyse the clonal life history of the species, by comparing and integrating demography of genets and ramets. Matrix population models were used to analyse demography of ramets and genets. A third, integrated, model coupled the dynamics of ramets and genets. In this model, ramets were classified based on their own size and that of the genet to which they belong. This integrated model allows a direct evaluation of the role of ramets in the species' life history. In demographic models that only consider ramet dynamics, such information is hidden. Small ramets had remarkably high stem growth rates. The study also revealed a positive influence of genet size on growth of small ramets. These patterns suggest the occurrence of establishment support through clonal integration. Genet mortality was very low and genet life span is calculated to be long (*c.* 300 yr). Genet reproductive output steeply increased with size, and genets did not show signs of senescence. In contrast, ramets are short-lived (on average 37 yr), and show increasing mortality risk with size. *Geonoma deversa* appears to cope well with climatic variation. During a dry year, seedling recruitment, sprout production and stem growth were considerably reduced, but population growth rate was only moderately reduced. This was explained by the fact that survival - by far the most important vital rate for population maintenance - was not affected. Time-varying matrix population models revealed that the sequence of normal and dry years did not affect long-term population growth rate. The clonal growth form in the study species appears to be beneficial in that it extends genet reproductive life span by continuous replacement of ageing ramets, and strongly increases reproductive output by increasing plant size. This hypothesis is supported by the observations on establishment support to new ramets and on rapid expansion of genet size by vegetative reproduction.

Introduction

In clonal plants, two types of 'individuals' can be distinguished: the genetic individual (genet or clone) and its vegetatively produced components (ramets) that are potentially independent (Harper 1977). A full understanding of the life history of clonal plants therefore requires information on the demography at these two organisation levels and their interaction. Since natural selection takes place at the level of genetic individuals, a demographic analysis of genets provides insight into life history trade-offs, *e.g.* on vegetative *vs.* sexual reproduction, or clonal integration *vs.* independence of ramets (Harper 1977, Cook 1985, Stearns 1992). Information on ramet demography, on the other hand, can be used to describe stand dynamics in clonal populations, as it reveals patterns of shoot recruitment and mortality (Sarukhan & Harper 1973, Huenneke & Marks 1987).

Demographic studies of clonal plants are often hampered by the difficulty or impossibility to identify genets when they possess below-ground or disappearing inter-ramet spacers (*e.g.* Eriksson & Bremer 1993, Nault & Gagnon 1993). Many clonal plant studies have therefore only considered ramet dynamics (*e.g.* Sarukhan & Harper 1973, de Kroon *et al.* 1987, Huenneke & Marks 1987, Nault & Gagnon 1993). Translation of results from ramet studies to genet demography is difficult and may lead to wrong conclusions concerning the species' life history (Cook 1985), as ramet and genet demography may differ substantially (Eriksson 1993, Damman & Cain 1998). Few studies have looked into the demography of both ramets and genets (*e.g.* Hartnett & Bazzaz 1985, Kull 1995, Damman & Cain 1998).

Physiological integration within clones and establishment support of small ramets is often found in clonal plants species (*e.g.* Callaghan 1984, Stuefer *et al.* 1996). As demography of ramets and genets are coupled, a complete analysis of clonal life histories also requires information on the interaction between ramets and genets (Cook 1985, Caswell 1985). Given the practical problems in the study of clonal plants, this interaction has hardly been analysed from a demographic point of view. Modelling tools to analyse the coupled demography of ramets and genets, however, are available (Goodman 1969, Caswell 1985).

Clustered understorey palms offer the opportunity to study both ramets and genets and their interaction in detail. In these species, which are commonly found among understorey plants in tropical forests (Wessels Boer 1968, Chazdon 1991a, Henderson *et al.* 1995), genets can be readily identified in the field (De Steven 1989, Chazdon 1992, Mendoza & Franco 1998). Clustered palms are widespread in the understorey of tropical forests, where they often occur at high densities (Wessels Boer 1968, Henderson *et al.* 1995).

The growth form of clustered palms can be considered intermediate between that of clonal plants which entirely depend on vegetative proliferation and that of a-clonal plants, as they do not have the ability to spread ramets horizontally (Chazdon 1992, Mendoza & Franco 1998). Thus, the advantage of foraging in clonal plants does not apply in these species (de Kroon & Hutchings 1995). However, other suggested benefits of a clonal life form may still apply: spreading risk of genet mortality among ramets (Eriksson & Jerling 1993), extending genet life span by replacing ageing ramets (Watkinson 1992), physiological integration among ramets (Pitelka & Ashmun 1985, Jonsdottir & Watson 1997, Marshall & Price 1997) and providing establishment support to new ramets (Callaghan 1984). Genets in a clustered understorey palm have indeed been estimated to have long life spans (Chazdon 1992). Given the clumped growth form and the supposed long life span of clustered palms, coping with (unpredictable) temporal variation is probably much more important than with spatial variation. This contrasts with the strong emphasis on spatial variation in clonal plant research (*e.g.* Oborny & Cain 1997), and asks for a different type of analysis (*e.g.* Eriksson 1994).

In this paper, we analyse genet and ramet demography of the clustered understorey palm *Geonoma deversa* in Northern Bolivia. We present a novel matrix population model that couples ramet and genet demography. In this model, ramets categories are 'nested' within genet categories, which allows for a more detailed analysis of the roles of ramets in different-sized genets. The goals of this study are (1) To analyse and compare demography of genets and ramets, and evaluate their integrated demography; (2) To evaluate the potential benefits of a clonal growth form for *Geonoma*, and (3) To evaluate the impact of climatic variation on demographic rates and population maintenance. This evaluation was conducted by comparing the species' demography during an observation year with normal precipitation with one that was exceptionally dry, and using time-varying population models.

Study species

Geonoma deversa (Poit.) Kunth is a clonal understorey palm species that is widespread and abundant in Central America and northern South America in non-flooded tropical rain forests (Wessels Boer 1968, Henderson *et al.* 1995). In Bolivia, the species often occurs at high densities in the Amazonian lowland forest area (Moraes 1996). Ramets (stems) may reach >4 m in stem length and produce up to 16 leaves (n=1160 ramets). Genets (clones) can consist of more than 20 ramets with a summed stem length of over 28 m and up to 107 leaves (n=248 genets). New ramets are formed vegetatively by basal sprouting just under the soil surface, and ramets are clustered within the genet. Genets can be easily identified in the field. Inflorescences (racemes) appear below the leaves and bear both male and female flowers (Henderson *et al.* 1995). Ramets may possess up to three reproductive racemes, although the majority of reproducing ramets only contain one. Flowers and fruits are present throughout the year (P.A. Zuidema *personal observation*).

Geonoma seeds germinate within four months after dispersal (Braun 1988). Recently germinated seedlings usually possess two bifid (juvenile) leaves. After establishment, number and size of bifid leaves increases and leaves change ontogenetically to a dissected (adult) form. The next developmental phase starts when the stem becomes visible above ground. Vegetative production of new ramets was observed for ramets of 50-100 cm stem length, and sexual reproduction at heights >100 cm.

Methods

Study site

The study was carried out in the Northern Bolivian Amazon, close to the forest community of El Turi (Pando Department, 11°45'S, 67°20'W). The region is covered by relatively undisturbed lowland moist forest. Mean annual precipitation amounts to 1703 mm in Riberalta (150 km east of study site) and 1803 mm in Cobija (175 km west; Beekma *et al.* 1996). The region has a dry season from May to September during which monthly precipitation does not exceed 100 mm; high rainfall months are December to March with >240 mm of rain per month.

During the second measurement year rainfall was strongly reduced: during the wet season (Dec '97-Mar '98) precipitation amounted to 874 mm compared to an average value of 1037 mm (SD=234 mm for '48-'98 data from Riberalta), during the subsequent dry season (May '98 - Sep '98) this was 94 mm compared to an average of 203 (SD=73 mm). The subsequent occurrence of two drier-than-normal seasons caused the 12-mo moving average precipitation to drop below 100 mm mo^{-1} which is considerably lower than average (143 mm mo^{-1}). Moving average values below 100 mm mo^{-1} were also observed in other years with very low rainfall in both wet and dry season (1956, '63, '69, '83 and '85), occurring at a frequency of 0.12 (=6/50) during the period 1948-1998. Three out of these six considerably drier years concurred with El Niño Southern Oscillation episodes (ENSO), but significant anomalies in monthly precipitation during ENSO episodes were not found (data not shown; *cf.* Ropelewski & Halpert 1996).

Study design

A 2-yr demographic study was performed in three high density stands of *Geonoma* in undisturbed primary forest. Stands were selected based on the following criteria: (1) no signs of recent *Geonoma* leaf cutting (leaves are used for thatching, Moraes *et al.* 1995), (2) no recent treefall gap within the stand, and (3) a reasonable number (>10) of large genets (>9 ramets) in the stand. In each of the three stands (A-C), a 30 × 30m plot was established to study population dynamics, subdivided into nine 10 × 10 m subplots. *Geonoma* genets and ramets were searched, tagged and measured in the entire plot or in as many subplots needed to obtain a sufficiently large sample. First measurements were conducted in November 1996 and repeated in October 1997 and October 1998. Seedling counts and measurements were carried out in nine 3 × 3 m seedling plots in each study plot. Seedlings were defined as having at least one unfolded leaf and <20 cm leaf length. Measurements on seedlings started in February 1997 and were repeated in March/April 1998 and February 1999. Seedling plots were also used to quantify recruitment.

Field measurements

Plant measurements were conducted at the level of ramets and genets. At the ramet level, the following parameters were measured of ramets >10 cm stem length: total stem length (distance between soil surface and base of youngest green leaf), number of green leaves (painting the petiole of the youngest leaf to determine leaf production), number of racemes bearing flowers or fruits, and whether the ramet had been or is currently is reproductive (by looking for reproductive buds). To determine stem growth without having to re-measure total stem length, the last visible internode was marked at initial measurement and stem length from this point to the base of the youngest green leaf was measured each year.

At the genet level, in addition to the ramet-based measurements, all ramets shorter than 10 cm stem length were counted and marked annually, thereby also determining the number of new vegetatively produced ramets. Thus, vegetative reproduction rates were only determined at the genet level. To be able to assign vegetative reproduction rates to different ramet categories, the 'mother' ramets of almost all (n=354) small ramets (<10 cm stem length) were identified in March 1999. Other genet-based parameters were derived from data on ramets (>10 cm stem length): summed stem length, growth in summed stem length (summing growth increments of surviving ramets), total number of leaves, and number of ramets with racemes bearing flowers or fruits. The following parameters were measured in small genets and seedlings: length of youngest leaf, number of bifid leaves and number of dissected leaves.

To characterise light conditions of the three study populations, hemispherical photographs were taken in the centre of each of the nine subplots at a height of 1.5 m in each of the three stands (using a Canon AE-1 camera with a 7.5 mm fisheye lens). Printed photographs were scanned (HP Scm6) and analysed to calculate canopy openness (Winphot 5.0; Ter Steege 1996). Canopy openness values were low, ranging from 2.9 to 7.3%, and did not differ among stands (Kruskal-Wallis ANOVA $\chi^2=1.96$, $n=3$, $p>0.05$; mean ± SD for plot A: 4.6 ± 1.1; B: 4.7 ± 1.0; C: 5.2 ± 0.9).

Statistical analysis

Statistical analyses were carried out for genets (>10 cm summed stem length) and ramets (≥1 dissected leaf) separately. Firstly, vital rates were tested for differences between years (using repeated measures ANOVA and McNemar's test). When significant differences between years were found, subsequent analyses were carried out for each year separately. Then, tests were performed to relate vital rates to genet and ramet size, and to detect differences among the stand (A-C), using linear and logistic regression.

Matrix population models

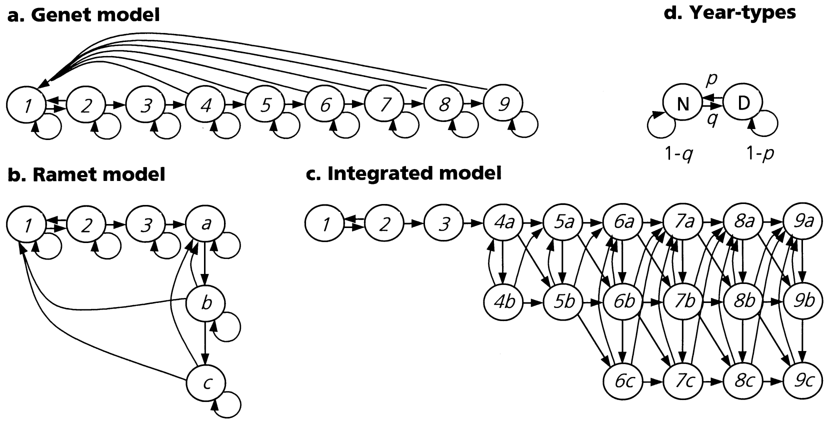
Stage-based matrix population models (Lefkovitch 1965) were used to describe dynamics of genets and ramets. These models use the equation

$$\mathbf{n}(t+1) = \mathbf{A}\ \mathbf{n}(t)$$

where $\mathbf{n}(t)$ and $\mathbf{n}(t+1)$ are population structures at time t and $t+1$, respectively, and $\mathbf{A}$ is a square matrix containing transition probabilities among categories. The asymptotic growth rate of the population is the dominant eigen value (λ) of matrix $\mathbf{A}$, the stable stage structure of the population is the right eigenvector $\mathbf{w}$, and the left eigenvector $\mathbf{v}$ contains the reproductive values of the categories (Caswell 1989a).

Transition matrices were constructed for genets, ramets and for ramets-within-genets (Figures 1 a-c), both for a normal (**N**) and a dry (**D**) year. The ramet-within-genet matrix model (further referred to as integrated model) is a combined matrix that describes ramet demography in relation to the genet to which they belong. That is, individual ramets are assigned to a category on the basis of their own size and that of the genet to which they belong. Thus, the model allows vital rates of equally sized ramets to differ among genet categories. As genet size can be important for ramet vital rates, this combined model may be more realistic than a model in which the demography of ramets is assumed independent of the genets to which they belong.

In the integrated model, ramets can grow to the next ramet category in a genet that remains in the same genet category, or in a genet that grows to the next category (Figure 1c). Similarly, ramets can remain in the same category in a genet that moves to the next category or in a genet that remains in the


a. Genet model

b. Ramet model

c. Integrated model

d. Year-types

Figure 1

Life cycle graphs for three population matrix models of the clonal understorey palm *Geonoma deversa* (a-c) and a Markov chain to describe sequence of normal and dry years (d). In the life cycle graphs, circles denote size categories: numbers refer to genet size and letters to ramet size. Arrows denote transitions among categories: self-loops are stasis probabilities (*P*), straight arrows are progression probabilities (*G*) if to a larger category, or retrogression if to a smaller category (*R*), curved arrows two category *1* denote sexual reproduction (*F*) and curved arrows to other categories denote vegetative reproduction (*V*). For the integrated model (c), transitions for stasis (present in all categories) and sexual reproduction (present in all categories except *1-3*) are not shown for the sake of clarity. In the Markov chain (d), N and D indicate matrices for a normal and a dry year respectively, *p* is the probability of occurrence of a dry year after a normal year and *q* is the reverse.

same category. Vegetative and sexual reproductive output at the genet level is the sum of the outputs of ramet categories contained in that genet category. Genet death causes all ramets to die, but ramets may die without influencing genet survival.

The integrated matrix has some resemblance with patch-specific matrix models in which population dynamics are described in the context of the dynamics of environmental conditions (Alvarez-Buylla & Garcia-Barrios 1993, Pascarella & Horvitz 1998), and with models in which individuals are classified by both age and size (Goodman 1969, Law 1983, van Groenendael & Slim 1988). An important difference, however, is that in our model there is a mutual dependence of the two levels (genets and ramets): an increase in ramet growth also increases genet growth, and genet death causes all ramets to die. In contrast, in patch-specific models, patch dynamics are independent of population dynamics, and in size-age models, transitions to higher age categories are independent of transitions among size categories.

Categorisation of individuals

Populations of ramets and genets were divided into size categories in order to construct transition matrices. Category boundaries were determined using information on size-dependent patterns of vital rates (survival, growth,

Table 1

Characteristics of genet and ramet categories used in three matrix models for *Geonoma deversa*. The first three categories are the same in all models. Category numbers refer to genet categories and letters to ramet categories. Ramet categories in the integrated model are nested within genet categories: in this case the number refers to the genet category to which a ramet belongs and the letter refers to the ramet size category, *e.g*. category *7c* are large (>230 cm) ramets being part of genets in category *7*. Number of leaves are annotated with b for bifid (juvenile) leaves and with d for dissected (adult) leaves. Classification criteria for stem length are upper class limits. Stem length for genets is summed over all ramets >10 cm. Leaf and ramet numbers are averages. σ = survival rate in normal year from regression equations; Clonal = percentage of clonal individuals in category; Repro = percentage of sexually reproductive individuals; *n* = number of measured individuals at the start of the study.

		Criteria			Characteristics					*n*
		Nr. leaves	Stem length genet [cm]	Stem length ramet [cm]	Nr. leaves	σ [%]	Clonal [%]	Repro [%]	Nr. ramets	
Model										
All	*1*	1-3 b				61.4	0	0	1.0	*135*
	2	4-6 b				93.3	0	0	1.0	*38*
	3	1-3 d	10		2.2	95.7	0	0	1.0	*17*
Genet	*4*	≥4 d	250		7.7	98.7	48	26	2.0	*39*
	5		500		21.7	99.5	100	100	3.8	*25*
	6		1000		32.3	99.5	100	100	5.9	*37*
	7		1500		46.7	99.5	100	100	7.8	*35*
	8		2000		63.4	99.5	100	100	11.3	*17*
	9		>2000		77.9	99.5	100	100	14.1	*12*
Ramet	*a*	≥ 4 d		120	6.3	99.1		4		*297*
	b			230	7.7	99.1		84		*458*
	c			>230	7.3	98.0		100		*333*
Integrated	*4a*	≥ 4 d	250	120	5.8	99.1		9		*44*
	4b	≥ 4 d	250	>120	8.2	99.2		60		*10*
	5a		500	120	7.7	99.1		21		*24*
	5b		500	>120	8.2	99.1		85		*40*
	6a		1000	120	6.3	99.1		13		*47*
	6b		1000	230	7.6	99.1		77		*87*
	6c		1000	>230	7.4	98.0		100		*30*
	7a		1500	120	6.5	99.1		8		*52*
	7b		1500	230	8.0	99.1		80		*89*
	7c		1500	>230	7.1	98.0		99		*83*
	8a		2000	120	5.7	99.1		0		*27*
	8b		2000	230	7.4	99.1		87		*61*
	8c		2000	>230	7.3	98.0		100		*61*
	9a		>2000	120	5.4	99.1		7		*27*
	9b		>2000	230	7.2	99.1		78		*40*
	9c		>2000	>230	7.2	98.0		100		*67*

reproduction), in order to maximise differences in demography among categories.

The first three categories (*1-3*) were equal for the three models, as they contain individuals consisting of just one ramet (Table 1). Seedlings with bifid leaves were classified in two categories: one with high mortality rate in which all newly recruited seedlings appeared, and one for somewhat larger seedlings with lower mortality. The third category contains established juveniles with 1-3 dissected leaves and a visible stem (<10 cm). The boundary between category *3* (based on leaf number) and the successive category (based on stem length) was established by a linear regression of stem length on number of dissected leaves (stem length[cm]=8.1+0.98 × leaf number, n=35, R^2=0.49, p<0.001).

In the genet model, genets in categories *4-9* were classified based on summed stem lengths of all ramets >10cm, using increments of 250 and 500 cm (Table 1). In the ramet model, ramets in categories *a-c* were classified based on stem length, in three categories with equal width (110 cm stem length). In the integrated model, ramets were classified based on their own size (applying the same categories as in the ramet model) and on the size of the genet to which they belong (applying the same categories as in the genet model).

Parameterisation of transition matrices

Matrix elements were parameterised in two ways. For categories *1-2* observed transition frequencies among categories were used to calculate transition probabilities. Observed transitions were used since many seedlings in category *2* (35%) regressed to category *1*. For categories *3* and higher, matrix elements were composites of different vital rates (survival, growth, reproduction). Values for vital rates were obtained by substituting the mean size of individuals in a category, into regression equations that relate a vital rate to one or more ramet or genet characteristics.

In the three types of transition matrices (genet, ramet and integrated) transitions among the categories *1-3* were equal. For category *3*, progression probability (G, moving to the next category) was calculated as $G_3 = \sigma_3 \times \gamma_3$, with σ_3 being survival probability, and γ_3 equals (leaf gain [leaves per yr]) / (category width [leaves]). The stasis probability (P) was calculated as $P = \sigma_3 - G_3$.

In the genet transition matrix, three types of matrix elements can be distinguished: probability of progression to the next highest category (G, horizontal arrows in Figure 1a), remaining in the same category (P, self-loops) and sexual production of new individuals (F, long loops to category 1). The calculation of these probabilities is shown in Table 2. As can be seen there, genet growth and reproduction is determined by summing these parameters

Table 2

Calculation of transition probabilities and their composites for three matrix models of *Geonoma deversa*. These equations do not apply to categories *1-3*; see Methods for quantification of transition probabilities in these categories. Transition values: *G* = progression probability; *P* = stasis probability; *F* = sexual reproduction ; *V* = vegetative reproduction. Vital rates and other parameters (in alphabetic order): γ = growth probability; σ = survival probability; *abnew* = abundance of new seedlings; *abrepro* = abundance of reproductive ramets; *c* = width of size category; *f* = number of new seedlings produced by a reproductive individual; *g* = growth rate (in stem length); *grow* = summed growth of surviving ramets; *loss* = genet stem length loss by ramet mortality; *Pr*{sex}= probability of being reproductive; *sl* = mean stem length; *slnew* = mean stem length of new ramets (equalled 15.3 cm ± 4.6 [SD], *n*=39); *veg* = contribution of new ramets to genet growth; *vp* = rate of new ramet production. Subscript *i* refers to genet category; subscript *k* to ramet category. Summations are over ramet categories and are weighted for the relative size of different ramet categories in a genet category. In the integrated model, transitions for ramet categories are calculated as for the categories in the ramet model. The transitions indicated with double letters are combinations of ramet and genet transition probabilities, e.g. G_kG_i denotes the probability that a ramet in category *k* grows to the next category, given that the genet to which it belongs also grows to the next category.

Genet model		Ramet model		Integrated model	
Var	Calculation	Var	Calculation	Var	Calculation
G_i	$= \sigma_i \times \gamma_i \times c_i^{-1}$	G_k	$= \sigma_k \times \gamma_k$	G_kG_i	$= G_k \times G_i$
P_i	$= \sigma_i - G_i$	P_k	$= \sigma_k - G_k$	G_kP_i	$= G_k \times P_i$
F_i	$= \Sigma(F_k)$	F_k	$= \sigma_k \times Pr\{\text{sex}\}_k \times f$	P_kG_i	$= P_k \times G_i$
γ_i	$= g_i / c_i$	V_k	$= \sigma_k \times vp_k$	P_kP_i	$= P_k \times P_i$
g_i	$= grow_i + veg_i - loss_i$	γ_k	$= g_k / c_k$	V_kG_i	$= V_k \times G_i$
$grow_i$	$= \Sigma(g_k)$	f	$= abnew / abrepro$	V_kP_i	$= V_k \times P_i$
veg_i	$= vp_i \times slnew_k$			F_k	$= \sigma_i \times \sigma_k \times Pr\{\text{sex}\}_k \times f$
$loss_i$	$= \Sigma\ ([1-\sigma_k] \times sl_k)$				

over the ramets contained in a genet category. Vegetative reproduction in genets is contained in progression probabilities as it adds to genet growth in summed stem length. On the other hand, ramet mortality reduces genet stem growth.

In the ramet transition matrix, an additional type of matrix element is present: vegetative reproduction (*V*). The mode of calculation for all matrix elements is in Table 2.

In the integrated model, demography of ramets and genets is coupled. Elements in the transition matrix are composites of genet and ramet vital rates (Table 2), and were calculated by multiplying vital rates for a genet category with those for a ramet category within that genet category. Growth, stasis and vegetative reproduction of ramets in categories *4a* and higher can occur within a genet that remains in the same category or a genet that moves to the next category (see Figure 1 and Table 2).

Analyses of simple matrices

Standard matrix analyses were carried out for each of the six matrices (three for a normal year: $\mathbf{N}_{\text{genet}}$, $\mathbf{N}_{\text{ramet}}$, and $\mathbf{N}_{\text{integrated}}$ and three for a dry year:

$\mathbf{D}_{\text{genet}}$ $\mathbf{D}_{\text{ramet}}$ and $\mathbf{D}_{\text{integrated}}$) to obtain finite rates of increase of the populations (λ), as well as the stable stage distributions (w) and reproductive value (v, Caswell 1989a). To relate model projections to reality, stable stage structures resulting from matrix models were compared to observed population structures (mean of three stands), using the similarity index PS (Horvitz & Schemske 1995): $PS = \Sigma(\min[ops_i, ssd_i]) \times 100$, where ops_i and ssd_i are vectors of observed population structures and stable size distributions respectively (both vectors scaled to sum to 1), and the sum is taken over all categories. High values of this index indicate a high level of similarity.

Elasticity analysis was performed to determine the proportional change population growth rate (λ) by a proportional change in one of the matrix elements (de Kroon *et al.* 1986). Several matrix elements in the integrated model (*4a* to *4a*, *5a* to *5a* etc) contained two added components - stasis (P) and vegetative production of new ramets (V). Elasticity for these elements reflects the contribution of both components. Flores-Martinez (1994) showed that in this case, the contribution of each component to elasticity is proportional to their contributions to the transition probability. Elasticity analysis was also conducted for vital rates (growth, survival and sexual reproduction) in the genet and ramet models, using the approach of Caswell (1989a p. 135). Both types of elasticities were calculated for the normal year matrix.

Age estimates for genets and ramets were obtained using the algorithms derived by Cochran & Ellner (1992). Mean and variance of age conditional on reaching a certain category (τ), and mean age of residence (S) were calculated using their equations 9-10 and 29-30 respectively. Age estimates for ramets in the integrated model were calculated for vegetatively produced ramets only (*i.e.* those produced in categories *4a*,*5a*,*6a*,*7a*,*8a* and *9a*) as it is very unlikely that the first ('mother') ramet of a clone is still alive in a large genet.

Time varying matrix models

Given the demographic differences between a normal and a dry year, time-varying matrix models were performed to describe long-term population dynamics for sequences of normal and dry years. Two types of models were used: deterministic (periodic) models and stochastic models. Time-varying models were applied to all three types of matrices (genet, ramet and integrated).

In deterministic matrix models, normal and dry years occur in a fixed sequence, and the model can be written as (Caswell 1989a, Silva *et al.* 1991):

$$\mathbf{n}(t + m) = \mathbf{D}^{x}\,\mathbf{N}^{m-x}\,\mathbf{n}(t) \tag{1}$$

where **D** and **N** are matrices for dry and normal years respectively, *m* is the period of the complete cycle and *x* is the number of dry years in the cycle (*x/m* being the frequency of dry years). The dominant eigenvalue of the matrix product $\mathbf{D}^x\mathbf{N}^{m-x}$ is the population growth rate over a period of *m* years, which can be transformed to an annual growth rate by taking the *m*-th root. The right eigenvector of the product matrix is cyclic, not allowing simple comparison with observed population structures (Caswell 1989a). Periodic population growth rates were determined for the estimated frequency of dry years (0.12) and for all other possible frequencies from 0 to 1 at 0.01 steps.

As dry years do not occur in strict cyclic pattern through time, the use of periodic models may lead to unrealistic projections of population dynamics. Stochastically time-varying models overcome this problem by randomly choosing year-types at each model time step, in proportion to their natural occurrence. Time-homogeneous stochastic models (*sensu* Caswell 1989a) were applied, based on a Markov chain containing probabilities of transitions among normal and dry years (Figure 1d). These models have the property that the probability distribution of stage structures eventually converges to a stationary distribution (Caswell 1989), so that final stage distributions are independent from initial population structures. Long-term population growth can be approximated numerically, by using population growth at each time step (Silva *et al.* 1991):

$$\log\lambda(t) = \log N(t+1) - \log N(t) \tag{2}$$

where *N* is the population size and $\log\lambda(t)$ is the instantaneous growth rate (*not* the dominant eigenvalue of a matrix). These instantaneous estimates can then be averaged over a long time interval (*T* yr; Silva *et al.* 1991):

$$\overline{\log \lambda_s} = \frac{1}{T-1}\sum_{t=1}^{T-1} \log\ \lambda(t). \tag{3}$$

In stochastic matrix models, autocorrelation (ρ) among year-types may play an important role (Tuljapurkar 1989). Autocorrelation is defined as $\rho = 1 - p - q$ (Silva *et al.* 1991), with positive values ($0<\rho<1$) when years of the same type tend to appear in sequence, and negative values ($-1<\rho<0$) when year-types tend to alternate. The frequency of dry years (π) is related to the degree of autocorrelation as

Stochastic analyses were performed for situations without autocorrelation ($\rho=0$ so that $\pi=q$) and with slight positive and negative autocorrelations ($\rho=0.1$ and $\rho=-0.1$), as no strong autocorrelation of the occurrence of normal and dry years was expected. In each of these three situations, average stochastic population growth rates (λ_s) and mean population structures were calculated over a period of 3000 simulation years (T=3000), after an initial period of 1000 years, and for dry-year frequencies (π) ranging from 0 to 1in steps of 0.1.

In the case of the rather infrequent occurrence of dry years, the occurrence of two successive dry years is unlikely. Therefore, a fourth stochastic analysis was performed, using the frequency of dry years as obtained from the meteorological records (π=0.12) and not allowing the occurrence of two consecutive dry years (p=1).

Results

Patterns of genet vital rates

Survival probability increased steeply from 0.61 in category *1* to 0.96 in category *3*. Mortality of genets occurred sporadically in intermediate-sized genets (category *4*) and was completely absent in large genets (*5-9*). The main cause for mortality of intermediate and large genets is probably falling trees or large branches as is the case for other understorey and sub-canopy palms (Piñero *et al.* 1984, De Steven 1989). It is unlikely that insufficient availability of light, nutrients or water causes large genets to die. We considered the mortality rate in all large genet categories (*5-9*) to be the same, since all experience approximately the same risk to be hit by a large branch or tree. The survival probability for large genets was calculated as the midpoint of the 95% confidence interval for survival probability (0.990-1.000, for 176 genets). For smaller genets, mortality rate was considered to be slightly higher as death of the main ramet could possibly cause genet death. One small genet died during the study period, providing a survival rate of ((39/40)=0.987; confidence interval 0.955-0.997).

All variables related to genet growth and reproduction exhibit a significant increase with genet size (Table 3). For all but one regression model, summed stem length was included as the explanatory variable, but total number of leaves or number of ramets in a genet could also be used, as these are highly correlated with summed stem length (all r>0.97, n≥216).

Net genet growth rate (g) increased with size up to category 7 mainly due to increased ramet growth (*grow*), and was reduced in the last two categories due to elevated mortality risk for large ramets and their larger *per capita* contribution to stem length loss (*loss*, Figure 2).

Category vital rates predicted by the regression models closely resembled observed category means (see *e.g.* Figure 2) except for one case: mean vegetative reproduction rate was observed to increase with genet size in the

Table 3

Relations between demographic rates and plant size for genets and ramets of *Geonoma deversa*. Possessing raceme refers to current reproductive activity; reproductive status to overall status. Genet stem length refers to summed stem length of all ramets in genet models (ln-transformed in the case of stem length growth) and to summed stem length of all other ramets in ramet models. Coefficients of determination for binary variables are calculated following Nagelkerke (1991). Per explaining variable, the sequence of values is: regression coefficient, significance level (ns: $p \geq 0.05$, *: $p < 0.05$, **:

Parameter	Period	R^2	Constant	Stem length [cm]					
				Genet			Ramet		
Genets									
Stem growth (*grow*)	'96-'97	0.53	0.9	0.40	***	(0.74)		-	
	'97-'98	0.57	1.0	0.37	***	(0.78)		-	
Possessing raceme	'96	0.15	-1.0	0.001	***	(0.30)		-	
	'97	0.39	-2.3	0.002	***	(0.39)		-	
Reproductive status (*Pr*{sex})	'96	0.54	-4.3	0.03	**	(0.24)		-	
Ramet production (*vp*)	'96-'97[1]	0.22	-2.3		ns			-	
	'97-'98	ns							
Clonality	'98	0.85	-3.7	0.05	***	(0.26)		-	
Ramets									
Survival (σ)	'96-'98	0.14	1.3		ns	-0.01		**	(-0.16)
Stem growth small ramets (*g*)	'96-'97	0.30	1.0		-		-0.08	***	(-0.31)
	'97-'98	0.44	-2.5		-		-0.11	***	(-0.46)
Stem growth large ramets (*g*)	'96-'97	0.35	1.8		-		-0.01	***	(-0.16)
	'97-'98	0.40	0.7		-		-0.02	***	(-0.30)
Possessing raceme	'96	0.11	-3.2	-0.0004	**	(-0.07)	0.01	***	(0.22)
	'97	0.17	-2.0	-0.0003	*	(-0.07)	0.01	***	(0.27)
Reproductive status (*Pr*{sex})	'96	0.76	-5.9		ns		0.04	***	(0.42)
New ramet attached (*vp*)	'98	0.06	-1.2	-0.0005	***	(-0.13)	0.003	**	(0.10)

[1] **Additional effect of number of ramets (notation as in Table): 0.18 *** (0.28)**

categories 4-7 and drop to lower values in the last two categories (Figure 2), whereas the logistic regression suggests a monotonic increase with genet size (Table 3). We therefore used category means to obtain transition probabilities.

Patterns of ramet vital rates

Ramet survival probability, stem growth and proportion of ramets with racemes all increased with number of leaves and decreased with ramet stem length (Table 3). Leaf number explained more variation in growth and survival than stem length, whereas for raceme production, reproductive status and vegetative reproduction influence of leaf number was smaller or not significant (Table 3). Stem growth was considerably lower in large ramets (5.6 ± 4.2 cm

Table 3 (continued)
$p<0.01$, ***: $p<0.001$), and partial correlation coefficients (between parentheses, as an indication of relative importance of variables). All rates are per year; stem length growth in cm yr^{-1}. When only one year is mentioned a static parameter is considered. The significance indications in column "Stand" specify differences among sites for the vital rate under consideration (this never increased R^2 considerably). Small ramets have a stem height of 10-120 cm, large ramets of >120 cm. Collinearity was taken into account in the analysis.

Parameter	Period	Leaf number		Stand	*n*
		Genet	Ramet		
Genets					
Stem growth (*grow*)	'96-'97	-	-	ns	*212*
	'97-'98	-	-	ns	*239*
Possessing raceme	'96	-	-	ns	*216*
	'97	-	-	ns	*248*
Reproductive status (*Pr*{sex})	'96	-	-	ns	*165*
Ramet production (*vp*)	'96-'97^{1}	ns	-	*	*249*
	'97-'98				*257*
Clonality	'98	-	-	ns	*216*
Ramets					
Survival (σ)	'96-'98	ns	0.49 *** (0.30)	ns	*1072*
Stem growth small ramets (*g*)	'96-'97	0.07 *** (0.24)	2.04 *** (0.54)	*	*281*
	'97-'98	0.09 *** (0.34)	2.31 *** (0.65)	ns	*268*
Stem growth large ramets (*g*)	'96-'97	ns	0.85 *** (0.47)	***	*768*
	'97-'98	ns	0.97 *** (0.52)	***	*781*
Possessing raceme	'96	-	0.12 ** (0.09)	*	*1082*
	'97	-	ns	**	*1048*
Reproductive status (*Pr*{sex})	'96	ns	ns	ns	*767*
New ramet attached (*vp*)	'98	-	0.08 * (0.06)	ns	*732*

yr^{-1} for ramets >120 cm stemlength, $n=560$), than in small ramets (10.7 ± 8.2 cm yr^{-1} for ramets 10-120 cm, $n=203$).

Variation in some vital rates could also be explained by variation in genet size, as indicated by significant effects of genet size (leaf number or summed stem length) in regression models for ramet performance (Table 3). Genet size was especially important for stem growth of small ramets, but also influenced reproduction.

Differences between years

Several vital rates differed between the dry and the normal year (Table 4). Recruitment of new seedlings in the population was severely reduced in the dry year. Whether this was due to decreased germination rates or elevated

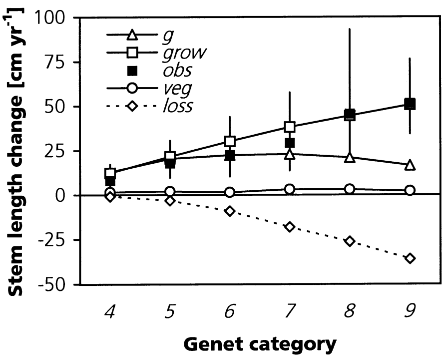


Figure 2
Change in genet stem length in *Geonoma deversa* in relation to size. Shown are the net genet growth rate in summed stem length (*g*) and its components: summed growth of surviving ramets (*grow*), contribution of vegetatively produced new ramets to stem length (*veg*) and loss of stem length due to ramet death (*loss*). Values for *grow* and *loss* were obtained from regression equations and *veg* is based on category means. Mean (± SD) of observed summed growth of surviving ramets (*obs*) is shown for comparison with regression values of *grow*.

mortality of recently germinated individuals could not be determined, as measurements were carried out on an annual basis. Newly emerged seedlings measured after the dry year (in March 1999) were also smaller than those found in 1998 (average number of leaves: 1.3 and 1.8 for n=106 and 203, respectively, t=5.9, $p<0.001$; leaf size: 6.2 and 7.1 respectively for same sample sizes, t=4.4, $p<0.001$). Seedling transition frequencies among the first two categories were comparable for the two measurement years. Leaf gain of juveniles in category *3* also did not differ between years (paired t-test, t_{13}=1.44, p=0.17).

For larger ramets and genets, most vital rates differed between the normal and dry year (Table 4). Stem growth of genets and large ramets was reduced by 15 to 30% in the dry year. Detailed observations on internode length and

Table 4
Between-year differences in vital rates of genets and ramets of *Geonoma deversa*. Averages (and SD) for a normal (1996-1997) and a dry year (1997-1998) are shown, as well as test results of repeated measures ANOVA for continuous variables (paired t-test for Recruitment, t-value underlined), and McNemar's or Chi-Square (italic) test for binary variables. Geometric means and upper back-transformed SD are shown for genet stem growth and recruitment rate; binomial SD is shown for binary variables. Small ramets have a stem height of 10-120 cm, large ramets of >120 cm. All rates are per year; stem length growth in cm yr^{-1}; recruitment as m^{-2} yr^{-1} ns: $p \geq 0.05$, *: $p<0.05$, **: $p<0.01$, ***: $p<0.001$.

	Parameter	Average		ANOVA - Within	McNemar	*n*
		Normal year	Dry year	F *p*	Chi^2 *p*	
Genets	Stem growth	24.4 (30.0)	20.9 (27.8)	18.7 ***		*163*
	Possessing raceme	0.69 (0.04)	0.76 (0.03)		4.4 *	*164*
	Recruitment	1.21 (0.47)	0.43 (0.17)	5.2 *		*3*
	Ramet production	0.15 (0.03)	0.03 (0.01)		12.9 ***	*165*
Ramets	Survival probability	0.98 (0.01)	0.98 (0.01)		*0.1* ns	*765*
	Stem growth small ramets	10.8 (8.1)	10.5 (8.2)	0.56 ns		*207*
	Stem growth large ramets	5.6 (4.1)	3.9 (3.5)	132.0 ***		*547*
	Possessing raceme	0.29 (0.02)	0.50 (0.02)		49.5 ***	*746*

Table 5

Population growth rates and similarity indices for different matrix models of *Geonoma deversa* for a normal year, a dry year and the stochastic model combining both years. Information for the stochastic model is for a dry year frequency of 0.12, the estimated value for the study region. PS is measure for similarity between observed population structure and stable stage structure; log(λ_s) is the average stochastic growth rate.

Model	Normal year (**N**)		Dry year (**D**)		Stochastic model	
	λ	PS	λ	PS	log(λ_s)	PS
Genet	1.059	95.7	1.030	97.3	0.054	96.2
Ramet	1.041	88.6	1.009	92.2	0.037	89.5
Integrated	1.037	89.5	1.003	93.4	0.033	90.5

leaf production rates (the two variables determining stem growth) showed that this pattern is mostly due to a strong decrease in internode length with ramet size rather than reduced leaf production rate. Vegetative production of new ramets was reduced by 80% during the dry year. However, the proportion of genets and ramets bearing racemes was higher at the end of a dry year than at the end of a normal year. Survival probability was not found to be different between measurement years for ramets, but this could not be tested for genets due to lack of observations on mortality.

Analysis of individual matrices

The three types of transition matrices for a normal year (**N**) are in Appendix A; those for dry year (**D**) in Appendix B. All matrices were characterised by high values for stasis probabilities. Matrix analyses showed that all asymptotic population growth rates (λ) were >1, but were lower for the dry than for the normal year and also varied among type of matrix (Table 5). Absolute values of λ should be interpreted with some care as survival probability for large genets was estimated.

Stable stage distributions of all models closely resembled observed population structures and values of the stable stage distribution did not deviate more than one standard deviation of the observed values in many size categories (Figure 3). Similarity index values (PS) of observed and stable stage structures were high to very high, both for normal and for dry year matrices (Table 5). Both results indicate that matrix projections resemble well the real population dynamics.

Reproductive values were low in all categories of the ramet and the integrated model; in the genet model they strongly increased with genet size (Figure 4). Elasticity values were highest for the early reproductive categories in the genet model, and were highest for intermediate-sized ramets in the ramet model (Figure 5). Using loop analysis (van Groenendael *et al.* 1994) in the genet model it was found that early and late reproductive pathways

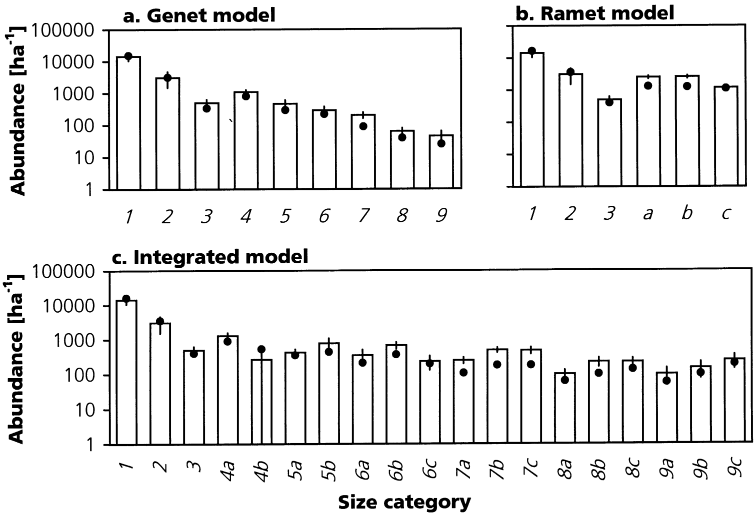


Figure 3

Observed population structures (mean ± SD) and stable stage structures resulting from matrix models for *Geonoma deversa*. Structures for genets (a), ramets (b) and ramets within genets (c, for integrated model) are shown. The same *y*-axis scaling is used to facilitate comparison. Numbers refer to genet size and letters to ramet size. Stable stage distributions is based on transition matrices for a normal year (N). Population structures are obtained from three stands in Northern Bolivia, in October 1996.

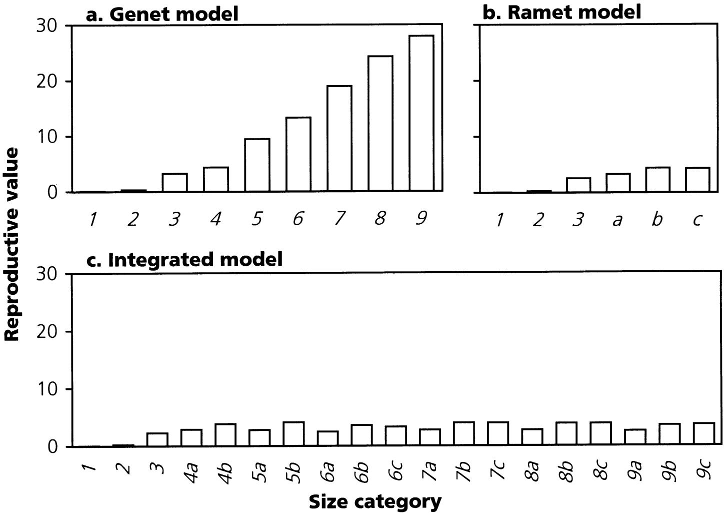


Figure 4

Reproductive values obtained for *Geonoma deversa* from a genet model (a), a ramet model (b), and an integrated model that combines ramets and genets. The same *y*-axis scaling is used to facilitate comparison. Numbers refer to genet categories and letters to ramet categories.

contributed less to the value of λ than medium-sized genets (highest loop elasticity in category *6* = 0.05). Loop analysis in the ramet model revealed that sexual reproduction loops were more important than vegetative reproduction loops (summed loop elasticities equal 0.12 and 0.03, respectively), and that elasticity of reproductive loops increases with ramet size. For the integrated model, no loop analysis could be performed due to the lack of unique loop elements (van Groenendael *et al.* 1994).

In the integrated model, ramet categories in small genets had larger elasticity than equally-sized ramet categories in large genets (Figure 5c), *e.g.* compare elasticities in *4a*, *5a*, ..., *9a*. Thus, ramets which belong to small genets contribute more to population growth than those that belong to large genets. This pattern is related to that obtained for the genet model: in that model elasticity is also higher in small genets. As a result, the sums of elasticities of all ramet categories pertaining to one genet category in the integrated model correlate closely with the elasticity for each genet category in the genet model (Figure 6a).

A comparison of the distribution of elasticities over matrix element types reveals strong similarities among the three models (Figure 6b). Stasis elasticities were highest, followed by growth, reproduction and retrogression. Sexual and vegetative reproduction transitions both had small contributions to population growth. Vital rate elasticity for the genet and ramet models were highest for

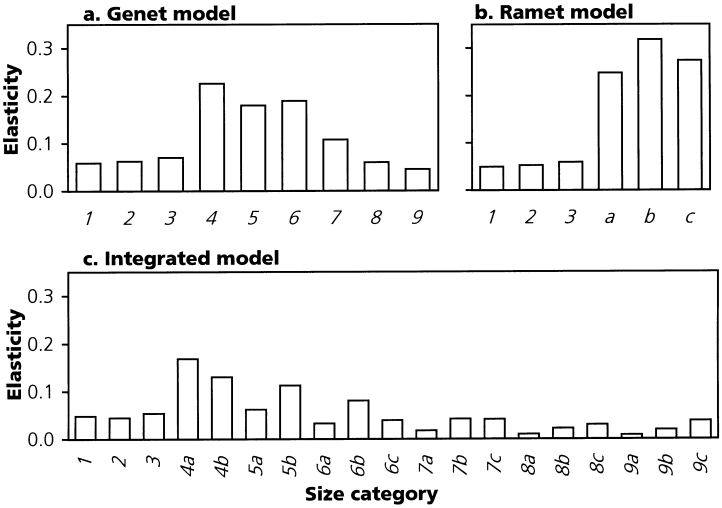


Figure 5

Elasticity values obtained for *Geonoma deversa* from a genet model (a), a ramet model (b), and an integrated model that combines ramets and genets. The same *y*-axis scaling is used to facilitate comparison. Numbers refer to genet categories and letters to ramet categories. Elasticities are for a situation with normal precipitation (matrix N), and are summed over all types of matrix elements for each categories.

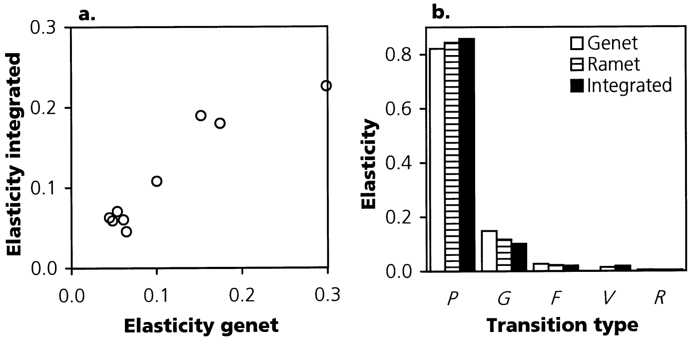


Figure 6

Comparison of elasticity output for population matrix models of *Geonoma deversa*. (a) Relation of elasticity output from genet and integrated model. Elasticity of genet model was summed over all matrix element types per genet category; elasticity of integrated model was summed over all matrix element types *and* over all ramet categories pertaining to a certain genet category (Correlation: r= 0.96, n=9, p<0.001). For instance, the x-value of the upper right symbol is the summed elasticity of the genet model for category *4* (0.23) and the y-value is the elasticity summed over all element types and over ramet categories pertaining to genet size *4* (*4a-c*; equals 0.30). (b) Summed elasticity values over all categories per type of matrix element: stasis probability (*P*), growth probability (*G*), sexual reproduction (*F*), vegetative reproduction (*V*) and retrogression (*R*). For the integrated model, stasis refers to staying in the same ramet-size category, and growth to growing to the next ramet-size category; thus, irrespective of the genet performance.

survival probability (σ, 89% of total elasticity for genet model, 88% for ramet model), followed by positive growth (γ, 7%, 5%), reproductive output (*f*, 2%, 2%) and vegetative reproductive output (only for ramet model: 4%).

Age estimates for ramets and genets differ considerably (Figure 7). Age conditional on entering the last genet category (τ) was estimated to be 97 yr,

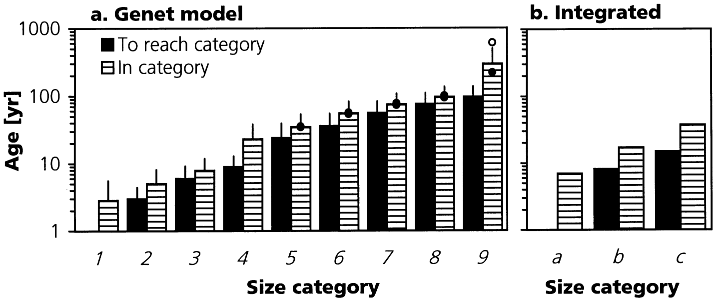


Figure 7

Age estimates for genets (a) and ramets (b) of *Geonoma deversa* as calculated using equations by presented by Cochran & Ellner (1992). Bars (mean ± SD) denote age conditional on reaching a category (τ) and mean age of residence in a category (*S*). Open dots in (a) for genet categories *5-9* indicate the mean age of residence when using a survival probability (σ) in these categories of 0.998; closed dots are estimates for σ=0.992. Numbers refer to genet categories and letters to ramet categories. Ages for ramets are from 10 stem length (an underestimation of 1-2 years), and were calculated by taking a weighted average over all categories with equal-sized ramets in the integrated model.

whereas the age to enter the largest ramet category for vegetatively produced ramets is only 14 yr. Similarly, mean age of residence (*S*) in largest genet category equalled 296 yr whereas that of large ramets amounted to only 37 yr. It should be noted that the values for ramet age are low estimates as vegetatively produced ramets enter the matrix model when they have attained a stem length of 10 cm, which probably takes 1-2 yr from the moment of emergence. Age estimates of the last genet category were accompanied by large standard deviations (*cf.* Boucher 1997) and were very sensitive to changes in survival probability, as indicated by the estimates using different genet survival probabilities (Figure 7).

Time-varying matrix analyses

Population growth rates for genets and ramets decreased linearly with frequency of dry years, both in deterministic and stochastic time-varying models (Figure 8). Different patterns of occurrence of dry years -deterministic *vs.* stochastic- had very similar influence on population growth rates. For stochastic time-varying models, positive and negative autocorrelation of year-types had very little effect on long-term population growth. Stochastic simulations using the estimated dry-year frequency obtained from precipitation patterns (π=0.12), and excluding the occurrence of two subsequent dry years (q=0), also yielded a population growth rate very close to that obtained in periodic matrix analysis (Figure 8). Stable stage structure of this stochastic model closely resembled the observed population structure, but similarity was almost equal to that of the normal or dry year matrices (Table 5).

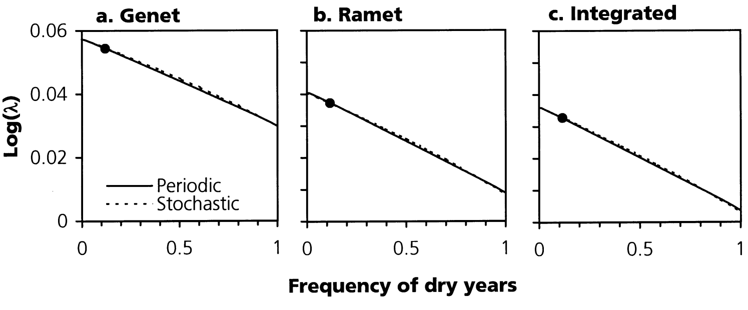


Figure 8

Influence of dry years on population growth rate in *Geonoma deversa*. Results of two time-varying matrix models (deterministic and stochastic) are shown for a genet model (a), a ramet model (b) and integrated model combining ramets and genets (c). Shown are the log(λ) for deterministic models and average log(λ_s) over 3000 model years for stochastic models. For stochastic models, simulation results for ρ=-0.1 and 0.1 (negative and positive autocorrelation) are not shown for the sake of clarity as they largely overlap with values for ρ=0 (no autocorrelation). The dot denotes the population growth for a model with a dry-year frequency (π) of 0.12 (the estimated value for the study region) and no successive occurrence of two dry years (q=1).

Discussion

Integrated matrix model

We applied a novel transition matrix model in which ramets are categorised by their own size and that of the genet to which they belong. The application of the combined model was suggested by the finding that genet size co-determines ramet performance (Table 3). Certain vital rates (growth and vegetative reproduction) of categories with equal-sized ramets therefore varied among genet categories.

Elasticity analysis of the combined model revealed that the contribution of ramet categories to population growth depends to a large extent on the genet category to which ramets belong (Figure 5). In other words, ramets in small genets are more important for population growth than equal-sized ramets in large genets. This result provides insight on the role of ramets in relation to the genet to which they belong. Such information could not be obtained from the ramet model. Therefore, demographic models that only consider ramet dynamics are likely to 'hide' information on the clonal demography that can assist in understanding a species' life history.

Furthermore, correlation between elasticity values between the genet and the integrated model (Figure 6a) shows that the integrated model can be interpreted as a refinement of the genet model. Thus, elasticity values in the genet model can be 'partitioned' into contributions of ramet categories. Elasticities in the integrated model, then, can be interpreted as the relative importance of ramet categories to genet population growth. This implies that, using a model that integrates genet and ramet demography, the role of ramets in the species' life history can be assessed. It should be noted, though, that the translation of ramet population growth to genet population growth assumes that the distribution of ramets over genets does not change; which is probably true for populations that are rather stable.

Ramet demography

Stem growth in small (<120 cm) ramets was twice that in large (>120cm) ramets. A relatively high growth rate of small ramets was also found in the congeneric *Geonoma congesta* (Chazdon 1992). In view of the low light availability in the understorey of tropical forests (Chazdon & Fetcher 1984, Chazdon 1986a), high growth rates in small shoots are remarkable and point to the occurrence of establishment support to small ramets by the rest of the clone (*cf.* Chazdon 1986a). This hypothesis is confirmed by the finding that growth of small ramets is positively related to genet size, suggesting that larger genets have more means to support growth of small ramets (Table 3). It is not clear, though, whether this support is mainly provided by the genet or by the 'mother' ramet. The establishment support probably consists of active support in the form of carbohydrate transport from the large mother ramet or other ramets (Callaghan 1984, Cook 1985). Apart from this, a small ramet may benefit from the rooting system of its mother ramet – or perhaps from that of the entire clone – as small vegetatively produced ramets do not possess roots yet (P.A. Zuidema, *personal observation*). In this way, initial ramet growth can be directed more to height growth, which is crucial as light availability gradually increases from the forest floor to *c*. 4 m height (Chazdon 1986a).

Low growth in large ramets may have different causes. The increasing reproductive output with ramet size and the high costs of reproductive structures may in part be responsible for the reduced growth (Piñero *et al.* 1982, Ash 1988). Indeed, during one of the measurement years, growth rate was lower in ramets that possessed racemes than in those that did not (data not shown). Similarly, large ramets produce more new ramets by vegetative reproduction (Table 3), and will probably experience higher costs of establishment support to small ramets. In addition, increasing maintenance costs for leaf support mass may also decrease the availability of carbohydrates for growth. Chazdon (1985, 1986b) showed that leaf support mass increases disproportionately with leaf area in two single-stemmed understorey palm species (*Geonoma congesta* and *Asterogyne martiana*). As a consequence, whole-shoot efficiency tends to decrease with ramet size (Chazdon 1986b). Another phenomenon that may explain low growth rates in large ramets is their instability. Stem diameter in clustered understorey palms typically amounts to 1-2 cm (Chazdon 1991a) and does not increase through secondary growth. Large ramets therefore tend to be physically unstable and susceptible to breakage (*cf.* Chazdon 1986b, 1992, Martinez-Ramos *et al.* 1988). High growth rates in large ramets could therefore increase breakage risk. In this study, dead ramets were observed both standing dead (an indication of senescence) and smashed down by falling debris (possibly the result of instability), but the small sample size did not allow a quantitative comparison of the importance of these causes. The combination of reduced leaf support efficiency, high reproductive output and increased breakage risk in large ramets may explain the relatively short life span for ramets found in this study (Figure 7b).

Genet demography

Genet demography is characterised by a large contrast in survival between seedlings and large individuals (Table 1). The low survival for small seedlings can be explained by the complete coverage of seedlings by fallen leaf litter during the dry season (P.A. Zuidema *personal observation*), and furthermore by the very low light availability at the forest understorey (canopy openness averaged 4.8 % at 1.5 height in the study plots; and is certainly lower at seedling level, *cf.* Chazdon 1986a). Once seedlings have reached the size category with adult-type leaves, they have a very high probability of surviving to maturity.

Genet death is probably caused by external factors such as tree and branch falls (*cf.* Piñero *et al.* 1984, De Steven 1989) and survival probability of established genets is very high. As a consequence, estimated genet life span is very long, amounting to at least several times that of vegetatively produced ramets (Figure 7). The importance of genet survival for population dynamics is reflected by the fact that survival accounts for almost 90% of the total vital rate elasticity in the genet model. For regular elasticities, stasis elements contain the largest proportion (0.82) of total elasticity (Figure 4), as generally found for long-lived species (Silvertown *et al.* 1993, Chapter 7).

Net genet growth and vegetative ramet production decreased in large genets (Figure 2). This pattern may be interpreted as a sign of senescence (Watkinson 1992), but this is not justified by the increasing sexual reproductive output with size, the very high reproductive values in large genets (Figure 4) and the equal survival probability assumed for all genet size categories. In addition, self-shading among ramets is more apparent in large genets. This is potentially important in *Geonoma* as the species' clustered growth form limits the distance among ramet crowns in a genet (*cf.* Chazdon 1986b). In the two largest genet categories, the number of large ramets (>120 cm) amount to 6.7 and 8.3, respectively, among which mutual shading can hardly be avoided.

Tolerance to climatic variation

The impact of reduced precipitation differed markedly among vital rates. Sexual reproduction and vegetative ramet production were most heavily affected, followed by stem growth, whereas survival probabilities were not different between a normal and a dry year (Table 4).

In spite of the large reductions of some vital rates in the dry year, population growth was only moderately decreased in the dry year model (Table 5). As a consequence, the sequence of occurrence of dry and normal years (random in stochastic models *vs.* cyclic in deterministic models) hardly affected long-term population growth rates (Figure 8).

The small reduction in population growth rate in the dry year model can be attributed to the fact that the most important vital rate – survival probability – was not affected by the dry year. The capacity of *Geonoma* individuals to survive dry years is therefore essential for its demographic tolerance to dry years.

Clonality in *Geonoma deversa*

Clonality is thought to have evolved several times in the genus *Geonoma* as clonal species are present in all sub-genera within *Geonoma* (Chazdon 1991, Wessels-Boer 1968). Apparently, a clonal growth form is an adequate strategy given the understorey conditions in which all *Geonoma* species grow. Clonality may be beneficial for these species in several ways.

One hypothesis is that mortality risk of genet is spread among ramets (Eriksson & Jerling 1990). The risk spreading hypothesis predicts that the risk of genet death (by simultaneous death of all ramets) is reduced as the number of ramets (each with a certain intrinsic mortality risk) is increased (Eriksson & Jerling 1990). It has to be kept in mind, though, that genet death in *Geonoma deversa* and related species is most likely caused by external factors, and not by simultaneous death of all ramets due to intrinsic factors.

Alternatively, a clonal growth form may be adaptive as it extends the genet's reproductive life span by continuous replacement of ageing ramets and increases the number of modules that can contribute to the genet's reproductive output (De Steven 1989, Chazdon 1992, Mendoza & Franco 1998). Several results from this study may confirm this hypothesis. Firstly, life span of genets is (very) long and genets do not show signs of senescence, whereas ramet life span is relatively short and ramet mortality increases with ramet size. The observed establishment support to new vegetatively formed ramets may contribute to the replacement of ageing ramets. Secondly, reproductive output in genets steeply increases with plant size, as can is seen in the reproductive values resulting from matrix models. Related to this, it appears that expansion of genet size is an important feature in *Geonoma*, as vegetative reproduction starts before sexual reproduction, and as strong establishment support is given to new ramets.

Following this line of reasoning, clonality in clustered understorey palms should be considered more a form of growth of an existing individual rather than a form of reproduction. The clonal strategy in *Geonoma* seems to ensure a large lifetime reproductive output of genets, which is important in view of the unfavourable light conditions in which new seedlings emerge.

Acknowledgements

We are grateful to Luis Apaza, Rene Aramayo and to the inhabitants of El Turi for their indispensable support during fieldwork, and to the community of El Turi for its hospitality during field evaluations. Geert Jan van Oldenborgh at the Royal Netherlands Meteorological Institute (KNMI) kindly provided long-term precipitation data. Roderick Zagt provided script files for age calculations. Rene Boot, Hans de Kroon, Graham Floater, Miguel Franco, Josef Stuefer and Jan van Groenendael gave valuable comments on draft versions of the manuscript. This study was partly funded by grant BO009701 from the Netherlands Development Assistance.

Appendix A

Population transition matrices for the genet model (1), ramet model (2), and the integrated model combining genets and ramets (3) for *Geonoma deversa* in a normal year (N). Life cycle graphs are shown in Fig. 1 and category characteristics in Table 1. Blocks in the integrated model group ramet matrix elements that are nested within one genet element: *e.g.* the block enclosing ramet transition *41-51* includes the transitions of ramets within a genet that grows from category *4* to *5*.

1. Category at *t*+1 / Category at *t*

Category at *t*+1	*1*	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*
1	0.506	0.351	0	0.7	4.9	10.0	16.1	23.3	29.7
2	0.108	0.539	0	0	0	0	0	0	0
3	0	0.043	0.658	0	0	0	0	0	0
4	0	0	0.299	0.934	0	0	0	0	0
5	0	0	0	0.053	0.914	0	0	0	0
6	0	0	0	0	0.081	0.951	0	0	0
7	0	0	0	0	0	0.044	0.949	0	0
8	0	0	0	0	0	0	0.046	0.953	0
9	0	0	0	0	0	0	0	0.042	0.995

2. Category at *t*+1 / Category at *t*

Category at *t*+1	*1*	*2*	*3*	*a*	*b*	*c*
1	0.506	0.351	0	0.2	2.9	3.4
2	0.108	0.539	0	0	0	0
3	0	0.043	0.658	0	0	0
a	0	0	0.299	0.905	0.023	0.026
b	0	0	0	0.1	0.937	0
c	0	0	0	0	0.054	0.98

3. Category at *t*+1 / Category at *t*

Category at *t*+1	*1*	*2*	*3*	*4a*	*4b*	*5a*	*5b*	*6a*	*6b*	*6c*	*7a*	*7b*	*7c*	*8a*	*8b*	*8c*	*9a*	*9b*	*9c*
1	0.506	0.351	0	0.15	2.21	0.15	2.91	0.15	2.91	3.42	0.15	2.91	3.42	0.15	2.91	3.42	0.15	2.91	3.42
2	0.108	0.539	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3	0	0.043	0.658	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4a	0	0	0.299	0.895	0.034	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4b	0	0	0	0.064	0.927	0	0	0	0	0	0	0	0	0	0	0	0	0	0
5a	0	0	0	0.051	0.001	0.855	0.039	0	0	0	0	0	0	0	0	0	0	0	0
5b	0	0	0	0.004	0.053	0.070	0.906	0	0	0	0	0	0	0	0	0	0	0	0
6a	0	0	0	0	0	0.076	0.003	0.868	0.015	0.007	0	0	0	0	0	0	0	0	0
6b	0	0	0	0	0	0.006	0.076	0.080	0.892	0	0	0	0	0	0	0	0	0	0
6c	0	0	0	0	0	0	0.004	0	0.050	0.932	0	0	0	0	0	0	0	0	0
7a	0	0	0	0	0	0	0	0.040	0.001	0.000	0.860	0.025	0.029	0	0	0	0	0	0
7b	0	0	0	0	0	0	0	0.004	0.042	0	0.090	0.889	0	0	0	0	0	0	0
7c	0	0	0	0	0	0	0	0	0.002	0.043	0	0.052	0.931	0	0	0	0	0	0
8a	0	0	0	0	0	0	0	0	0	0	0.041	0.001	0.001	0.855	0.025	0.030	0	0	0
8b	0	0	0	0	0	0	0	0	0	0	0.004	0.043	0	0.098	0.891	0	0	0	0
8c	0	0	0	0	0	0	0	0	0	0	0	0.002	0.045	0	0.054	0.934	0	0	0
9a	0	0	0	0	0	0	0	0	0	0	0	0	0	0.037	0.001	0.001	0.882	0.015	0.025
9b	0	0	0	0	0	0	0	0	0	0	0	0	0	0.004	0.039	0	0.110	0.928	0
9c	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.002	0.041	0	0.058	0.975

Appendix B

Population transition matrices for the genet model (1), ramet model (2), and the integrated model combining genets and ramets (3) for *Geonoma deversa* in a dry year (D). See Appendix A for explanation.

1\. Category at t+1 / Category at t

Category at t+1	*1*	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*
1	0.506	0.351	0	0.3	1.8	3.5	5.7	8.3	10.5
2	0.108	0.539	0	0	0	0	0	0	0
3	0	0.043	0.658	0	0	0	0	0	0
4	0	0	0.299	0.946	0	0	0	0	0
5	0	0	0	0.041	0.933	0	0	0	0
6	0	0	0	0	0.062	0.963	0	0	0
7	0	0	0	0	0	0.032	0.968	0	0
8	0	0	0	0	0	0	0.027	0.974	0
9	0	0	0	0	0	0	0	0.021	0.995

2\. Category at t+1 / Category at t

Category at t+1	*1*	*2*	*3*	*a*	*b*	*c*
1	0.506	0.351	0	0.1	1.0	1.2
2	0.108	0.539	0	0	0	0
3	0	0.043	0.658	0	0	0
a	0	0	0.299	0.923	0.005	0.006
b	0	0	0	0.071	0.949	0
c	0	0	0	0	0.042	0.98

3\. Category at t+1 / Category at t

Category at t+1	*1*	*2*	*3*	*4a*	*4b*	*5a*	*5b*	*6a*	*6b*	*6c*	*7a*	*7b*	*7c*	*8a*	*8b*	*8c*	*9a*	*9b*	*9c*
1	0.506	0.351	0	0.05	0.78	0.05	1.03	0.05	1.03	1.21	0.05	1.03	1.21	0.05	1.03	1.21	0.05	1.03	1.21
2	0.108	0.539	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3	0	0.043	0.658	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4a	0	0	0.299	0.897	0.002	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4b	0	0	0	0.048	0.939	0	0	0	0	0	0	0	0	0	0	0	0	0	0
5a	0	0	0	0.039	0.000	0.874	0.009	0	0	0	0	0	0	0	0	0	0	0	0
5b	0	0	0	0.002	0.041	0.055	0.925	0	0	0	0	0	0	0	0	0	0	0	0
6a	0	0	0	0	0	0.058	0.001	0.890	0.003	0.001	0	0	0	0	0	0	0	0	0
6b	0	0	0	0	0	0.004	0.059	0.065	0.916	0	0	0	0	0	0	0	0	0	0
6c	0	0	0	0	0	0	0.002	0	0.038	0.944	0	0	0	0	0	0	0	0	0
7a	0	0	0	0	0	0	0	0.030	0.000	0.000	0.884	0.006	0.007	0	0	0	0	0	0
7b	0	0	0	0	0	0	0	0.002	0.031	0	0.077	0.921	0	0	0	0	0	0	0
7c	0	0	0	0	0	0	0	0	0.001	0.032	0	0.038	0.948	0	0	0	0	0	0
8a	0	0	0	0	0	0	0	0	0	0	0.025	0.000	0.000	0.882	0.006	0.007	0	0	0
8b	0	0	0	0	0	0	0	0	0	0	0.002	0.026	0	0.086	0.928	0	0	0	0
8c	0	0	0	0	0	0	0	0	0	0	0	0.001	0.027	0	0.038	0.955	0	0	0
9a	0	0	0	0	0	0	0	0	0	0	0	0	0	0.019	0.000	0.000	0.891	0.003	0.006
9b	0	0	0	0	0	0	0	0	0	0	0	0	0	0.002	0.020	0	0.096	0.946	0
9c	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.001	0.020	0	0.040	0.975

Leaves of the 'jatata' palm Geonoma deversa *, prepared for roof thatching.*

Chapter 5

Impact of artificial defoliation on ramet and genet demography in a Neotropical understorey palm

Pieter A. Zuidema & Marinus J.A. Werger

Summary

A defoliation experiment was carried out in the clustered understorey palm *Geonoma deversa* from which leaves are harvested for high-quality roof thatches. The treatment consisted of cutting all leaves of all large ramets once. Survival, growth and reproduction of defoliated palms were recorded during two years following treatment, and population-level consequences were assessed using matrix population models. Responses to defoliation varied widely among vital rates: no increase in mortality was observed after defoliation; leaf production rate of defoliated ramets decreased by 16 and 9% (first and second year, respectively); stem growth by 43 and 29%; probability of reproduction by 40 and 60% and rate of vegetative production of new ramets by an estimated 70% for both years. Undisturbed small ramets in defoliated clones were not affected by the treatment, as they showed no changes in growth rate and reproductive effort. Thus, the impact of defoliation appears to be localised in the treated ramets. After one year defoliated ramets had regained 36% of their initial leaf number, after two years this amounted to 68%. It is argued that stored reserves are likely to have partly covered the large costs for recuperation after leaf removal. Population growth rate was only moderately reduced in defoliated populations compared to an undisturbed population, both during the first and second year after leaf removal. This can be attributed to the combination of a high sensitivity of population growth for changes in survival and a lack of a defoliation impact on survival. Time-varying, periodic matrix models were used to simulate the effect of varying the frequency of leaf cutting (every 16, 8 and 4 yr) on population size and future availability of leaves. Model projections show that leaf availability in defoliated populations always remains below that in an undisturbed population. Nevertheless, at low harvest frequency, leaf availability of exploited populations remained close to those for undisturbed ones. These results suggest that there are good prospects for sustained leaf extraction from *Geonoma deversa*.

Introduction

Extraction of non-timber forest products (NTFP) is considered a locally important source of income from tropical rain forests (Peters *et al.* 1989b, Richards 1993, FAO 1997a). Palms are probably the most widely used plant family for NTFP collection, with a large number of useful species that yield many different types of products (Balick & Beck 1990, Johnson 1991, Kahn & de Granville 1992, FAO 1997b). All plant parts of palms are used: leaves for roofing and basketry, trunks for construction and furniture, apical meristem for palm heart, fruits for juices, and roots for medicine.

Leaves of understorey palm species in the genera *Chamaedorea, Geonoma* and others are intensively used for thatching, basketry and ornamental purposes (Hodel 1992, FAO 1997b). The small size (generally <5 m height, Wessels Boer 1968, Henderson *et al.* 1995) of these species makes them especially suitable for leaf extraction. Furthermore, leaf harvesting generally does not kill the individual and therefore has the potential to be carried out repeatedly.

Whether palm leaf extraction may be sustained over longer periods depends on the ability of individuals to survive defoliation and recuperate their leaf area after leaves have been removed. Impact of defoliation has been studied for a number of understorey palms belonging to the genera *Astrocaryum* (Mendoza et al 1987), *Calytrogyne* (Cunningham 1997), *Chamaedorea* (Oyama & Mendoza 1990), *Geonoma* (Chazdon 1991b) and *Livistonia* (O'Brien & Kinnaird 1996). These studies point out that defoliation generally does not increase mortality, although mortality risk may be higher for juveniles that have been completely defoliated (Mendoza *et al.* 1987). Responses of other vital rates (growth and reproduction) were found to vary among species and defoliation intensities. Post-defoliation leaf production remained equal in some species (Chazdon 1991b, partial defoliation in Mendoza *et al.* 1987), and was more than doubled in others (partial and complete defoliation in Oyama & Mendoza 1990). Similarly, reproductive effort was found to be severely reduced in some species-treatment combinations (complete defoliation in Mendoza *et al.* 1987), and increased in others (partial defoliation, Oyama & Mendoza 1990). In spite of the variation in responses to defoliation, the general pattern emerging from these studies is that of a tolerance for (high levels of) defoliation and the ability to recuperate rather well after treatment.

The tolerance of individuals of understorey palms to defoliation makes these species potentially suitable for commercial leaf extraction. However, this suitability also depends on how populations respond to defoliation, as changes in individual performance due to defoliation may alter population growth. Simulations of population-level leaf availability through time can indicate the consequences of different leaf cutting regimes and in this way assist in the design of management systems for sustained leaf extraction. In spite of the considerable attention given to the individual-level impact of leaf removal in undergrowth palms, the population-level consequences of leaf cutting practices have not been quantified so far. For other non-timber forest products, however, population-level analyses of NTFP extraction have been carried out using matrix models (Caswell 1989b, Peters 1990a, b, Pinard & Putz 1992, Pinard 1993, Olmsted & Alvarez-Buylla 1995, Bernal 1998, Peña-Claros & Zuidema 1999).

This paper analyses the impact of defoliation in the clustered understorey palm *Geonoma deversa*, both at the level of the individual and that of the population. Leaves of this species are harvested from natural stands in Neotropical forests and used for thatching (Wessels Boer 1968, FAO 1997a). The study species has a clonal growth form (*i.e.* produces new shoots by vegetative reproduction) and all shoots (ramets) within a clone (genet) remain connected. Therefore, leaf cutting does not only influence the defoliated shoot, but also other shoots within the clone. We report on a defoliation experiment in which all leaves of large ramets were removed. The impact of leaf removal on survival, growth and reproduction of genets and ramets is evaluated. We then quantify the impact of defoliation on population dynamics using population matrix models and simulate the development of population size and leaf availability for different defoliation regimes.

The following questions are addressed. (1) What is the impact of defoliation of large ramets on vital rates (survival, growth and reproduction)? We consider the effect of leaf removal at three levels: large defoliated ramets, small undisturbed ramets, and genets. (2) What are the consequences of defoliation for population growth of ramets and genets? And, (3) how do different defoliation regimes influence future population size and availability of leaves?

Study species

The study species

Geonoma deversa (Poit.) Kunth (hereafter mentioned by its generic name only) is a clonal understorey palm which is widespread in the Neotropics (Wessels Boer 1968, Henderson *et al.* 1995), and frequently occurs in high-density stands (Wessels Boer 1968, Moraes 1996). Leaves of large ramets (≥ *c.*120 cm stem length) are cut. Harvested leaves are irregularly dissected and have a leaf blade length of *c.*30 cm. Leaves are tightly woven on poles at a density of 100-150 per m. The thick panels thus formed are used for high quality thatching that may last for several decades. An estimated 1000 leaves is needed for 1 m^2 of roof thatch. In Northern Bolivia and Peru, panels are used locally in forest communities and traded to urban centres (Rioja 1992, Moraes *et al.* 1995).

Geonoma has a clustered growth form and genets may contain up to 11 large ramets. Genets possess on average 32 (SD =18, *n*=186 genets) leaves that may be harvested. Ramets may attain a height of over 4 m and possess 7.4 ± 2.3 harvestable leaves (*n*=798 ramets). Total abundance of large ramets in our study plots amounted to 38 ± 8 per $100m^2$, possessing a total of 319 ± 76 harvestable leaves per $100m^2$. A detailed description of genet and ramet demography in three undisturbed populations is provided in Chapter 4.

Methods

Defoliation experiment

The study was carried out in the Northern Bolivian Amazon, close to the forest community of El Turi (Pando Department, 11°45'S, 67°20'W), from late 1996 to early 1999. The area is covered by lowland moist forest with a mean annual precipitation of 1703 mm and a dry spell from May to September during which monthly precipitation does not surpass 100 mm.

The defoliation experiment was conducted parallel to a demographic study on undisturbed populations which also served as a control for the experiment (Chapter 4). Information on the selection of stands and the design of the undisturbed population study can be found in Chapter 4. The defoliation experiment was carried out in an area of 20 × 30m adjacent (at 5 m distance) to the plot used for the undisturbed population study populations, and replicated in three stands (A-C). In each experimental plot, all genets with at least one ramet >120 cm stem length were identified and subsequently 4 genets were randomly selected from this pool for each of the following size categories: 1-3 ramets (of >120 cm stem length), 4-6, 7-9, and >9. Selected genets were tagged and measured, and were defoliated in November 1996. The defoliation treatment consisted of cutting all green leaves of ramets >120 cm stem length, without damaging the developing leaf or the ramet itself. This treatment mimics the leaf harvest as practised in Bolivia and Peru. Subsequent measurements on defoliated genets were carried out simultaneously with those on undisturbed individuals, in October 1997 and October 1998.

Field measurements

Survival, growth and reproductions of defoliated individuals were monitored in the same way as in the study on undisturbed population dynamics

(Chapter 4), but did not include any measurements on genets without a ramet of >120 cm. The parameters measured are listed briefly here; details can be found in Chapter 4.

At the level of ramets, the following parameters were recorded at each census: total stem length, number of green leaves, number of racemes bearing flowers or fruits, and whether ramet has been or currently is reproductive. Leaf production rate, stem growth rate and length of new internodes (quotient of rates of stem growth and leaf production) were calculated for both measurement years.

At the level of genets the number of recently emerged ramets (<10 cm stem length) was noted at each census to estimate the rate of vegetative reproduction. Other genet-based parameters were derived from data on ramets (>10 cm stem length): summed stem length, growth in summed stem length (summing growth rates of surviving ramets), total number of leaves, total leaf production, and number of ramets with racemes bearing flowers or fruits. Leaf blade length, an indicator for leaf size, was determined for all ramets (>10 cm stem length) of 18 randomly selected genets in the three undisturbed population plots and 20 genets in the defoliation experiment. Recruitment of new seedlings was determined in seedling plots in the undisturbed populations.

Statistical analysis

The second of the two measurement years was unusually dry, causing various vital rates to be markedly different (see Results). The different climatic conditions in the second year interfered with the process of recuperation after defoliation. To identify how treatment effects differed between years, a repeated measures ANOVA was performed. Further per-year analyses were performed to determine effects of defoliation on vital rates at the level of genets and ramets. This was done using regression models with size-related parameters as covariates and the defoliation treatment as factor. In all analyses, data obtained from the undisturbed population study (Chapter 4) were used as a control for the defoliated individuals.

Construction of transition matrices

Size-based matrix population models (Lefkovitch 1965, Caswell 1989a) were applied to describe population dynamics in the first and second year after defoliation. These models are of the form: $\mathbf{n}(t+1) = \mathbf{A}\ \mathbf{n}(t)$, where $\mathbf{n}(t)$ and $\mathbf{n}(t+1)$ are population structures at time t and $t+1$ respectively and $\mathbf{A}$ is a square matrix containing transition probabilities among categories. When projected over a long time period, the predicted size structure becomes stable and the population grows or decreases at a constant rate. This stable stage structure can be shown to be the right eigenvector w of matrix $\mathbf{A}$ and the

Table 1

Classification criteria and defoliation treatment for genet and ramet categories of *Geonoma deversa*. Number and percentage of leaves cut in defoliation treatment are given under Defoliation, and sample sizes for undisturbed (Und) and defoliated (Def) populations under *n*. Category numbers refer to genet size and letters to ramet size. Ramet categories are nested within genet categories *e.g*. category *7c* are large (>230 cm) ramets being part of genets in category *7*. Number of leaves are annotated with b for bifid (juvenile) leaves and with d for dissected (adult) leaves. Classification criteria for stem length are upper class limits. Stem length for genets is summed over all ramets >10 cm.

		Leaves	Stem length		Defoliation		*n*	
			Genet	ramet	nr	%	Und	Def
Model			[cm]	[cm]	leaves	leaves		
Genet	*1*	1-3 b					*135*	
	2	4-6 b					*38*	
	3	1-3 d	<10				*17*	
	4	≥ 4 d	250		2.3		*39*	*1*
	5		500		13.3	55	*25*	*7*
	6		1000		24.5	77	*37*	*20*
	7		1500		37.6	83	*35*	*11*
	8		2000		53.2	82	*17*	*9*
	9		>2000		64.8	78	*12*	*3*
Ramet	*1*	1-3 b					*135*	
	2	4-6 b					*38*	
	3	1-3 d	<10	<10	0.0	0	*17*	
	4a	≥ 4 d	250	120	0.0	0	*44*	*1*
	4b	≥ 4 d	250	>120	8.2	100	*10*	
	5a		500	120	0.0	0	*24*	*11*
	5b		500	>120	8.2	100	*40*	*12*
	6a		1000	120	0.0	0	*47*	*26*
	6b		1000	230	7.5	100	*87*	*43*
	6c		1000	>230	7.4	100	*30*	*20*
	7a		1500	120	0.0	0	*52*	*15*
	7b		1500	230	7.9	100	*89*	*27*
	7c		1500	>230	7.1	100	*83*	*29*
	8a		2000	120	0.0	0	*27*	*21*
	8b		2000	230	7.4	100	*61*	*32*
	8c		2000	>230	7.2	100	*61*	*32*
	9a		>2000	120	0.0	0	*27*	*10*
	9b		>2000	230	7.2	100	*40*	*17*
	9c		>2000	>230	7.2	100	*67*	*11*

population growth rate the dominant eigenvalue λ of $\mathbf{A}$ (Caswell 1989a).

Transition matrices were constructed for both genets and ramets, to allow quantification of the impact of defoliation at both levels. Ramet dynamics were described in relation to the genet to which they belong as ramet vital rates were shown to be co-determined by genet characteristics (Chapter 4). The ramet model (introduced as "integrated model" in Chapter 4) couples the dynamics of ramets and genets. In this model, ramets are categorised by their own size and that of the genet to which they belong, so that ramet categories are nested in genet categories (Table 1, Figure 1). The first three categories are identical for the genet and ramet models.

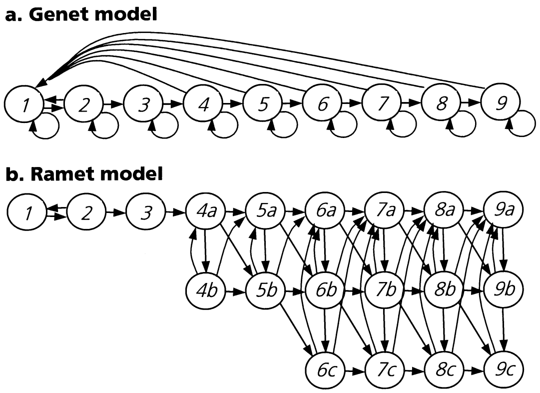


Figure 1
Life cycle graphs for genets (a) and ramets (b) of *Geonoma deversa*. Arrows indicate transitions among categories. Classification criteria and category descriptions are in Table 1. In the ramet life cycle (b), ramets can grow to the next ramet category in a genet that remains in the same genet category (vertical arrows), or in a genet that grows to the next category (diagonal arrows); similarly, ramets can remain in the same category in a genet that moves to the next category (horizontal arrows) or a genet that remains in the same category (stasis self-loops of ramet categories not shown); ramets may vegetatively produce a new ramet (bending arrows to categories *41*, *51*, etc.; straight horizontal arrows from *41* to *51* etc. also include vegetative ramet production); and ramets may produce new individuals by sexual means (from categories *41* and higher to *11*, arrows not shown). Underlined numbers indicate categories of which all (b) or part (a) of the leaves were removed.

Year-based transition matrices were constructed for genet and ramet populations during the first (**C**1) and the second (**C**2) year after defoliation. Both matrices are modifications of the matrices for an undisturbed population in a normal year (**N**) which were presented in Chapter 4.

Transition probabilities among categories *1-3* for the defoliation matrices are equal to those in the undisturbed population matrix (**N**) as defoliation does not affect these transitions. An influence of leaf cutting on seedling dynamics by altering light conditions is unlikely. Values for all other matrix elements were calculated by combining category-specific values for vital rates, obtained from regression models or category means. Further information on the parameterisation of matrices is provided in Chapter 4.

To determine values of matrix elements in matrices **C**1 an **C**2, those vital rates that were found to be significantly altered by defoliation were changed with respect to their value in a transition matrix of an undisturbed population (**N**). That is, the proportional change due to defoliation was applied to the value for the undisturbed population. For both defoliation matrices (**C**1 and **C**2), the impact of defoliation on production of sexually produced offspring was estimated by the drop in the proportion of ramets possessing reproductive racemes. Observations on reproductive status were conducted at the end of the first and second measurement year, and not during the course of the years. It was assumed that this proportion was indicative for the raceme production during that year. Furthermore, it was assumed that a reduction in the proportion of ramets with flowers or fruits causes an equal proportional reduction in recruitment of new individuals in the population.

For the elaboration of matrices for the second year after defoliation (**C**2) some assumptions were made with regard to the combination of recuperation after harvest and the occurrence of a dry year. Effects of relative drought and of recuperation after defoliation interacted (see Results). As these two effects could not be separated, it was assumed that the dry conditions during the second measurement year had equally affected undisturbed and defoliated individuals. This assumption is reasonable when root capacity per unit leaf area is the same in defoliated and undisturbed plants. For herbs it has been shown that growth response after defoliation is directed towards a rapid return to the original root:shoot ratio (Ryle & Powell 1975, Oesterheld 1992). Although for understorey palms no such data are available, it is probable that a similar regulation of root:shoot ratio takes place in order to optimise growth rate after defoliation (Hilbert 1990). We therefore applied the proportional changes in vital rates observed in the second year to the values for undisturbed individuals in a normal year. When our assumption does not hold, *e.g.* due to a slow response of root:shoot ratio, the defoliation effect in the second year matrix (**C2**) underestimates the real impact.

The rate of vegetative reproduction was very low during the second measurement year, probably due to reduced rainfall (see Table 4). As a result, no difference could be found between defoliated and undisturbed individuals. As vegetative reproduction was strongly reduced during the first year (see Table 4), it was likely to be similarly affected during the second year. Therefore, vegetative reproduction in the second year was reduced by the same proportion as in the first year.

Matrix analyses

Matrix analyses were performed on single, time-invariant matrices and on sequences of matrices (time-varying models). The analysis of single matrices consisted of calculating population growth rates (λ, Caswell 1989a) and performing elasticity analysis (de Kroon *et al.* 1986).

Time-varying matrix models were used to project population dynamics after (repeated) defoliation. In such models, sequences of matrices are applied to determine the effect of temporal changes in population dynamics (*i.e.* different transition matrices) on population development. Deterministic and stochastic time-varying models can be distinguished, of which the former (periodic matrix models) may be analysed analytically (Caswell 1989a). In a study on undisturbed demography of *Geonoma* (Chapter 4), it was shown that both methods yielded very similar population growth for sequences of normal and dry years, probably related to the fact that differences among matrices were not large. As differences between transition matrices of defoliated (**C1** and **C2**) and undisturbed (**N**) populations presented here are comparable with those for normal and dry years (see Results), we expected to find similar results using both methods, and choose to use the analytically solvable periodic matrix models.

The study region experiences dry years at an estimated frequency of 12% and *Geonoma* demography in dry years differ from that in normal years (Chapter 4). A sequence of seven normal years followed by one dry year ($\mathbf{DN}^7$) was therefore used as the basis for simulations of defoliation impact on population dynamics. Three periodic matrices were constructed to simulate defoliation once every 16, 8 and 4 years. Population dynamics after defoliation was described as follows: for the first year after defoliation transition matrix **C1** was applied; for the second and third year **C2**, and thereafter the matrix for an undisturbed population during a normal (**N**) or a dry (**D**) year. Matrix **C2** was used for the third year after defoliation as no demographic data were available for that year. After three years, the leaf number of defoliated individuals has probably recovered completely, since treated palms regained one-third of their original leaf number per year during the first two years (see Results). It therefore seemed reasonable to use matrices for undisturbed populations (**N** or **D**) for the fourth year onwards.

The following models were used to describe time-varying population dynamics for a situation without defoliation (Eq. 1) and for situations with repeated defoliation every 16, 8 and 4 yr (Eqs. 2, 3 and 4 respectively):

$$\mathbf{n}(t+8) = \mathbf{D}\ \mathbf{N}^7\ \mathbf{n}(t) \qquad \text{[Undisturbed]} \qquad (1)$$

$$\mathbf{n}(t+16) = \mathbf{D}\ \mathbf{N}^7\ \mathbf{D}\ \mathbf{N}^5\ \mathbf{C2}^2\ \mathbf{C1}\ \mathbf{n}(t) \qquad \text{[Defoliated 1/16]} \qquad (2)$$

$$\mathbf{n}(t+8) = \mathbf{D}\ \mathbf{N}^4\ \mathbf{C2}^2\ \mathbf{C1}\ \mathbf{n}(t) \qquad \text{[Defoliated 1/8]} \qquad (3)$$

$$\mathbf{n}(t+8) = \mathbf{D}\ \mathbf{C2}^2\ \mathbf{C1}\ \mathbf{N}\ \mathbf{C2}^2\ \mathbf{C1}\ \mathbf{n}(t) \qquad \text{[Defoliated 1/4]} \qquad (4)$$

It should be noticed that the chronological order in these equations is from right to left, *e.g.* starting with a first-year defoliated matrix (**C1**) in equation 2. For each of these models, annual population growth rate (λ) of the product matrix was calculated (Caswell 1989a). As λ is calculated for the product matrix, normal sensitivity or elasticity analyses cannot be applied. An alternative analysis was developed by Caswell & Trevisan (1994), which indicates the influence of changes in matrix elements during the cycle on the population growth rate of the product matrix. For each of the four periodic matrix models, elasticity analyses were carried out using this approach.

Leaf availability was projected in time for an undisturbed population and for the different leaf cutting regimes. To do so, population distributions were projected using the four periodic matrix models (Eqs 1-4), both for genets and ramets. For each simulation step, the projected abundance of individuals in a category was multiplied by the *per capita* number of harvestable leaves, and these values were summed over all size categories to obtain the leaf availability at population level. The number of harvestable leaves needed for these calculations was obtained by regressing leaf number on (summed) stem length and subsequently filling in category midpoints of (summed) stem length for each size category. In case regression models were non-significant, the overall mean leaf number was used for all categories. From the third year after defoliation onwards, leaf number was assumed to be equal to that in an undisturbed population.

Results

Impact of defoliation on individual vital rates

The impact of defoliation on a number of vital rates appeared to be different in the two measurement years, as shown by the significant interaction terms of defoliation and year in ANOVA results (Table 2, Figure 2). Stem growth (undisturbed large ramets and genets) and internode length (large ramets) were lower in the second measurement year, whereas those for defoliated individuals were equal or higher. Lower values in undisturbed individuals are most likely due to the influence of the dry conditions during the second year. As a consequence, the stable values for defoliated individuals should actually be interpreted as a process of recuperation

In genets and large ramets, effect of defoliation was apparent for stem growth, and this was mainly due to the reduction in internode length and to

Table 2

Effect of defoliation, year of measurement and their interaction on vital rates of *Geonoma deversa*. Results of a repeated measures ANOVA (ns: $p \geq 0.05$, *: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$) are shown with defoliation as between-subjects factor and both year and defoliation × year interaction as within-subject factors. Genets with summed stem length >120 cm were included in analyses; small ramets are 10-120 cm stem length; large ramets >120 cm.

	Parameter	Defoliation		Year		Defol × Year		*n*
		F	*p*	F	*p*	F	*p*	
Genets	Stem growth	8.10	**	4.04	*	7.35	**	*184*
	Leaf production	0.02	ns	0.96	ns	0.54	ns	*186*
Small ramets	Stem growth	1.96	ns	0.02	ns	0.52	ns	*280*
	Leaf production	0.02	ns	9.99	**	6.19	*	*270*
	Internode length	3.84	ns	1.08	ns	0.19	ns	*253*
	Leaf length	0.92	ns	2.36	ns	0.56	ns	*50*
Large ramets	Stem growth	111.41	***	31.69	***	32.75	***	*754*
	Leaf production	27.00	***	39.71	***	0.93	ns	*754*
	Internode length	131.21	***	16.19	***	21.66	***	*723*
	Leaf length	4.07	*	18.85	***	12.32	**	*137*

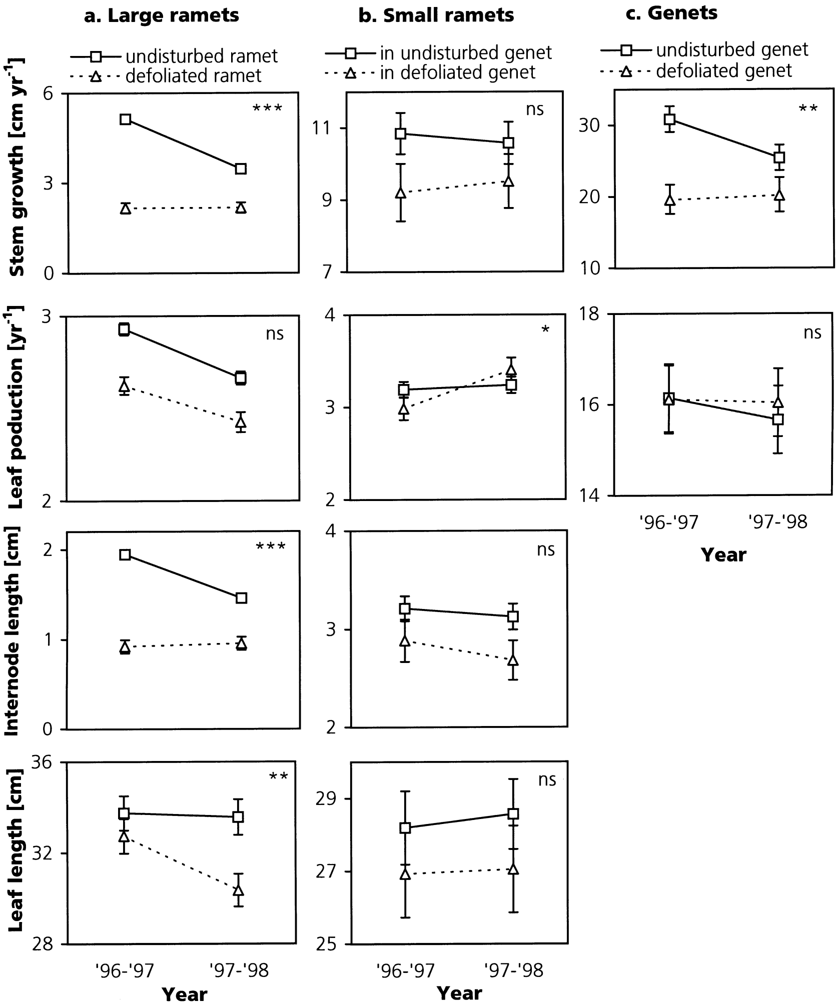


Figure 2

Effects of defoliation on vital rates of large ramets (a), small ramets (b) and genets (c) of *Geonoma deversa* during two years with contrasting precipitation. For large ramets and genets, defoliated and undisturbed individuals are compared, whereas for small ramets a comparison is made between ramets in undisturbed genets and those in defoliated genets. Averages and 1 standard error of the mean are given; for internode length and leaf length, values were first averaged per ramet. Significance indications (ns: $p \geq 0.05$, *: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$) in the top right corner of each graph denote significance of interaction of defoliation treatment and year in a repeated measures ANOVA (see Table 2).

a much smaller extent to reduced leaf production (Figure 2a, Table 3). In genets leaf production was not changed by defoliation and in large ramets the reduction in leaf production was small compared to that in internode length: 16% and 9% in the first and second year for leaf production compared to a 66% and 36% for internode length (Table 3). Surprisingly, leaf length in large

Table 3

The effect of defoliation and plant size on vital rates in genets and ramets of *Geonoma deversa*. Shown are results from multiple forward regression models for two years following defoliation treatment. Ramet survival was analysed using a logistic regression model, all other parameters with linear regressions. Shown are coefficient of determination ($R^2_{Nagelkerke}$ for logistic regression, Nagelkerke 1991), regression coefficient and significance level (-: not tested, ns: $p \geq 0.05$, *: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$). The percentages in the column "Change" indicate the proportional change in a vital rate due to defoliation for an average genet in category *7* (genets) or an average ramet in category *7a* (small ramets) or *7b* (large ramets). This value was obtained by filling in the regression equation. Genet stem length refers to summed stem length of all ramets in genet models (ln-transformed in the case of stem length growth) and to summed stem length of all other ramets in ramet models. Positive effects of defoliation in leaf production and internode length for large ramets are due to the fact that number of leaves is much lower: defoliated individuals actually have lower values for these parameters. Significance indications under "Stand" specify differences among studied stands (tested by entering as dummy variables). Genets with summed stem length >120 cm were included in the analysis; small ramets are 10-120 cm stem length; large ramets >120 cm. All rates are per year; stem length growth in cm yr^{-1}; internode length in cm.

	Parameter	Period	R^2	Constant	Defoliation			Stem length		Leaf number		Stand	*n*
					Genet	Ramet	Change	Genet	Ramet	Genet	Ramet		
Genets	Stem growth	'96-'97	0.53	0.90	-0.42 ***	-	-38%	0.40 ***	-	-	-	ns	*212*
		'97-'98	0.57	0.95	-0.24 **	-	-24%	0.37 ***	-	-	-	ns	*239*
	Leaf production	'96-'97	0.66	-52.0	ns	-		0.82 ***	-	-	-	ns	*184*
		'97-'98	0.60	-51.4	ns	-		0.78 ***	-	-	-	*	*184*
All ramets	Survival	'96-'98	0.14	1.32	-	ns		-	-0.01 **	ns	0.49 ***	ns	*1072*
Small ramets	Stem growth	'96-'97	0.30	0.38	ns	-		-	-0.08 ***	0.07 ***	2.03 ***	*	*281*
		'97-'98	0.43	-0.50	ns	-		-	-0.12 ***	0.07 ***	2.29 ***	ns	*245*
	Leaf production	'96-'97	0.27	1.83	ns	-		-	-0.06 **	ns	0.27 ***	ns	*287*
		'97-'98	0.43	1.35	0.29 *	-	13%	-	-0.01 ***	ns	0.29 ***	***	*280*
	Internode length	'96-'97	0.16	1.49	ns	-		-	-0.02 ***	0.36 ***	0.01 *	ns	*272*
		'97-'98	0.22	1.48	ns	-		-	-0.02 ***	0.31 ***	0.01 **	ns	*264*
Large ramets	Stem growth	'96-'97	0.35	1.54	-	-2.98 ***	-43%	-	-0.01 ***	0.01 *	0.86 ***	***	*768*
		'97-'98[1]	0.39	0.38	-	3.41 ***	-29%	-	-0.02 ***	ns	0.97 ***	ns	*781*
	Leaf production	'96-'97	0.24	1.68	-	-0.26 ***	-16%	-	ns	ns	0.18 ***	***	*769*
		'97-'98	0.26	0.71	-	0.93 ***	-9%	-	ns	ns	0.22 ***	***	*753*
	Internode length	'96-'97	0.25	1.36	-	-0.98 ***	-66%	-	-0.003 ***	ns	0.16 ***	***	*757*
		'97-'98[2]	0.21	1.30	-	0.32 *	-36%	-	-0.004 ***	ns	0.17 ***	*	*729*
	Leaf length	'96-'97	ns										*138*
		'97-'98	0.05	33.60		-3.22 **	-10%						*137*

[1] **Additional effect of possessing raceme 1997: -1.2 *** (regression coefficient and significance)**

[2] **Additional effect of possessing raceme 1997: -0.3 *** (regression coefficient and significance)**

Table 4

Results of Chi-square tests to determine the impact of defoliation on reproduction of ramets and genets of *Geonoma deversa* in two years following treatment (undisturbed and defoliated). New ramet is a binomial parameter indicating whether the genet contained one or more new ramets of >10 cm stem length. Possessing raceme denotes whether a ramet possesses one or more racemes bearing flowers or fruits. Small ramets are 10-120 cm stem length; large ramets >120 cm.

	Parameter	Period	Proportion		Change	χ^2	*p*	*n*	
			Undis	Defol				Undis	Defol
Genets	New ramet	'96-'97	13%	4%	-70%	3.48	0.06	*205*	*51*
		'97-'98	4%	0%		2.28	ns	*136*	*50*
Small ramets	Possessing raceme	'97	4%	4%		0.06	ns	*205*	*80*
		'98	11%	13%		0.19	ns	*203*	*79*
Large ramets	Possessing raceme	'97	39%	23%	-40%	16.5	***	*558*	*220*
		'98	64%	26%	-60%	92.0	***	*540*	*212*

ramets was not reduced during the first year and by 10% during the second year following defoliation. Reproductive activity was more reduced than growth: vegetative production of new ramets on the level of genets decreased by some 70% (difference marginally significant, Table 4) and the proportion of ramets possessing racemes was decreased by 40-60% (Table 4).

Small ramets (10-120 cm) pertaining to defoliated genets were hardly affected by defoliation treatment: stem growth and internode length were not changed, but leaf production actually increased in the second year after treatment (Table 3). Reproductive activity of small ramets was also not affected by defoliation of larger ramets within the same clone (Table 4).

Survival probability was not influenced by defoliation treatment in ramets (Table 3). For genets, there is presumably no impact of defoliation on survival as none of the defoliated genets died during the study period, against one genet (category *4*) of the undisturbed population.

Leaf number recovered rapidly following defoliation: after one year defoliated ramets had regained 36 ± 11% (mean ± SD, n=219) of their original number of leaves, and after two years this had doubled to 68 ± 19% (n=215). For genets recuperation of harvestable leaves was comparable: 38 ± 17 % (n=51) after the first year and 71 ± 26 % (n=50) after the second. High leaf production rates (2.5-3 leaves yr^{-1}) cause leaf turnover to be rather high in *Geonoma* ramets: leaf life span (calculated as $[(N_o+p)/f]-1$ where N_o is leaf number at the start of the year, and p and f are annual rates of leaf production and loss, respectively, Cunningham 1997) was estimated to be 3.4 ± 2.0 yr (mean ± SD, n=518) for large (>120 cm) ramets and somewhat higher, 4.0 ± 2.2 yr (n=166) for small ramets.

Table 5

Vital rates used for the construction of transition matrices for genets and ramets of *Geonoma deversa*. Included are vital rates for an undisturbed population in a normal year (N, derived in Chapter 4) and proportional differences for a defoliated population during the first (C1) and second year (C2) after defoliation. Parameters shown are survival probability (σ), summed growth of all surviving ramets for genets (*grow*), stem growth for ramets (*g*), loss of genet stem length by ramet death (*loss*), the contribution of vegetatively produced ramets to increase in summed stem length (*veg*), rate of new ramet production (*vp*), and the number of seedlings produced by a genet or a ramet (*Pr*{sex} *f*). Further explanation of the variables is provided in Chapter 4. The difference percentages were obtained by filling in regression equations (growth related parameters, see Table 3) or applying an overall change based on frequencies (reproduction-related parameters, see Table 4).

		N					**C1**				**C2**			
		σ	*grow*	*loss*	*veg*	*Pr*{sex}×*f*	*grow*	*loss*	*veg*	*Pr*{sex}× *f*	*grow*	*loss*	*veg*	*Pr*{sex}× *f*
Model		[yr^{-1}]	[cm yr^{-1}]	[cm yr^{-1}]	[cm yr^{-1}]	[yr^{-1}]	[%]	[%]	[%]	[%]	[%]	[%]	[%]	[%]
Genet	*4*	0.987	12.4	1.0	1.5	0.7	-48	0	-70	-30	-31	0	-70	-46
	5	0.995	21.6	3.2	1.9	5.0	-42	0	-70	-38	-27	0	-70	-58
	6	0.995	30.1	9.1	1.3	10.0	-40	0	-70	-39	-25	0	-70	-59
	7	0.995	38.1	18.2	3.0	16.2	-38	0	-70	-39	-24	0	-70	-60
	8	0.995	44.3	26.4	2.9	23.4	-38	0	-70	-39	-24	0	-70	-60
	9	0.995	50.6	36.1	2.0	29.9	-37	0	-70	-39	-24	0	-70	-60
		σ	*g*		*vp*	*Pr*{sex}× *f*	*g*		*vp*	*Pr*{sex}× *f*	*g*		*vp*	*Pr*{sex}× *f*
		[yr^{-1}]	[cm yr^{-1}]		[yr^{-1}]	[yr^{-1}]	[%]		[%]	[%]	[%]		[%]	[%]
Ramet	*4a*	0.991	7.6		0.04	0.2	0		-70	0	0		-70	0
	4b	0.992	5.9		0.01	2.3	-51		-70	-40	-17		-70	-60
	5a	0.991	8.5		0.02	0.2	0		-70	0	0		-70	0
	5b	0.991	5.7		0.04	3.0	-52		-70	-40	-21		-70	-60
	6a	0.991	9.4		0.01	0.2	0		-70	0	0		-70	0
	6b	0.991	5.9		0.02	3.0	-51		-70	-40	-25		-70	-60
	6c	0.980	4.5		0.01	3.5	-66		-70	-40	-34		-70	-60
	7a	0.991	10.6		0.01	0.2	0		-70	0	0		-70	0
	7b	0.991	6.1		0.03	3.0	-49		-70	-40	-26		-70	-60
	7c	0.980	4.6		0.03	3.5	-64		-70	-40	-40		-70	-60
	8a	0.991	11.4		0.01	0.2	0		-70	0	0		-70	0
	8b	0.991	6.2		0.03	3.0	-48		-70	-40	-24		-70	-60
	8c	0.980	4.8		0.03	3.5	-62		-70	-40	-43		-70	-60
	9a	0.991	12.3		0.01	0.2	0		-70	0	0		-70	0
	9b	0.991	6.4		0.02	3.0	-46		-70	-40	-26		-70	-60
	9c	0.980	5.0		0.03	3.5	-59		-70	-40	-44		-70	-60

Table 6

Population growth rates (λ) and elasticity values for single and periodic matrices of genets and ramets of *Geonoma deversa*. Data for periodic matrices are based on deterministic sequences of normal and dry years without defoliation (Undisturbed, see Eq. 1), and for different frequencies of defoliation that also include dry years (Defoliated, see Eqs 2-4). Elasticity values for genet matrices are summed per matrix element. For periodic matrices elasticities are averages (and SD; *n*=16 yrs for Defoliated 1/16 and *n*=8 for other models) of the component matrices that constitute the product matrix. The single transition matrices for undisturbed populations (N and D) were derived in Chapter 4.

Matrices	λ		Elasticity in genet model [%]			
	Genet	Ramet	Stasis	Growth	Reprod	Retro
Single matrices						
N (undisturbed, normal yr)	1.059	1.037	82	15	3	0.4
D (undisturbed, normal yr)	1.030	1.003	88	10	2	0.3
C1 (defoliated, first yr)	1.032	1.013	89	9	2	0.3
C2 (defoliated, second yr)	1.030	1.007	89	10	2	0.3
Periodic matrices						
Undisturbed	1.056	1.033	83 (1)	14 (1)	3 (1)	0.4 (0.0)
Defoliated 1/16	1.051	1.028	84 (2)	13 (1)	2 (1)	0.4 (0.0)
Defoliated 1/8	1.046	1.024	85 (2)	13 (1)	2 (1)	0.4 (0.0)
Defoliated 1/4	1.035	1.013	87 (2)	11 (1)	2 (1)	0.4 (0.0)

Impact of defoliation on population dynamics

Vital rates used for the construction of matrices describing dynamics in defoliated populations are shown in Table 5 as the proportional change to vital rate values found for the undisturbed population (**N**). Transition matrices for genets and ramets during the first (**C1**) and second (**C2**) year following defoliation are in Appendices 1 and 2, respectively.

Population growth rates (λ) of time-invariant transition matrices describing dynamics during the first and second year after defoliation are lower than those for an undisturbed population in a normal year although the decrease in λ is not large (Table 6). Population growth for matrix **C2** is slightly lower than that for **C1**, probably due to a stronger reduction in reproduction in **C2** (Table 5). Elasticity analysis of **C1** and **C2** showed a very similar pattern of contributions to λ as for the undisturbed populations (Table 6). In all genet matrices, stasis transitions account for a very large proportion of the total elasticity, followed by growth and reproduction. In defoliated matrices, the contribution of stasis elements to population growth is slightly higher (Table 6). Elasticity values calculated for vital rates (instead of matrix elements), using the approach of Caswell (1989a, p 135), show that the importance of survival is somewhat higher than for an undisturbed population: 93% of the total vital rate elasticity is accounted for by survival in the genet models for both **C1** and **C2**, compared to 89% in **N**.

Analyses of time-varying periodic matrix models for different defoliation regimes showed that population growth decreased with the frequency of defoliation (Table 6, Figure 3). However, changes in λ were relatively small,

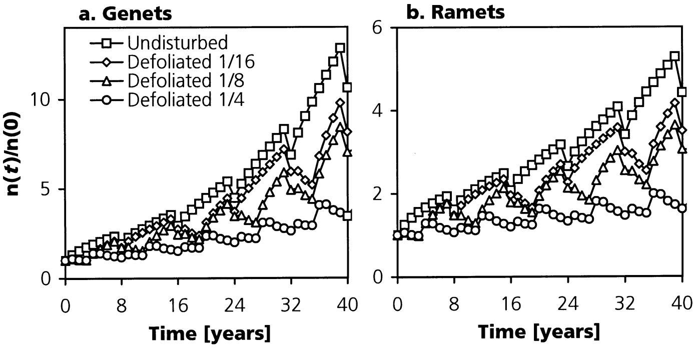


Figure 3
Projected population changes relative to initial population size for genets (a) and ramets (b) of *Geonoma deversa* under different defoliation regimes. Shown are projections using periodic matrix models described in Eqs 1-4, for an undisturbed population and for populations defoliated once every 16, 8 and 4 years. Initial population sizes are total observed abundance per hectare, averaged over the three studied stands: 20,048 for genets and 24,179 for ramets.

probably due again to the fact that survival probability was not altered as a result of defoliation. Elasticity analyses of periodic matrix models revealed that also in periodic matrix models λ is mainly determined by stasis elements in the matrices: total elasticity in stasis elements always accounted for > 84% of the total value (Table 6). Furthermore, the distribution of elasticity values among matrix element types (stasis, growth, reproduction and retrogression) was very constant throughout the defoliation cycles, as indicated by small standard deviations of elasticity values in Table 6.

Projections of leaf availability show that leaf number restored rapidly in all defoliation treatments, even when repeating defoliation every 4 years (Figure 4). In the undisturbed population, relative leaf availability increases continuously and exponentially. When disregarding the sharp drops directly after defoliation, this is also the case for defoliated populations, although at a lower rate (Figure 3). Furthermore, in all defoliation treatments, the relative leaf availability ($n_L(t)/n_L(0)$) always recovered to values >1 after defoliation. Leaf availability increased more rapidly in genets than in ramets, due to higher intrinsic population growth rate of the genet matrices (Table 6).

Discussion

Individual recuperation after defoliation

Genets and ramets of *Geonoma* were remarkably tolerant to complete defoliation: leaf removal did not increase mortality and treated individuals rapidly recovered their leaf area. Complete recovery of leaf area was expected

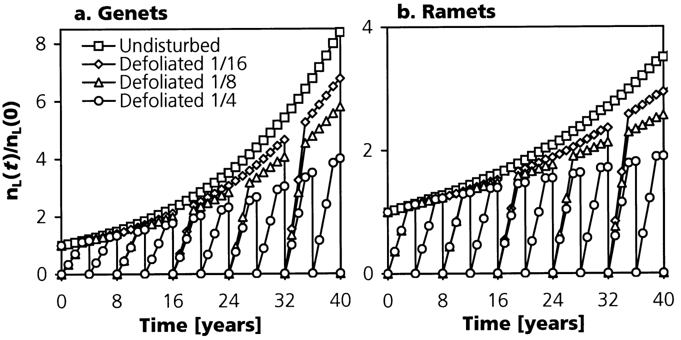


Figure 4

Projected changes in leaf availability relative to initial availability for genets (a) and ramets (b) of *Geonoma deversa* under different defoliation regimes. Shown are projections using periodic matrix models (Eqs 1-4) and category-specific values of leaf number, for an undisturbed population and for populations defoliated once every 16, 8 and 4 years. Only leaves of ramets > 120 cm stem length are included.

after three years, as two thirds of the harvested leaves had been replaced after two years and size of newly produced is only slightly reduced.

Defoliated clones had lost a large portion of their leaves, 77% on average (n=51). Recovery of those leaves imposes a large cost for the individual as a whole. Given the clonal nature of the species, these costs may be covered by active support of defoliated ramets by other ramets (Pitelka & Ashmun 1985, Schmid *et al.* 1988, Jonsdottir & Watson 1997) and/or by retrieval of stored carbohydrates (Suzuki & Stuefer 1999). Active support by small, non-defoliated, ramets was not apparent from our data, as growth and reproduction were not reduced in small ramets within defoliated genets. Also, possibilities for elevated photosynthetic activity in small ramets are probably limited due to low understorey light levels (Chazdon 1986a). For the congeneric clonal palm *Geonoma congesta* small (<150 cm) ramets often had a negative carbon balance (Chazdon 1986a). Therefore it is more likely that carbohydrates necessary to restore leaf area and support growth and reproduction were largely retrieved from stored reserves in the defoliated ramet itself or elsewhere in the clone (Chapin *et al.* 1990, Suzuki & Stuefer 1999). A similar mechanism was suggested for the recovery of *Geonoma congesta* clones after leaf and/or ramet removal treatments (Chazdon 1991b), and for single-stemmed understorey palms (Mendoza *et al.* 1987, Oyama & Mendoza 1990). Thus, it appears that, in spite of low light availability, understorey palms are able to establish considerable reserves. The evolutionary background for this behaviour may be that plants completing their life cycle in the forest understorey have a high probability of being hit by falling debris, causing damage to leaves or stem (Bullock 1980, Martinez-Ramos *et al.* 1988, Clark & Clark 1989, Chazdon 1992). These plants may have adapted to this unpredictable risk of damage by building reserves that can (partly) cover recuperation costs.

Impact of leaf removal differed strongly among vital rates: leaf production and leaf size decreased by 16% at most while reproduction was reduced by 40-70% (Tables 3 and 4). Of the two components determining stem growth, leaf production rate and internode length, the latter was far lower for defoliated ramets (Table 3). These differences suggest that the recuperation process in *Geonoma* was directed more to restoring lost leaf area than at keeping stem growth or reproductive output constant, thus securing the rapid recuperation of photosynthetic capacity (Crawley 1983). A stronger decrease in reproductive output compared to leaf production was also found in completely defoliated adults of the understorey palm *Astrocaryum mexicanum* (Mendoza *et al.* 1987), but not for other palm species (Oyama & Mendoza 1990, Chazdon 1991, Cunningham 1997).

Defoliation impact was restricted to the defoliated ramets, as no impact was found on the non-defoliated smaller ramets within treated genets. These results are comparable with findings in defoliation experiments of branches in trees (Stephenson 1980, Marquis 1992). It is therefore suggested that large ramets in *Geonoma*, and perhaps also in other undergrowth palms, may be considered as functioning rather independently from the clone to which they belong (*cf.* Chapter 4).

Population responses to defoliation

Population growth rates (λ) obtained in this study were generally high (Table 6). The absolute values of λ should be interpreted with some care as survival probability for large genets was estimated (Chapter 4). High growth rates such as calculated for undisturbed genet and ramet models will probably be adjusted by density-dependent regulation (Hubbell *et al.* 1990, Alvarez-Buylla 1994, Condit *et al.* 1994), or by the rare occurrence of very unfavourable climatic conditions.

Population growth rates were only slightly lower after defoliation compared to an undisturbed situation (Table 6). In time-varying periodic matrices the impact of different frequencies of leaf cutting also had little impact on population growth (Table 6). This contrasts with the strong reductions observed in reproduction and stem growth at the level of individuals (Tables 3 and 4). However, it can be understood when considering that survival rate was not affected by defoliation and this is by far the most important vital rate determining population growth (largest vital rate elasticity). Thus, the combination of a long-lived species and the fact that exploitation does not influence survival appears to be responsible for the limited impact of leaf removal on population growth. Similar results were found in simulations of fruit harvesting from tree and palm species: population growth only slightly decreased when reproduction by seeds was strongly decreased (Peters 1990a, b, Bernal 1998). In contrast, simulations of harvest practices that eliminate adult or pre-adult individuals show a much stronger impact on population growth of long-lived palm species (Pinard 1993, Olmsted & Alvarez-Buylla 1995, Peña-Claros & Zuidema 1999).

Harvest simulations using population matrix models usually consider the impact of repeated harvests on population size without considering changes in population structures and their consequences for resource availability (Peters 1990a,b, Pinard 1993, Olmsted & Alvarez-Buylla 1995, but see Chapter 3, Zagt 1997, Peña-Claros & Zuidema 1999). In the present study, the impact of exploitation was evaluated for the population growth rate, the population structure and the availability of leaves. This method allows to simulate extraction regimes and judge their sustainability based on the future resource availability, and not only on a stable population size.

In the leaf availability simulations we used matrix **C2** to describe population dynamics during the third year after defoliation, as no data were available on vital rates for that year and as it was expected that the population had not completely recuperated. The use of this matrix has probably led to conservative projections of population growth and leaf availability. To investigate the sensitivity of projected leaf availability for the type of matrix used to describe dynamics three years after defoliation, we exchanged **C2** for **N**, the matrix of an undisturbed population. This change caused the proportional availability of leaves to be somewhat higher in all defoliation regimes: after 10 defoliation cycles availability was projected to be approximately 60% in stead of 50% for all regimes.

Simulations of leaf availability showed that population-level leaf number recovers rapidly after defoliation and that even frequent leaf cutting does not cause this to drop below the initial value (Figure 4). Nevertheless, when compared to the undisturbed situation, leaf availability is lower for all defoliation regimes. This is not due to a *per capita* reduction in leaf number, as is shown by the steep increases in leaf availability (Figure 3), but can be attributed to the fact that population growth after defoliation is lower than that for an undisturbed situation.

Suitability for leaf extraction

Several characteristics make *Geonoma* a particularly suitable species for commercial leaf extraction. Firstly, the species occurs in high densities, thus making efficient leaf harvesting possible. Secondly, removal of all leaves was not found to cause ramet or genet death, and defoliated individuals were observed to recuperate rapidly. And, most importantly, defoliated populations also recuperated well and were shown to maintain their initial leaf availability even when complete defoliation is repeated every 4 years. Nevertheless, compared to undisturbed populations, leaf availability in defoliated populations lags behind and caution should therefore be taken with too frequent harvests. Given these considerations, sustained leaf availability is probably assured when harvests are conducted at a low frequency (*e.g.* once every 16 yr as used in our simulations).

Acknowledgements

We are grateful to Luis Apaza, Rene Aramayo and the inhabitants of El Turi for their indispensable support during fieldwork, and to the community of El Turi for hospitality during field evaluations. We thank Niels Anten, Rene Boot, Graham Floater and Jan van Groenendael for valuable comments on a draft version of this paper. This study was partly funded by grant BO 009701 from the Netherlands Development Assistance.

Appendix A

Population transition matrices for genets (1) and ramets (2) of *Geonoma deversa* in the first year after defoliation (C1). Life cycle graphs are in Fig. 1; classification criteria and category descriptions in Table 1. Blocks in the ramet model group ramet matrix elements that are nested within one genet element: e.g. the block enclosing ramet transition *4a*-*5a* includes the transitions of ramets within a genet that moves from category *4* to *5*. Note that net genet growth in the last category is negative, causing a part of the individuals in that category to retrogress to the previous category, which also influences the structure in the ramet matrix.

1.

Category	Category at *t*								
at *t*+1	*1*	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*
1	0.506	0.351	0	0.5	3.0	6.1	9.8	14.2	18.1
2	0.108	0.539	0	0	0	0	0	0	0
3	0	0.043	0.658	0	0	0	0	0	0
4	0	0	0.299	0.963	0	0	0	0	0
5	0	0	0	0.024	0.956	0	0	0	0
6	0	0	0	0	0.039	0.976	0	0	0
7	0	0	0	0	0	0.019	0.983	0	0
8	0	0	0	0	0	0	0.012	0.991	0.005
9	0	0	0	0	0	0	0	0.004	0.990

2.

Category	Category at *t*																		
at *t*+1	*1*	*2*	*3*	*4a*	*4b*	*5a*	*5b*	*6a*	*6b*	*6c*	*7a*	*7b*	*7c*	*8a*	*8b*	*8c*	*9a*	*9b*	*9c*
1	0.506	0.351	0	0.15	1.33	0.15	1.76	0.15	1.76	2.06	0.15	1.76	2.06	0.15	1.76	2.06	0.15	1.76	2.06
2	0.108	0.539	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3	0	0.043	0.658	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4a	0	0	0.299	0.898	0.010	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4b	0	0	0	0.066	0.956	0	0	0	0	0	0	0	0	0	0	0	0	0	0
5a	0	0	0	0.023	0.000	0.879	0.012	0	0	0	0	0	0	0	0	0	0	0	0
5b	0	0	0	0.002	0.024	0.073	0.947	0	0	0	0	0	0	0	0	0	0	0	0
6a	0	0	0	0	0	0.036	0.000	0.887	0.004	0.002	0	0	0	0	0	0	0	0	0
6b	0	0	0	0	0	0.003	0.038	0.082	0.942	0	0	0	0	0	0	0	0	0	0
6c	0	0	0	0	0	0	0.001	0	0.025	0.957	0	0	0	0	0	0	0	0	0
7a	0	0	0	0	0	0	0	0.017	0.000	0.000	0.883	0.008	0.009	0	0	0	0	0	0
7b	0	0	0	0	0	0	0	0.002	0.018	0	0.094	0.947	0	0	0	0	0	0	0
7c	0	0	0	0	0	0	0	0	0.000	0.018	0	0.027	0.963	0	0	0	0	0	0
8a	0	0	0	0	0	0	0	0	0	0	0.011	0.000	0.000	0.883	0.008	0.009	0.005	0.000	0.000
8b	0	0	0	0	0	0	0	0	0	0	0.001	0.012	0	0.102	0.953	0	0.001	0.005	0
8c	0	0	0	0	0	0	0	0	0	0	0	0.000	0.012	0	0.029	0.971	0	0.000	0.005
9a	0	0	0	0	0	0	0	0	0	0	0	0	0	0.004	0.000	0.000	0.873	0.004	0.007
9b	0	0	0	0	0	0	0	0	0	0	0	0	0	0.000	0.004	0	0.110	0.950	0
9c	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.000	0.004	0	0.031	0.970

Appendix B

Population transition matrices for genets (1) and ramets (2) of *Geonoma deversa* in the second year after defoliation (C2). See Appendix A for explanation.

1\.

Category	Category at *t*								
at *t*+1	*1*	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*
1	0.506	0.351	0	0.4	2.1	4.1	6.5	9.4	12.0
2	0.108	0.539	0	0	0	0	0	0	0
3	0	0.043	0.658	0	0	0	0	0	0
4	0	0	0.299	0.954	0	0	0	0	0
5	0	0	0	0.033	0.943	0	0	0	0
6	0	0	0	0	0.052	0.968	0	0	0
7	0	0	0	0	0	0.027	0.972	0	0
8	0	0	0	0	0	0	0.023	0.979	0
9	0	0	0	0	0	0	0	0.016	0.995

2\.

Category	Category at *t*																		
at *t*+1	*1*	*2*	*3*	*4a*	*4b*	*5a*	*5b*	*6a*	*6b*	*6c*	*7a*	*7b*	*7c*	*8a*	*8b*	*8c*	*9a*	*9b*	*9c*
1	0.506	0.351	0	0.15	0.88	0.15	1.16	0.15	1.16	1.36	0.15	1.16	1.36	0.15	1.16	1.36	0.15	1.16	1.36
2	0.108	0.539	0	0	0	0	0	0	0.975 0	0	0	0	0	0	0	0	0	0	0
3	0	0.043	0.658	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4a	0	0	0.299	0.890	0.010	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4b	0	0	0	0.066	0.947	0	0	0	0	0	0	0	0	0	0	0	0	0	0
5a	0	0	0	0.031	0.000	0.867	0.012	0	0	0	0	0	0	0	0	0	0	0	0
5b	0	0	0	0.002	0.033	0.072	0.934	0	0	0	0	0	0	0	0	0	0	0	0
6a	0	0	0	0	0	0.048	0.001	0.879	0.004	0.002	0	0	0	0	0	0	0	0	0
6b	0	0	0	0	0	0.004	0.050	0.082	0.921	0	0	0	0	0	0	0	0	0	0
6c	0	0	0	0	0	0	0.002	0	0.038	0.948	0	0	0	0	0	0	0	0	0
7a	0	0	0	0	0	0	0	0.025	0.000	0.000	0.874	0.008	0.009	0	0	0	0	0	0
7b	0	0	0	0	0	0	0	0.002	0.026	0	0.093	0.924	0	0	0	0	0	0	0
7c	0	0	0	0	0	0	0	0	0.001	0.027	0	0.039	0.953	0	0	0	0	0	0
8a	0	0	0	0	0	0	0	0	0	0	0.021	0.000	0.000	0.872	0.007	0.009	0	0	0
8b	0	0	0	0	0	0	0	0	0	0	0.002	0.022	0	0.101	0.928	0	0	0	0
8c	0	0	0	0	0	0	0	0	0	0	0	0.001	0.022	0	0.042	0.959	0	0	0
9a	0	0	0	0	0	0	0	0	0	0	0	0	0	0.015	0.000	0.000	0.877	0.004	0.007
9b	0	0	0	0	0	0	0	0	0	0	0	0	0	0.002	0.015	0	0.110	0.944	0
9c	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.001	0.016	0	0.042	

*Sun flecks on a leaf of the 'palla' palm (*Attalea butyracea*).*

Chapter 6

Integrating vital rate variability into perturbation analysis: a simulation approach for population matrix models

Pieter A. Zuidema & Miguel Franco

Summary

Population matrix models are usually constructed employing average values of vital rates for each size or age category. Variation in vital rates (survival, growth and reproduction) among individuals is normally not taken into account in matrix analysis. Perturbation analyses of matrix models assess the importance of vital rates or matrix elements for population growth rate. They consider the impact of either an unstandardised (sensitivity) or a mean-standardised (elasticity) change in a model component, but do not take into account that certain vital rates are intrinsically more variable than others. We present a variance-standardised perturbation analysis in which random values are drawn from frequency distributions of vital rates that are constructed using field data. The effect of this sampling procedure on population growth rate (λ) is then evaluated. This is done for each combination of a vital rate and a size category, allowing evaluation of the impact of *probable* vital rate changes on λ. This perturbation analysis was applied to six plant species with different life histories. The degree of variation of vital rates for these species was negatively correlated to the vital rates' effect on λ (sensitivity or elasticity). Simulation results show that the relationship between λ and vital rates was close to linear, when the latter were varied within their range of probable values (95% confidence interval). Therefore, and as predicted by first-order approximation, variability of λ resulting from variation of vital rates could be approached by the product of sensitivity (or elasticity) and degree of variability (measured by 95% confidence interval or coefficient of variation) of the vital rate. For our sample species, 95% of the variation in λ was explained by this product. Because the parameters used for this calculation can easily be obtained from transition matrices and field data, this method provides a simple estimation of the degree of variation in λ due to among-individual variation in vital rates. When the need arises to quantify the impact of either true variation or uncertainty in the estimation of certain vital rate values on population growth rate, this variance-standardised perturbation technique provides additional insight to that obtained by standard mean-based approaches.

Introduction

Matrix population models are a widely used tool of demographic analysis (Caswell 1989a). Their popularity stems from the fact that they are easy to construct and yield useful indices of population dynamics (*e.g.* population growth rate) and life history (*e.g.* size-dependent reproductive values). An important development of these models is the family of techniques known as perturbation analyses which compare the importance of different model components to model output, usually population growth. The most popular perturbation techniques, sensitivity (Caswell 1978) and elasticity (de Kroon *et al.* 1986) analyses, have become standard procedures in a number of research fields, including conservation biology, population management, evolutionary ecology and comparative ecology (Silvertown et al 1993, 1996, Franco & Silvertown 1996, Benton & Grant 1999, de Kroon *et al.* 2000, Grant & Benton 2000, Heppell *et al.* 2000, Saether & Bakke 2000).

In their basic and most widely used form, population matrix models are constructed using average values of demographic rates, and their projections assume dynamics to be constant over time and space. As demographic attributes vary among individuals, among populations and in time, population growth rate varies accordingly. It is therefore important to evaluate the effect of demographic variation on output generated by matrix models. Several techniques have been developed to assess the impact of observed variation in time (*e.g.* Caswell & Trevisan 1994, Tuljapurkar 1989), space (*e.g.* Alvarez-Buylla & Garcia-Barrios 1993, Alvarez-Buylla 1994, Pascarella & Horvitz 1998), or both (*e.g.* Caswell 1989ab, 1996a, 2000, Horvitz *et al.* 1997). Most of these techniques consider variation 'among' several matrices that have been constructed for different (sub-)populations or observation periods.

Relatively little attention has been paid to the influence of 'within-matrix' variation in demographic rates on population growth, although a formal first-order approximation of variation in population growth rate is available (Caswell 1989a). Within-matrix variation may result from genetic and phenotypic variation among individuals, from differences in micro-environmental conditions experienced by different individuals, and from the grouping of heterogeneous individuals in a size category (Wisdom & Mills 1997, Wisdom *et al.* 2000). The significance of this variation for matrix model output, however, is widely acknowledged (Sarukhan *et al.* 1982, Alvarez-Buylla & Slatkin 1991, 1993, 1994, Silvertown *et al.* 1996, van Tienderen 1995, 2000, Ehrlén & van Groenendael 1998, Benton & Grant 1999, Bierzychudek 1999, de Kroon *et al.* 2000). An additional source of 'within-matrix' variation is uncertainty in parameter estimates, which, given the difficulty of quantifying certain vital rates, may have considerable influence on model output (Caswell *et al.* 1998, Wisdom & Mills 1997, Wisdom *et al.* 2000).

Among-individual variation in vital rates may differ between types of vital rates (survival, growth and reproduction) and between size categories (Pfister 1998, Gaillard *et al.* 1998) either as a result of inherent differences or because of methodological constraints. Some vital rates (in certain categories) are, therefore, more variable than others, and changes in these vital rates are more probable than changes in other vital rates. In standard perturbation analyses (sensitivity and elasticity), differences in the likelihood of changes in vital rates are not taken into account. The first of these techniques, sensitivity analysis, considers the effect on population growth of a fixed infinitesimal change in a vital rate (*unstandardised* perturbation), whereas elasticity analysis quantifies the influence of a infinitesimal change that is proportional to the average value of a vital rate (*mean-standardised* perturbation). A perturbation technique that takes into account the fact that certain vital rates are more likely to change than others, applies changes in a vital rate proportional to their variability (*variance-standardised* perturbation; van Tienderen 1995).

In this paper, we present a variance-standardised perturbation technique that incorporates vital rate variability into matrix model projections. This technique employs Monte Carlo simulations to evaluate the influence of large but realistic (*i.e.* probable) changes in vital rates for population growth rate. We apply this technique to investigate the importance of variability in vital rates for population growth in six plant species with different life histories for which size-based matrix models have been constructed. We then compare the results to those obtained by standard perturbation analyses. Our simulation technique considers the effect of a change in one vital rate (and one size category) at a time, and is in this sense comparable to sensitivity and elasticity analyses which evaluate one model parameter at a time while keeping all other elements constant. Thus, we do not take covariation of vital rates into account. Perturbations are carried out directly on the lower-level parameters (vital rates: survival, growth and reproduction), not on matrix elements (Caswell 1989a). This is justified by the fact that vital rates are the parameters directly determined in field studies and they are the focus of interventions for conservation and management of natural populations (Caswell 1996a, Mills *et al.* 1999). More specifically, the goals of our study are: (1) to examine patterns of variability of vital rates for a number of plant species with different life histories; (2) to determine the effect of this variability on population growth, and (3) to compare the results obtained from the variance-standardised perturbation analysis to those obtained with mean-based sensitivity and elasticity analysis.

Methods

Construction of transition matrices

Stage-based, Lefkovitch (1965) matrix models use the standard time-invariant matrix model: $\mathbf{n}(t+1) = \mathbf{A}\ \mathbf{n}(t)$, where $\mathbf{A}$ is a square $m \times m$ matrix with transitions among m categories and $\mathbf{n}$ is the population vector containing densities of individuals in m size categories. The dominant eigenvalue (λ) of matrix $\mathbf{A}$ is equivalent to the growth rate of the population (Caswell 1989a).

Typically, elements a_{ij} (with i denoting row number, and j column number) of transition matrix $\mathbf{A}$ may contain the following (notation follows Caswell 1989a): P_j is the probability of surviving and remaining in stage j (*stasis*; main diagonal of transition matrix), G_{ij} is the probability of surviving and growing from stage j to a stage with larger individuals i ($i>j$; *progression*; lower diagonals), R_{ij} is the probability of surviving and going back from stage j to a category with smaller individuals i ($i>j$; *retrogression*; upper diagonals), and F_j is the number of sexual offspring (as number of seeds or seedlings) produced by an individual of stage j from one time interval to the next (*fecundity*; first row).

Essential for the simulations carried out in the present study is that these matrix elements are built from underlying *vital rates* (we use the term vital rate exclusively to denote these lower-level parameters, as opposed to matrix-elements): survival (σ_j), growth (positive: γ_{ij}; negative: ρ_{ij}) and reproductive output (f_j). The relationships between matrix elements and vital rates are as follows:

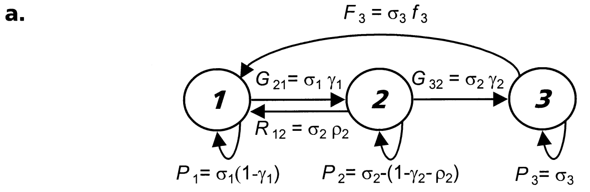
Stasis: $$P_j = \sigma_j \left(1 - \sum_i \gamma_{ij} - \sum_i \rho_{ij}\right) \qquad (1)$$

Progression: $$G_{ij} = \sigma_j\, \gamma_{ij} \qquad (2)$$

Retrogression: $$R_{ij} = \sigma_j\, \rho_{ij} \qquad (3)$$

Fecundity: $$F_j = \sigma_j\, f_j \qquad (4)$$

Notice that although a pair of subscripts is implicit in each element we only employ them when several possible transitions may occur (*e.g.* progression and retrogression in one time interval to non-adjacent categories). This is usually the case for G, R, γ and ρ. Otherwise, if matrix elements involve a single transition (production of seeds or seedlings and permanence in the same class),we only employ the subscript corresponding to the source category (matrix column j) . An example of how a transition matrix is built from the



b.

$$\begin{array}{ccccc} & & & \text{Category at } t & \\ & & 1 & 2 & 3 \\ \text{Category at } t+1 & 1 & P_1 & R_{12} & F_3 \\ & 2 & G_{21} & P_2 & 0 \\ & 3 & 0 & G_{32} & P_3 \end{array}$$

c.

$$\begin{array}{ccccc} & & & \text{Category at } t & \\ & & 1 & 2 & 3 \\ \text{Category at } t+1 & 1 & \sigma_1 - \sigma_1 \gamma_1 & \sigma_2 \rho_2 & \sigma_3 f_3 \\ & 2 & \sigma_1 \gamma_1 & \sigma_2 - \sigma_2 \gamma_2 - \sigma_2 \rho_2 & 0 \\ & 3 & 0 & \sigma_2 \gamma_2 & \sigma_3 \end{array}$$

Figure 1
Life cycle (a) and corresponding transition matrix with symbols for matrix elements (b) and for vital rates (c) of a hypothetical species classified into three size categories.
Uppercase letters denote matrix elements:
***G* = progression;**
***R* = retrogression;**
***P* = stasis;**
***F* = fecundity.**
Lowercase letters denote vital rates:
σ = survival;
γ = positive growth;
ρ = negative growth;
***f* = reproductive output.**

life cycle of a hypothetical plant species and parameterised in terms of vital rates is shown in Figure 1.

Progression may be parameterised in various ways: (1) based on observed transitions, as the proportion of surviving individuals that is found in another category at the next time interval t+1; (2) based on observed growth of individuals in the category, as

$$\gamma_j = g_j / c_j , \tag{5}$$

where g_j is mean growth rate in category j (*e.g.* in cm height increment per yr) and c_j is category width (*e.g.* in cm height; Chapters 2-4, Zagt 1997 see also Batista *et al.* 1998 for a related approach); or (3) based on estimated stage durations (for different options, see Caswell 1989a p. 83-91). To date, transition matrices for plant species have mainly been constructed using the first method, although for long-lived species with few observed transitions and low values of *G* this may not be the most appropriate approach. Progressions to non-adjacent categories can only be estimated using the first method; this also applies for retrogressions. If multiple life cycle pathways occur, matrix elements can only be estimated using observed transitions.

Depending on whether seeds or seedlings are recruited from one time interval to the next, reproductive output f_j is derived from a combination of the following parameters: the probability that an individual in category j be reproductive, the number of seeds (or seedlings) produced by an average individual in class j, and, when necessary, the proportion of seeds that become seedlings (or survive) within the time interval chosen for iteration.

Vital rate sensitivity and elasticity

In their standard form, sensitivity and elasticity analyses consider the impact of changes in *matrix elements* on population growth rate (λ). However, they can also be applied to the *vital rates* mentioned above, sometimes referred to as lower-level parameters (Caswell 1989a, 1996a, Brault & Caswell 1993, Mills *et al.* 1999).

Sensitivity s_{ij} of matrix element a_{ij} is defined as (Caswell 1978):

$$s_{ij} = \frac{\partial \lambda}{\partial a_{ij}} = \frac{v_i \, w_j}{\langle \mathbf{w}, \mathbf{v} \rangle} \tag{6}$$

where v_i and w_j are the corresponding i and j elements of the left ($\mathbf{v}$) and right ($\mathbf{w}$) eigenvectors associated to λ, and $<\mathbf{w}, \mathbf{v}>$ denotes the scalar product. Sensitivity can be calculated for lower level parameters by tracking the changes in λ resulting from changes in the vital rates implicit in matrix elements a_{ij}. For the four types of vital rates distinguished here, and from equations 1-4, the sensitivities of vital rates are (following Caswell 1989a, p. 126-129 and Caswell 1996a):

Survival:

$$\begin{aligned} s_{\sigma_j} &= \frac{\partial \lambda}{\partial \sigma_j} = \frac{\partial \lambda}{\partial P_j}\frac{\partial P_j}{\partial \sigma_j} + \sum_i \frac{\partial \lambda}{\partial G_{ij}}\frac{\partial G_{ij}}{\partial \sigma_j} + \sum_i \frac{\partial \lambda}{\partial R_{ij}}\frac{\partial R_{ij}}{\partial \sigma_j} + \frac{\partial \lambda}{\partial F_j}\frac{\partial F_j}{\partial \sigma_j} \\ &= s_{jj}\Big(1 - \sum_i \gamma_{ij} - \sum_i \sigma_{ij}\Big) + \sum_i s_{ij}\,\gamma_{ij} + \sum_i s_{ij}\,\rho_{ij} + s_{1j}\, f_j \end{aligned} \tag{7}$$

Positive growth ($i>j$)

$$\begin{aligned} s_{\gamma_{ij}} &= \frac{\partial \lambda}{\partial \gamma_{ij}} = \frac{\partial \lambda}{\partial P_j}\frac{\partial P_j}{\partial \gamma_{ij}} + \frac{\partial \lambda}{\partial G_{ij}}\frac{\partial G_{ij}}{\partial \gamma_{ij}} \\ &= s_{jj}\,(-\sigma_j) + s_{ij}\,\sigma_j \end{aligned} \tag{8}$$

Negative growth ($i<j$):

$$\begin{aligned} s_{\rho_{ij}} &= \frac{\partial \lambda}{\partial \rho_{ij}} = \frac{\partial \lambda}{\partial P_j}\frac{\partial P_j}{\partial \rho_{ij}} + \frac{\partial \lambda}{\partial R_{ij}}\frac{\partial R_{ij}}{\partial \rho_{ij}} \\ &= s_{jj}\,(-\sigma_j) + s_{ij}\,\sigma_j \end{aligned} \tag{9}$$

Fecundity: $$s_{f_j} = \frac{\partial \lambda}{\partial f_j} = \frac{\partial \lambda}{\partial F_j} \frac{\partial F_j}{\partial f_j} = s_{1j}\, \sigma_j \tag{10}$$

Notice that sensitivities for positive and negative growth only differ with respect to the matrix elements that are included in the calculation (usually, like here, subdiagonals for positive growth and upper diagonals for negative growth, but this depends on how the life cycle has been coded into the matrix).

Elasticity is the proportional change in λ due to a proportional change in a parameter. For matrix element a_{ij} its elasticity e_{ij} is defined as (de Kroon *et al.* 1986):

$$e_{ij} = \frac{\partial \log \lambda}{\partial \log a_{ij}} = \frac{\partial \lambda / \lambda}{\partial a_{ij} / a_{ij}} = \frac{\lambda}{a_{ij}} s_{ij} \tag{11}$$

where s_{ij} is sensitivity of the element. Consequently, elasticity for vital rates can be calculated by multiplying vital rate sensitivity by x/λ (Caswell 1989a, p.135), where x is the value of the vital rate under consideration, in this case σ_j, γ_{ij}, ρ_{ij}, or f_j. Notice also that, in contrast to the sensitivity and elasticity of matrix elements, which are always positive, vital rate sensitivity and elasticity can be negative. Because we are interested in measuring the magnitude of the change and not its sign, throughout the paper we use the absolute value of sensitivity and elasticity of these vital rates. Lastly, it should be noticed that – in contrast to matrix element elasticities – vital rate elasticities do not sum to 1 (de Kroon *et al.* 1986, Caswell 1989a).

Variance-standardised perturbation analyses

The goal of the variance-standardised perturbation analysis is to assess the influence of variability in each demographic parameter on the population growth rate (λ). We focus our attention on the impact of variation in vital rates (survival, growth and reproduction) and not matrix elements. This is because, unlike matrix coefficients which contain a combination of demographic processes, vital rates isolate each of these. The perturbation technique outlined here considers the influence of variation in *one* vital rate of *one* size category at a time, and is in this sense analogous to standard sensitivity and elasticity analyses. Finally the among-individuals demographic variation that is considered using this technique may be caused by genetic variation, size and morphology differences within a category, environmental heterogeneity or temporal variation (in case vital rates are measured over more than one year).

The first step in the analysis identifies the frequency distributions of the vital rates from which values are drawn. These distributions are based on variation in vital rates among studied individuals in each category. In the case of observed transitions, growth rate (both γ_{ij} and ρ_{ij}) can be described using a binomial frequency distribution (as the basic observations are whether an individual jumps to another category or not). If growth in size is measured for all individuals (eq. 5), growth rates will mostly follow a normal or lognormal distribution. Survival probability (σ_j) will follow a binomial distribution. Finally, reproductive output (f_j) may follow either a normal or a binomial distribution, or may be made up of several parameters, each with a different frequency distribution (*e.g.* probability of reproducing [binomial] × number of offspring produced per reproductive individual [normal]). In this case, values are drawn from the respective distributions and then multiplied. For each category, the frequency distributions of observed vital rates are described by their mean and standard deviation. Binomial standard deviations are used when necessary (Sokal & Rohlf 1995).

The second step in the analysis involves the perturbations themselves. For each combination of size category and vital rate (survival in category 1, 2, etc., growth in category 1, 2, etc., etc.), 1,500 values are randomly drawn with the following restriction: draws have to fall within the 95% confidence interval of the observed vital rate distribution, and (bio)logically impossible values (negative γ_{ij} and f_j values, probability values outside the $< 0,1 >$ interval) are excluded. For vital rates with a binomial frequency distribution, values are drawn from a normal distribution, as this approximates the binomial distribution fairly well for moderately large samples (Sokal & Rohlf 1995) and the sampling process is greatly simplified in this way. For each sampled value of a vital rate in a certain category, a matrix is constructed using equations 1–4. Unchanged values are used for all other vital rates of the category under consideration. The unchanged elements of the mean matrix are used for all other categories. Population growth rate (λ) is then computed for each of the 1,500 simulated matrices.

The third step is the analysis of simulation results. Several parameters are derived from the drawn vital rate values and the resulting values of λ: mean, standard deviation, 95% confidence interval (calculated using the SD of the distribution of λ; henceforth referred to as CI95) and coefficient of variation (CV). Using these parameters, the magnitude of changes in λ due to the simulated variation in vital rates is compared among species and vital rates, and related to both their degree of variation and to their effect on population growth (sensitivity and elasticity). The relationship between each vital rate and population growth is also assessed. Absolute (sensitivity, CI95) as well as relative (elasticity, CV) measures of variability and importance of vital rates are calculated, as both are commonly used in demographic studies. In the analysis of simulation results, absolute and relative measures are compared amongst themselves.

Table 1

Characteristics of the six sample species used for variance-standardised perturbation analysis. The value of population growth (λ) is that of the transition matrix using mean vital rates; size is number of categories in matrix. Estimates of life span come from the cited references for the first two species, and mean age (and standard deviation) in the last category obtained with equations 29 and 30 in Cochran & Ellner (1992; S_1 - mean age of residence) for the remaining species. More information on study methods, matrix construction and vital rates of the sample species is presented in the Appendix.

Species	Life form	λ	Size	Life span	Reference
Primula vulgaris	woodland understorey herb	1.038	5	10 -30	Valverde & Silvertown 1998
Geonoma deversa	understorey palm - ramets	1.041	6	*c.* 37	Chapter 4
Euterpe precatoria	(sub)canopy palm	0.977	11	106 (35)	Chapter 3
Duguetia neglecta	understorey tree	1.006	12	255 (95)	Zagt 1997
Bertholletia excelsa	emergent tree	1.007	17	360 (106)	Chapter 2
Chlorocardium rodiei	canopy tree	0.998	15	444 (156)	Zagt 1997

We apply the perturbation analysis outlined above to six plant species spanning a range of life histories and life spans (Table 1), and including small to large-sized transition matrices. More detailed information on demographic studies, matrix construction and vital rates of the sample species can be found in the Appendix.

Results

Variability and sensitivity of vital rates

Variability of vital rates varied widely among types of vital rates and species, with coefficients of variation ranging from 0 to 77 (MedianCV=27.1, $n=188$). Vital rate types differed significantly in variability, both for absolute (CI95; Kruskal-Wallis: $\chi^2_3=42.7$, $p<0.001$) and relative (CV; $\chi^2_3=120.7$, $p<0.001$) measures of variation. Confidence intervals were narrower for survival than for positive growth and reproduction (Multiple comparisons Kruskal-Wallis, $p<0.05$; Siegel & Castellan 1988). No difference in vital rate variability was found among species, for absolute (CI95 of drawn values; Kruskal-Wallis: $\chi^2_5=8.9$, $p=0.11$) and relative measures ($\chi^2_5=3.9$, $p=0.57$).

Considered over all vital rates and species, there was a negative correlation between the variability of a vital rate and its effect on λ, both when measured in absolute (CI95(λ) *vs.* sensitivity) or relative (CV(λ) *vs.* elasticity) terms (Figure 2, Table 2). Looking at the contribution that each vital rate makes to this relationship, it is clear that, by spanning almost the entire range of values, reproductive output is mostly responsible for this relationship when absolute measures are considered (Figure 2c; Table 2: Spearman's $r=-0.90$). Looking at the contribution by species, the points with lowest sensitivity and highest vital rate's CI95 correspond to the reproductive output values of the two longest-

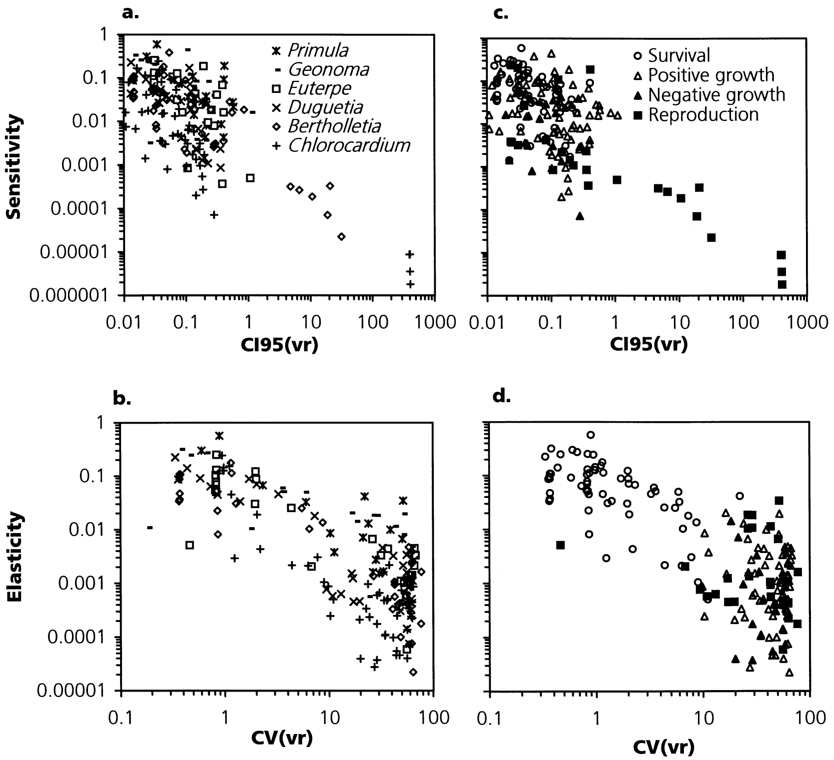


Figure 2
Relation between the contribution of a vital rate to lambda (its 'importance') and the vital rate's variability for six plant species, using (a,c) absolute measures (sensitivity and CI95(vr), see text for definition) and (b,d) relative measures (elasticity and CV(vr)). Right and left panels differentiate species from vital rates, but otherwise provide the same data. Correlation analyses are presented in Table 2.

living tree species *Chlorocardium rodiei* and *Bertholletia excelsa* (lower right-hand side of Figure 2a). In contrast, when considering relative measures (Figures2b and 2d), elasticity and CV of reproduction are not correlated and survival is mostly responsible for the overall correlation (Table 2), spanning the widest range of CV and elasticity. Within the range of survival probabilities, survival in adult categories occupies the high elasticity-low variability end of the relationship, while seedling survival occupies the opposite end (Kruskal-Wallis for CV of drawn values in seedling, juvenile and adult categories: $\chi^2_2=29.4$, $n=65$; $p<0.001$). When evaluated at the species level, negative correlations between vital rate variability and their effect on λ (sensitivity and elasticity) were found for most of them (Table 2). The range of values for each species tended to overlap more in the case of relative measures (Figure 2b) than in the case of absolute ones (Figure 2a).

Table 2

Correlation between measures of importance and variability of vital rates for six plant species. Correlations were performed for absolute (sensitivity *vs.* CI95) and relative (elasticity *vs.* CV) measures. Sensitivities and elasticities are calculated for vital rates (*not* matrix elements; see Methods). Values are Spearman's *r* with significance level (-: $p \geq 0.05$; *: $p<0.05$; **: $p<0.01$; ***: $p<0.001$).

Species	Vital rate	Sensitivity *vs.* CI95(vr)	Elasticity *vs.* CV(vr)	*n*
All	All	-0.54 ***	-0.70 ***	*188*
Primula	All	-	-0.63 **	*17*
Geonoma	All	-0.63 **	-0.61 **	*18*
Euterpe	All	-0.61 **	-0.73 ***	*25*
Duguetia	All	-0.77 ***	-0.72 ***	*34*
Bertholletia	All	-0.72 ***	-0.53 ***	*39*
Chlorocardium	All	-0.74 ***	-0.75 ***	*55*
All	Survival	-0.47 ***	-0.56 ***	*65*
All	Positive growth	-0.27 *	-	*75*
All	Negative growth	-	-	*20*
All	Reproductive output	-0.90 ***	-	*28*

Variance-standardised perturbation results

The variation in population growth rate (λ) resulting from the variance-standardised perturbations over all vital rate types and species ranged from CI95(λ)=0.000 to CI95(λ)=0.077 and CV(λ)=0.001 to CV(λ)=1.891. Significant differences were found among vital rate types, both for CI95(λ) (Kruskal-Wallis: $\chi^2_3=14.6$, $p<0.01$) and CV(λ) (Kruskal-Wallis: $\chi^2_3=29.4$, $p<0.001$), with negative growth having less influence on the variation of λ than other vital rates (Figure 3a; Kruskal-Wallis: multiple comparisons, $p<0.05$). Similarly, species differed in the magnitude of variation in λ resulting from vital rate variability (Kruskal-Wallis: $\chi^2_5=52.3$, $p<0.001$ for CI95(λ) and $\chi^2_5=51.3$, $p<0.001$ for CV(λ)). Variability of λ generally decreased with species life span (Figure 3b).

The relationship of λ and vital rates is intrinsically non-linear, but the results of our simulations show a low degree of curvature leading to almost linear relations. Three examples of contrasting differences in curvature are shown in Figure 4. With some exceptions, the relationship between λ and either survival or negative growth was concave (43 out of 63 cases and 16 out of 20, respectively; as in Figure 4a). Relations with positive growth and reproductive output were mainly convex (67 out of 75 and 19 out of 28, respectively; as in Figure 4b). Figure 4 also shows that vital rate sensitivity is equal to the slope of the relation between λ and the vital rate (vr) evaluated at the mean value (arrows). By analogy, elasticity is the slope of the curve relating log(λ) to log(vr), also evaluated at the mean vital rate value.

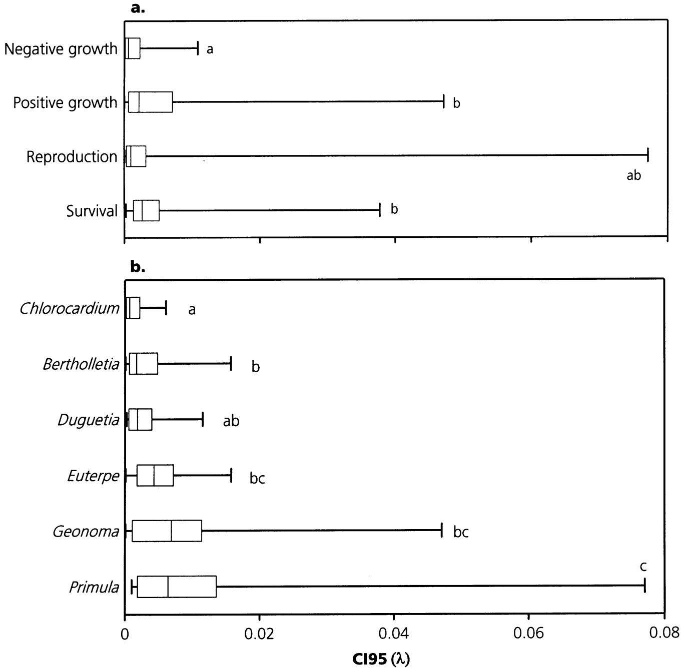


Figure 3

Distribution of confidence intervals for λ resulting from variance-standardised perturbation analyses for six plant species, grouped by type of vital rate (a) and species (b; ordered from bottom to top by increasing life span). Midline in boxes denotes the median value, borders of boxes the 25 and 75% percentiles, and whiskers the minimum and maximum values. Different letters indicate significant differences among groups (p<0.05) in a nonparametric multiple comparison test (Siegel & Castellan 1988 p.213).

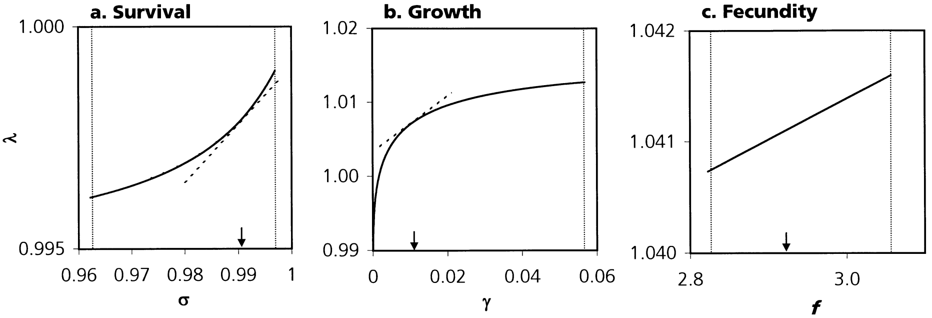


Figure 4

Examples of the relationship between a vital rate and population growth rate (λ). (a) A concave relation for survival in category 13 of *Chlorocardium*, (b) a convex relation for growth in category 5 of *Bertholletia* and (c) a linear relation for fecundity in category 5 of *Geonoma*. The dashed lines in (a) and (b) are the slopes of the relationship between λ and the vital rate (the sensitivity of λ to changes in that vital rate) evaluated at the mean value (indicated by arrow). The dotted vertical lines represent the borders of the 95% confidence interval for the vital rate. Evidently, the slope (sensitivity) in (c) is the same at all values of *f*.

Table 3

Correlation between variability of population growth rate (λ) and measures of importance and variability of vital rates for six plant species. Correlations were performed between absolute changes in lambda (CI95(λ)) and the absolute measures of vital rate importance (sensitivity) and vital rate variation (CI95(vr)), as well as between relative changes in lambda (CV(λ)) and the relative measures of vital rate importance (elasticity) and vital rate variation (CV(vr)). Values are Spearman's *r* with significance (-: $p \geq 0.05$; *: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$). Sample sizes as in Table 2.

Species	Vital rate	CI95(λ) *vs.*		CV(λ) *vs.*	
		Sensitivity	CI95(vr)	Elasticity	CV(vr)
All	All	0.66 ***	0.20 **	0.60 ***	-
Primula	All	0.73 **	-	0.78 **	-
Geonoma	All	-	-	-	0.45 $^{0.063}$
Euterpe	All	-	0.49 *	-	0.54 **
Duguetia	All	0.64 **	-	0.61 **	-
Bertholletia	All	-	0.47 **	-	0.30 $^{0.065}$
Chlorocardium	All	0.69 **	-	0.82 **	-
All	Survival	0.59 ***	0.31 *	0.53 ***	0.26 *
All	Positive growth	0.69 ***	0.45 ***	0.90 ***	0.30 *
All	Negative growth	0.84 ***	-	0.95 ***	-
All	Reproductive output	-	-	0.48 **	0.55 **

The variation in λ found in our simulations is the result of both variation of vital rates (range between the vertical dotted lines in Figure 4) and the responsiveness of λ to modifications of the vital rates (evaluated by sensitivity or elasticity; slopes in Figure 4). To check to what extent these two factors explained variation in λ, we related the magnitude of variation in λ (CI95(λ) or CV(λ)) to that in vital rates (CI95(vr) or CV(vr)) and to sensitivity or elasticity. The results of the analysis are in Table 3. Considering the patterns among species, it appears that either sensitivity (or elasticity) or the variability of vital rates is correlated with variation in λ. This pattern seems not to be related to differences in life history. Among vital rates, both sensitivity (or elasticity) and vital rate variation were positively correlated with variation in λ in several cases.

The fact that the relationships between λ and vital rates were often close to linear implies that the slope of the relation at the mean vital rate value is a good predictor of the vital rate's 'importance' over its complete range of possible values (see Caswell 2000). We therefore evaluated to what extent the product of vital rate variability (range of values along x-axis in Figure 4) and the sensitivity (slope indicated in Figure 4) would predict variability in λ (range of values along y-axis in Figure 4). For strictly linear relations (Figure 4c) this product would provide the exact value of the range of variation of λ. This approach was derived from the basic equation for variation in λ due to variation in matrix elements (Caswell 1989a). In the formula presented by Caswell, the first-order approximation of Var(λ) is calculated by multiplying

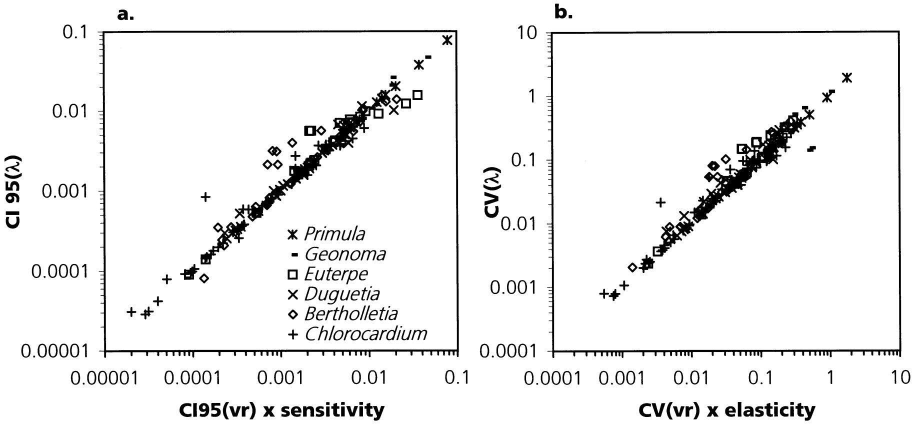


Figure 5

The relation between variation in λ (CI95(λ) or CV(λ)) and the product of vital rate importance (sensitivity or elasticity) and its variability (CI95(vr) or CV(vr)) for six plant species. (a) absolute measures, (b) relative measures. Notice that all types of vital rates are well spread over the whole range of values.

the variance in matrix element a_{ij} by its squared sensitivity, and summing these products over all cells in the matrix: $\mathrm{Var}(\lambda)=\Sigma(\mathrm{Var}[a_{ij}] \times s_{ij}^2)$.

We found a strong correlation between the product of sensitivity (or elasticity) and vital rate variability, with the variability of λ (Figure 5). This, and the regression analyses on log-transformed data (Table 4) confirm the approximate linearity of the relationship between λ and vital rates. Because

Table 4

Relation between variability in population growth rate (CI95(λ) or CV(λ)) and the product of vital rate importance (sensitivity or elasticity) and variability (CI95(vr) or CV(vr)) for six plant species. Both dependent and independent variables were ln-transformed prior to analysis. The Table shows coefficients of determination, value of constant, regression coefficient (and standard error) and significance level for t-test to assess whether regression coefficient is different from 1 (*: $p<0.05$; **: $p<0.01$; ***: $p<0.001$). All regression coefficients were highly significantly different from 0 ($p<0.001$). Sample sizes as in Table 2.

Species	Vital rate	CI95(λ)			CV(λ)		
		R²	Constant	CI95 × Sens	R²	Constant	CV × Elast
All	All	0.96	-0.23	0.95 (0.01) ***	0.95	0.06	0.96 (0.02) *
Primula	All	1.00	-0.01	1.00 (0.00) ns	1.00	0.01	1.00 (0.01) ns
Geonoma	All	1.00	0.12	1.02 (0.02) ns	0.88	-0.31	0.91 (0.08) ns
Euterpe	All	0.91	-0.55	0.90 (0.05) ns	0.92	0.40	1.03 (0.06) ns
Duguetia	All	0.97	-0.38	0.94 (0.03) *	0.96	0.03	0.97 (0.03) ns
Bertholletia	All	0.89	-0.29	0.93 (0.05) ns	0.90	0.17	0.97 (0.05) ns
Chlorocardium	All	0.96	-0.45	0.93 (0.03) **	0.95	0.02	0.97 (0.03) ns
All	Survival	0.95	-0.51	0.92 (0.03) **	0.95	-0.27	0.90 (0.03) ***
All	Positive growth	0.94	-0.19	0.95 (0.03) *	0.96	0.43	1.02 (0.03) ns
All	Negative growth	1.00	-0.19	0.97 (0.01) *	0.99	0.04	0.99 (0.02) ns
All	Reproductive output	1.00	-0.10	0.99 (0.01) ns	0.94	-0.52	0.87 (0.04) **

coefficients of determination and slopes obtained from these regressions were close to one, they indicate a tight, linear relationship.

Discussion

Variability and importance of vital rates

Variation in vital rates differed widely among the six sample species. In general, survival probability was the least variable vital rate, particularly in adult categories (Figure 2). A negative relationship between vital rate importance (sensitivity or elasticity) and vital rate variability was found for all species and vital rates combined, but also separately for the six sample species and for most of the vital rates (Figure 2, Table 2). Similar inverse relations between demographic variation and sensitivity (or elasticity) have been found for temporal variation in a large number of plant and animal species (Pfister 1998), and for a combination of spatial and temporal variation in the perennial herb *Lathyrus vernus* (calculated from Ehrlén & van Groenendael 1998: Spearman correlation of CV and elasticity of matrix elements: r=-0.74, p<0.001, n=31). These results suggest that natural selection promotes population stability by reducing variability in relation to the importance of the life history traits involved (*cf.* Pfister 1998).

Significance of vital rate variation

Our simulations show that variation in vital rates as observed in demographic field studies may influence the estimates of population growth rate λ to different degrees (Figure 3). Variation in survival probability and growth rate had the strongest impact on λ (Table 3), despite the fact that the former was the least variable vital rate. Clearly, these results reflect the life histories of our sample species. Comparing species, variation in λ is large for short-lived species and smaller for the longer-lived species (Figure 3b). This pattern may be influenced by differences in matrix dimension, as transition matrices for long-lived species were larger and the distribution of elasticities among matrix elements is influenced by matrix dimension (Enright *et al.* 1995, Chapter 7).

The functional relations between λ and vital rates approached linearity in many instances (*e.g.* Caswell 1996a, b, 2000, de Kroon *et al.* 2000, but see Huenneke & Marks 1987), despite the intrinsic non-linear relation between the dominant eigenvalue and matrix elements. This implies and confirms that sensitivities and elasticities perform well beyond the point for which they are calculated (Caswell 2000, de Kroon *et al.* 2000). Given this linearity, an estimate of the variability of λ due to variation in a vital rate is obtained by multiplying the importance of the vital rate (expressed as sensitivity or elasticity) and its variability (expressed as either its 95% confidence interval or its coefficient of variation). When applying this to our six sample species, very strong relationships were found (Figure 5, Table 4).

The implication of this result is that a good predictor of the first-order approximation for variance in λ (Caswell 1989a) can be obtained by multiplying two readily available parameters. That is:

$$\mathrm{CI}(\lambda) \approx \mathrm{CI95}(\mathrm{vr}_j) \times s_j \tag{12}$$

or, if relative measures are used:

$$\mathrm{CV}(\lambda) \approx \mathrm{CV}(\mathrm{vr}_j) \times e_j \tag{13}$$

where CI95(λ) and CV(λ) are measures of variability in λ, $\mathrm{CI95}(\mathrm{vr}_j)$ and $\mathrm{CV}(\mathrm{vr}_j)$ are measures of variability of a specific vital rate in category j, and s_j (sensitivity) and e_j (elasticity) are measures of the importance to population growth of that vital rate in that category. Estimates of variability can be obtained from field data (or from the literature; Mills *et al.* 1999, Wisdom *et al.* 2000), and sensitivity and elasticity for vital rates can be calculated using equations 7–10 (or Caswell 1989a, 1996a). Whether one applies absolute or relative measures does not influence the predictive strength of the relationship (in our simulations, either of them explained more than 88% of the variation in ln(λ); Table 4).

Covariation among vital rates

Vital rates are likely to co-vary and this can happen either within the same stage of the life cycle or between different stages. In particular, the finite resources available to an organism at a particular time, limits the amount that can be allocated to different activities. For example, current reproduction may be inversely related to future survival if the drain of resources for the former becomes limiting to the latter (*e.g.* Piñero *et al.* 1982). What an organism does at one stage of its life cycle (*e.g.* reproduce early) may affect its chances of doing the same thing (*i.e.*, reproduce again), or even something else (grow or survive) in the future (*e.g.* Dick *et al.* 1990, Geber 1990, Geber *et al.* 1997). Covariation, however, does not necessarily imply negative relationships or trade-offs: a population growing in a rich soil may grow and reproduce more than one in a poorer patch; habitat perturbation may have a negative effect on several life cycle stages and demographic processes.

As a consequence, certain combinations of vital rates will be more probable than others, and specific combinations may be impossible. In our simulations, we varied one vital rate in one category at a time, while keeping other vital rates in the focal category and all vital rates in all other categories, constant. Our variance-standardised perturbations did not adjust for covariance among vital rates. Some unrealistic combinations of vital rates may have resulted from this. However, by drawing values of vital rates only from the 95% confidence interval, we prevented unrealistic values and unrealistic combinations of values from having a large influence on the variability of λ. Also, when varying one vital rate of one category at a time (as is the case in the perturbation technique applied here), far less unrealistic combinations of values are obtained than when doing so for several (Mills *et al.* 1999) or all vital rates in all categories at a time ("life stage simulation analysis"; Wisdom *et al.* 2000). Finally, our approach shows resemblance with the application of large perturbations, as commonly applied for the planning of conservation measures (Heppell *et al.* 1996, Mills *et al.* 1999, de Kroon *et al.* 2000, Caswell 2000). In that application, perturbation is also generally applied to one vital rate or category at a time. thus ignoring the intricacies of possible covariation with other life history traits or stages.

In spite of the availability of several techniques (Caswell 1989ab, 1996a, van Tienderen 1995, 2000), the influence of demographic covariance on variation in population growth has only sporadically been assessed (Brault & Caswell 1993, Horvitz *et al.* 1997, Caswell 2000). Inclusion of covariance in matrix models is probably hampered by diverse interpretations of covariance and by important practical limitations. The two main techniques that assess the role of covariance have different starting points. In integrated elasticities (van Tienderen 1995, 2000) covariance between vital rates is specifically modelled using observed or assumed trade-off relations. In life table response experiments (LTRE; Caswell 1989ab, 1996a, 2000), on the other hand, covariances appear as an integral part of the quantification of contributions to observed variation in λ, providing empirical evidence of the role of covariation. As LTRE consider differences among (sub)populations or different observation periods, to a certain extent they disregard trade-offs that only become apparent at the individual level (these may be included, however, in integrated elasticities). In addition, difference in sample size or uncertainty in parameter estimation among populations included in LTRE may also be a source of (co)variance in demographic rates and consequently in λ (*e.g.* Brault & Caswell 1993).

The use of both integrated elasticity and LTRE is limited by the amount of information gathered in a particular study: detailed knowledge on covariance structures necessary for integrated elasticities is not always available and sets of transition matrices from different populations or time periods are necessary for LTRE. These are available for only a fraction of the species

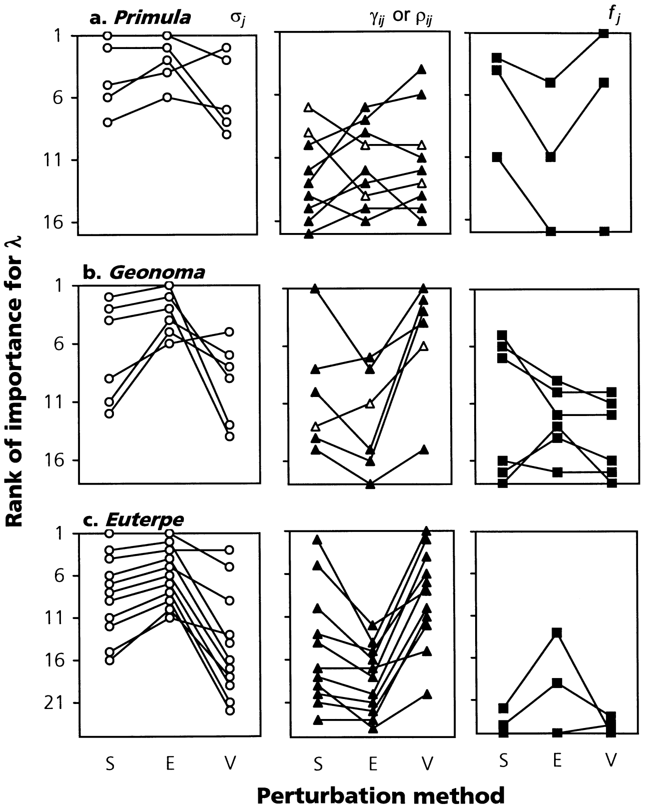


Figure 6

Ranking of vital rates according to their contribution to changes in λ for six plant species. The results of three perturbation methods are shown: vital rate sensitivity (S), vital rate elasticity (E) and variance-standardised perturbation analysis (V). Lines connect the same vital rate among the three

studied so far (see Menges 2000). Furthermore, the variety of sources of covariation, the large number of categories in many transition matrices and the complexity of real life cycles has limited the inclusion of covariance into matrix analysis.

Comparing perturbation methods

A variety of perturbation methods have been developed for population matrix models (Benton & Grant 1999, Caswell 2000, de Kroon *et al.* 2000, Grant & Benton 2000, van Tienderen 2000, Wisdom *et al.* 2000). Some of these methods are widely used and well-known (sensitivity and elasticity analysis), whereas others have been much less used so far (LTRE, integrated elasticities, density-dependent elasticities). Conceptually, perturbation methods may be grouped into two families (Caswell 1997, Horvitz *et al.* 1997): prospective and retrospective analyses. While prospective analyses "explore the

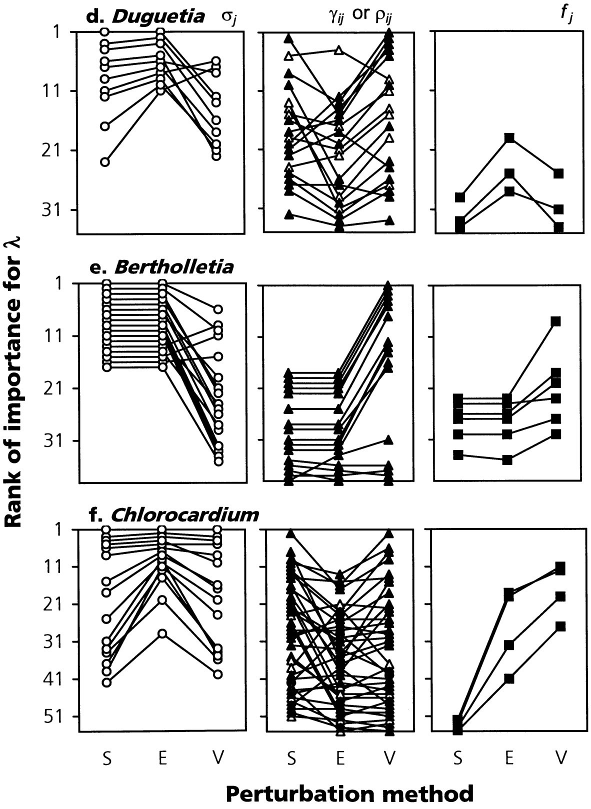


Figure 6 (continued)
methods. Rank 1 means the highest value of sensitivity, elasticity or CI95(λ), respectively. For clarity, the Figures have been split by type of vital rate: left panels represent survival (σ_j), centre panels include both positive (γ_{ij}) and negative (ρ_{ij}),growth, and right panels contain reproductive output (f_j).

functional dependence of λ" on either matrix elements or lower-level parameters (vital rates), retrospective analyses determine how an observed pattern of variation has affected variation in λ (Caswell 2000). Our variance-standardised perturbation analysis adds another dimension to the body of perturbation methods, combining aspects of both families. On the one hand, it considers variation in λ due to observed variation in vital rates (an aspect of retrospective analysis). On the other hand, the effect of vital rate variability on the variation of λ depends on the functional relationship of λ to that vital rate (a subject of prospective analysis; Figure 4). Variance-standardised perturbation analysis can be considered an extension of traditional sensitivity or elasticity analysis: whereas sensitivity analysis considers the influence of unstandardised changes, and elasticity analysis deals with mean-standardised changes, our approach focuses on the probable changes in a vital rate, by applying variance-standardised changes.

Given the variety of perturbation methods available, it becomes relevant to know which method to use for what question. This is of special importance since, as expected, different methods yield different results. Figure 6 compares the ranking of sensitivity, elasticity and variance-standardised perturbation analysis for the six sample species. There are marked differences in the 'importance' of vital rates suggested by the different methods. Overall, when comparing the last two (elasticity and the variance-standardised method), survival decreases in importance while growth increases its importance from the former to the latter method. Survival probability is the vital rate with the highest elasticity: 93% of the top-5 ranked vital rates correspond to σ_j. In many cases this implies low mortality in adult categories or slow growth (long residence times) in juvenile stages. Ranks resulting from the variance-standardised perturbation method, on the other hand, show a much lower contribution of survival to the top-5 ranks (30%). Using this technique, positive growth is in many cases (60%) the most important vital rate. Here, the top-5 ranks mainly include growth of juveniles in categories with highly variable growth rate. In particular, the plastic response of juveniles of tropical forest trees (such as *Euterpe precatoria* and *Bertholletia excelsa*) to the large variation in light availability in their forest environments, may be responsible for the large simulated variation in population growth rate.

Although the topic "When to use what method?" has been covered elsewhere (Caswell 2000, de Kroon *et al.* 2000), we shortly re-state the different questions that can be addressed using the most important perturbation methods and relate our variance-standardised approach to these. Firstly, elasticity and sensitivity analyses evaluate the *potential* effect on λ of a change in a vital rate and, therefore answer the question "What would happen if a particular demographic rate were modified?". This also includes the large perturbation vital rates that are used to assess conservation measures (*e.g.* Heppell *et al.* 1996, Mills *et al.* 1999, Caswell 2000). Secondly, life table response experiments (LTRE) evaluate the importance of demographic variation on variation in λ, addressing the question "What are the contributions of different demographic rates to observed variation in population growth rate?". LTRE use a set of transition matrices for different populations or observation periods, and consider the influence of demographic variation among these transition matrices for population growth. They are therefore especially useful to disentangle complex demographic consequences of particular environmental changes. Finally, the question posed by variance-standardised perturbation is: "What are the consequences for population growth of observed variation in vital rates among individuals?". This addresses either the effect that random variation among individuals in the population have on the perceived rate of population growth or the effect that error introduced by sampling a subset of individuals has on the estimated rate of population growth. That is, it focuses on the variation 'within' the transition matrix, which is 'hidden' in each element of the transition matrix when performance of individuals in a category is summarised by the average value. Thus, the latter two techniques differ in the starting point (departing from observed variation in population growth rate (LTRE) *vs.* observed variation in vital rates (variance-standardised perturbation analysis)) and therefore in necessary information (several transition matrices *vs*. one transition matrix and information on vital rate variability). The sources of demographic variation, however, are related and often overlap: variation among populations can be considered as aggregated among-individuals variation, spatial variation may be included in one transition matrix or specified in several patch-specific matrices, and similarly, demographic data from different years may be combined in one average model or used for several annual models. Therefore, the form in which demographic data are presented also determines what method can be applied.

It is evident that different questions require different approaches, and that differences in output of perturbation analyses (Figure 6, Horvitz *et al.* 1997) do not imply inconsistencies, but rather provide answers to different questions. The variance-standardised technique, and more importantly, the approximation of variation in λ by the product of vital rate variability and either its sensitivity or elasticity (eqs. 11 and 12), represent an addition to the existing techniques, without the purpose of replacing any of these. Rather, the method presented here provides a ranking that shows which vital rates in which categories should be given special attention as they may have a considerable influence on population growth due to variation among individuals. Why these vital rates have such large contributions to variation in population growth may depend on life history, the condition of the population, sampling effects or uncertainty in parameter estimates.

Acknowledgements

We thank Teresa Valverde and Roderick Zagt for allowing us the use of their data. Heinjo During, Xavier Pico and Marinus Werger provided useful comments on a draft version. PZ acknowledges the Instituto de Ecología, UNAM, Mexico, and the Open University, UK, for their hospitality. Part of this study was financed by grant BO009701 from the Netherlands Development Assistance. MF thanks Conacyt, Mexico, DGAPA, UNAM, Mexico, the Ferguson Trust, and the Open University for support and hospitality during a sabbatical period.

Appendix

In this appendix we present information on the matrix models used for the simulations in the paper, including the mean and SD of vital rates used for the simulations. The vital rate values for the six sample species are presented in tables. Symbols as in main text; numbers between parentheses refer to the number of steps of a transition (*e.g.* 2 for a 2-step transition).

- *Primula vulgaris*. Of the various populations studied by Valverde & Silvertown (1998), a population under intermediate canopy openness was chosen (SF), located in Northamptonshire, UK, using data for 1992-1993. Due to large differences in survival and reproduction between years, data from different years were not combined (Valverde & Silvertown 1998). In the original matrix, five categories were distinguished based on rosette size. Progression and retrogression elements in the matrix were based on directly observed transitions. One transition (a_{45}) based on one individual was omitted from the simulations. Reproduction (capsule production) was calculated by multiplying the probability of being reproductive and the number of capsules produced per reproductive individual.

Stage	σ	$\gamma(1)$	$\gamma(2)$	ρ	Pr{rep}	Seedling prod.
1 Seedling	0.471 (0.121)	0.625 (0.171)	0.375 (0.171)			
2 Juvenile	0.900 (0.067)	0.389 (0.115)	0.333 (0.111)		0.150 (0.080)	2.000 (1.000)
3 Adult 1	0.954 (0.026)	0.484 (0.063)	0.113 (0.040)		0.292 (0.056)	2.737 (1.910)
4 Adult 2	0.992 (0.008)	0.362 (0.045)		0.052 (0.021)	0.720 (0.041)	4.588 (2.744)
5 Adult 3	0.988 (0.012)			0.173 (0.042)	0.963 (0.021)	10.228 (6.592)

- *Geonoma deversa*. We used a ramet matrix model in which data from three nearby populations in a moist tropical forest in Northern Bolivia were combined for one year (1996-1997; Chapter 4). The population was divided into six size categories, based on number of juvenile-type leaves (categories 1-2), number of adult-type leaves (3), and stem-length (4-6). Transitions for categories 1 and 2 were based on observed transitions; progression from 3 to 4 on leaf production and in categories 4-6 on stem length growth (category values from linear regression of growth *vs*. size). Production of new seedlings was modelled as the product of the probability of being reproductive (category values from logistic regression) and the number of new seedlings encountered per reproductive ramet (based on densities of seedlings and reproductive ramets; this equalled 3.5). Production of new ramets was calculated as the probability that a ramet in a certain category would produce a new ramet.

Stage	σ	γ	ρ	Ramet prod.	Pr{rep}
1 Seedling	0.614 (0.042)	0.176 (0.033)			
2 Seedling	0.933 (0.041)	0.046 (0.034)	0.376 (0.079)		
3 Juvenile	0.957 (0.049)	0.313 (0.442)			
4 Adult	0.991 (0.006)	0.101 (0.072)		0.014 (0.007)	0.044 (0.012)
5 Adult	0.991 (0.004)	0.055 (0.042)		0.023 (0.007)	0.840 (0.017)
6 Adult	0.980 (0.008)			0.027 (0.009)	0.998 (0.003)

- *Euterpe precatoria*. A transition matrix for a population in moist tropical forest in Northern Bolivia was used for a year with normal precipitation (Chapter 3). The population was divided into 11 categories, of which the first four were based on leaf blade length, and the remaining (5-11) on stem height. For categories 1-4, transitions were based on direct observations (1-2) or average leaf blade growth (3-4); for categories 5-11, mean growth rate was determined using the Hossfeld IV equation (Zeide 1993), a non-linear function that relates growth to initial size. Category values were obtained by entering the mid point of a category in the fitted function. Standard deviations for growth rates were based on a measure of deviation from the mean curve. The difference between observed growth and that predicted by the equation was used to obtain an estimate of the standard deviation for growth rate per category (SD_i): $SD_i = \mathrm{Sqrt}(\Sigma[(o\text{-}p)^2]/n)$, where *o* is observed diameter increment of an individual, *p* the value predicted by the equation for an individual of the same size, *n* the sample size and the summation is over all individuals in a category. Survival probability was lower for category 1

than for all other categories, but for the remaining categories no size-dependent patterns were found. Average values were therefore used for categories 2-4 and 5-11. Production of new seedlings was calculated as the product of the probability of being reproductive (from logistic regression) and the number of new seedlings encountered per reproductive ramet (this equalled 5.9).

Stage	σ	γ	ρ	Pr{rep}
1 Seedling	0.722 (0.036)	0.061 (0.019)		
2 Seedling	0.941 (0.021)	0.098 (0.042)	0.133 (0.048)	
3 Seedling	0.941 (0.021)	0.047 (0.179)		
4 Seedling	0.941 (0.021)	0.024 (0.090)		
5 Juvenile	0.957 (0.009)	0.050 (0.141)		
6 Juvenile	0.957 (0.009)	0.086 (0.170)		
7 Juvenile	0.957 (0.009)	0.127 (0.092)		
8 Juvenile	0.957 (0.009)	0.115 (0.071)		
9 Adult	0.957 (0.009)	0.076 (0.095)		0.027 (0.021)
10 Adult	0.957 (0.009)	0.035 (0.031)		0.685 (0.052)
11 Adult	0.957 (0.009)			0.998 (0.005)

- *Duguetia neglecta*. The matrix model for a population in undisturbed, evergreen rain forest in central Guyana was used, containing data collected in 1991-1995 (Zagt 1997). The population was divided into 12 size categories: four for seedlings (classified by stem length and number of leaves per unit stem length), two for juveniles and six for reproductive individuals (both classified by diameter). Transitions among seedling categories were based on observed transitions, and contained many multiple-step transitions. Growth rates for juvenile and adult categories were determined using Hossfeld IV equations (see description for *Euterpe*). Survival for juvenile and adult categories was based on a double logistic regression of survival against diameter (Zagt 1997), allowing for a lower survival probability for both small and large individuals. Production of new seedlings was calculated as the product of the probability of being reproductive (using category means) and the number of new seedlings encountered per adult (which equalled 1.5).

Stage	σ	γ (1)	γ (2) or ρ(2)	ρ(1)	Pr{rep}
1 Seedling	0.749 (0.064)	0.162 (0.063)	0.009[1] (0.017)		
2 Seedling	0.943 (0.039)	0.115 (0.056)		0.030 (0.030)	
3 Seedling	1.000 -	0.066 (0.045)		0.044 (0.038)	
4 Seedling	0.976 (0.028)	0.047 (0.040)	0.011[2] (0.020)	0.047 (0.040)	
5 Juvenile	0.992 (0.004)	0.057 (0.011)		0.007 (0.004)	
6 Juvenile	0.994 (0.004)	0.016 (0.051)			
7 Adult	0.994 (0.006)	0.032 (0.056)			0.110 (0.024)
8 Adult	0.993 (0.008)	0.047 (0.062)			0.290 (0.044)
9 Adult	0.991 (0.011)	0.057 (0.080)			0.535 (0.060)
10 Adult	0.990 (0.013)	0.061 (0.049)			0.535 (0.066)
11 Adult	0.988 (0.023)	0.058 (0.067)			0.535 (0.106)
12 Adult	0.984 (0.026)				0.535 (0.104)

[1] Refers to γ(2); [2] refers to ρ(2)

- *Bertholletia excelsa*. A matrix model for a population in moist tropical forest located in Northern Bolivia was used (site 'El Sena'; Chapter 2), with data for a year with normal precipitation. The population was divided into 17 size categories: four for seedlings (classified by stem length), seven for juveniles and six for reproductive individuals (both classified by diameter). Transitions among seedling categories were based on growth in stem height (using linear regression of growth *vs*. size); those for juvenile and adult categories on diameter growth (using Hossfeld IV equation, see description for *Euterpe*). Survival was constant within categories 1-4, 5-7, 8-11 and 12-17, as no size-dependent patterns were found. Production of new seedlings was calculated by multiplying the probability of being

reproductive, the number of fruits produced and the number of new seedlings per fruit produced (from densities of fruits and seedlings; this equalled 0.07).

Stage	σ	γ	Pr{rep}	Fruit prod.
1 Seedling	0.546 (0.041)	0.167 (0.196)		
2 Seedling	0.735 (0.073)	0.200 (0.366)		
3 Seedling	0.914 (0.064)	0.146 (0.220)		
4 Seedling	0.988 (0.020)	0.169 (0.135)		
5 Juvenile	0.985 (0.016)	0.010 (0.024)		
6 Juvenile	0.985 (0.016)	0.028 (0.039)		
7 Juvenile	0.995 (0.005)	0.047 (0.042)		
8 Juvenile	0.995 (0.005)	0.110 (0.053)		
9 Juvenile	0.995 (0.005)	0.148 (0.085)		
10 Juvenile	0.995 (0.005)	0.157 (0.082)		
11 Juvenile	0.995 (0.005)	0.143 (0.092)		
12 Adult	0.995 (0.005)	0.053 (0.031)	0.971 (0.032)	4.083 (0.479)
13 Adult	0.995 (0.005)	0.032 (0.035)	0.998 (0.007)	4.225 (0.298)
14 Adult	0.995 (0.005)	0.019 (0.009)	1.000 (0.002)	4.368 (0.864)
15 Adult	0.985 (0.011)	0.011 (0.012)	1.000 (0.001)	4.511 (0.482)
16 Adult	0.985 (0.011)	0.007 (0.019)	1.000 (0.000)	4.654 (0.668)
17 Adult	0.985 (0.011)		1.000 (0.000)	4.832 (0.858)

- *Chlorocardium rodiei*. The matrix model for an undisturbed population in evergreen rain forest in central Guyana was used, containing data collected in 1991-1995 (Zagt 1997). The population was divided into 15 size categories: one for seeds, six for seedlings (classified by stem length and number of leaves per unit stem length), four for juveniles and four for reproductive individuals (both classified by diameter). Progression, retrogression and stasis transitions for seedlings, juveniles and adults were calculated as for *Duguetia*. Seed production was calculated as the density of current year's seeds divided by density of adult trees. Information on among-individuals variation in seed production was derived from a seed-fall study of 16 trees in the same area (Ter Steege *et al*. 1996, p 30). Note that for *Geonoma*, *Euterpe*, *Duguetia* and *Bertholletia* no information on variation in seedling production was included.

Stage	σ	γ (1)	γ (2)	ρ(1)	ρ(2)	γ or ρ
1 Seedling	0.377 (0.032)	0.456 (0.033)	0.134 (0.023)			0.096[1] (0.020)
2 Seedling	0.280 (0.029)	0.138 (0.022)	0.220 (0.027)			0.078[1] (0.017)
3 Seedling	0.457 (0.060)	0.110 (0.038)	0.089 (0.034)	0.358 (0.058)		
4 Seedling	0.495 (0.025)	0.070 (0.013)	0.031 (0.009)		0.045 (0.010)	0.004[1] (0.003)
5 Seedling	0.870 (0.022)	0.006 (0.005)	0.032 (0.012)	0.277 (0.029)	0.031 (0.011)	0.029[2] (0.011)
6 Seedling	0.683 (0.049)	0.114 (0.033)	0.006 (0.008)	0.059 (0.025)	0.129 (0.035)	0.005[3] (0.008)
7 Seedling	0.963 (0.014)	0.027 (0.012)		0.072 (0.019)	0.032 (0.013)	0.008[2] (0.006)
8 Juvenile	0.985 (0.011)	0.014 (0.023)				
9 Juvenile	0.990 (0.015)	0.016 (0.030)				
10 Juvenile	0.993 (0.020)	0.014 (0.009)				
11 Juvenile	0.993 (0.016)	0.007 (0.005)				Seed prod
12 Adult	0.992 (0.016)	0.014 (0.007)				116 (156)
13 Adult	0.991 (0.015)	0.007 (0.003)				116 (156)
14 Adult	0.988 (0.018)	0.006 (0.003)				116 (156)
15 Adult	0.986 (0.033)					116 (156)

[1] Refers to 3-step progression; [2] refers to 3-step retrogression; [3] refers to 4-step retrogression.

*Emergent individual of the Brazil nut tree (*Bertholletia excelsa*)*

Chapter 7

Using population matrices for long-lived species: a review of published models for 35 woody plants

Pieter A. Zuidema & Roderick J. Zagt

Summary

Matrix models developed for 35 woody species were reviewed. Model construction and parameterisation (population classification, calculation of matrix elements, data constraints) was related to model output (population growth rate, elasticity, age estimates). In addition, in two matrix models for long-lived tropical trees, the number of categories was increased to determine the influence of stage duration on model output. Median stage duration in the reviewed models varied from 2 to 42 yr. In most studies observed transition frequencies for model parameterisation were used. Survival probability averaged 94% for all size categories and 97% for adults. Population growth rates were very sensitive to changes in stasis elements (83% of total elasticity for matrix elements), and low for progression (15%) and fecundity (3%) elements. Vital rate elasticity (for lower-level parameters) showed very high elasticity for survival (92% of total elasticity) compared to growth (6%) or reproductive output (2%). Elasticity values were compared in two demographic triangles: the existing triangle for regular matrix element elasticity and an alternative one for vital rate elasticity. The position of species in the original triangle was more strongly influenced by stage duration than in the alternative triangle. Similarly, elasticity values covaried more strongly with population growth rate using element elasticities. Adults constituted only 20% (average 126 individuals) of total sample size used for model construction, but accounted for 60% of the total elasticity. Adult survival contributed 50% of the total vital rate elasticity. More than 40% of the studied reported difficulties with the estimation of adult survival. High (and often unrealistic) survival and stasis probabilities increased λ and age estimates. We recommend the use of overall size-dependent patterns of vital rates to calculate matrix elements. Furthermore we argue to increase sampling effort in adult categories and to combine demographic data of different years or sites into one model, particularly if no differences are found among them.

Introduction

Matrix population models are a popular tool to analyse plant and animal demography as they apply a standardised model structure and yield output with clear biological interpretation (van Groenendael *et al.* 1988, Caswell 1989a, Tuljapurkar & Caswell 1997). In their standard form, matrix models use the equation $\mathbf{n}(t+1) = \mathbf{A}\ \mathbf{n}(t)$, where $\mathbf{A}$ is a square $m \times m$ matrix with transitions among the m categories into which the population is divided (based on age or size) and $\mathbf{n}$ is the population vector containing densities of individuals in the m categories. The asymptotic growth rate of the population is the dominant eigenvalue (λ) of matrix $\mathbf{A}$ (Caswell 1989a); the left and right eigenvectors ($\mathbf{v}$ and $\mathbf{w}$) corresponding to λ can be interpreted as the contributions of categories to the total reproductive output and as the asymptotic population structure, respectively. The sensitivity of the population growth rate λ to changes in elements a_{ij} of the transition matrix $\mathbf{A}$, can be assessed in two ways. The sensitivity s_{ij} of matrix element a_{ij} considers the absolute change in λ due to an absolute change in a_{ij} (Caswell 1978, 1989). Elasticity analysis, on the other hand, calculates the proportional change in λ due to a proportional change in a_{ij} (de Kroon *et al.* 1986, 2000, Benton & Grant 1999). Finally, for size-classified population models, several age estimates can be derived using algorithms developed by Cochran & Ellner (1992).

The set of standardised output parameters provides the opportunity to compare the demography of different species (Silvertown *et al.* 1993, 1996, Franco & Silvertown 1996, Heppell *et al.* 2000, Sæther & Bakke 2000) or that of different populations of the same species (*e.g.* Ehrlen 1995, Horvitz & Schemske 1995, Oostermeijer *et al.* 1996, Valverde & Silvertown 1998, Hoffmann 1999). As the use and usefulness of matrix models is gradually disseminated, more modelling studies will become available, increasing the scope and strength of comparative studies. To date, matrix models have been constructed for at least 250 species, including birds (Sæther & Bakke 2000), mammals (Heppell *et al.* 2000) and plants (Silvertown *et al.* 1993, Franco & Silvertown 1996).

In spite of the high degree of standardisation of model form and output of matrix models, there are inevitably differences among studies with respect to model construction and model parameterisation. Recent papers on matrix models have shown that such differences may have considerable impact on model output. That is, the number of categories into which the population is divided influences patterns of elasticities and within-stage age distributions (Enright *et al.* 1995, Boucher 1997, de Matos & Silva Matos 1998). Furthermore, Caswell (1989) demonstrated that different ways of calculating transition probabilities using the same data results in different model output. More recently, it was shown that uncertainty in parameter estimates and

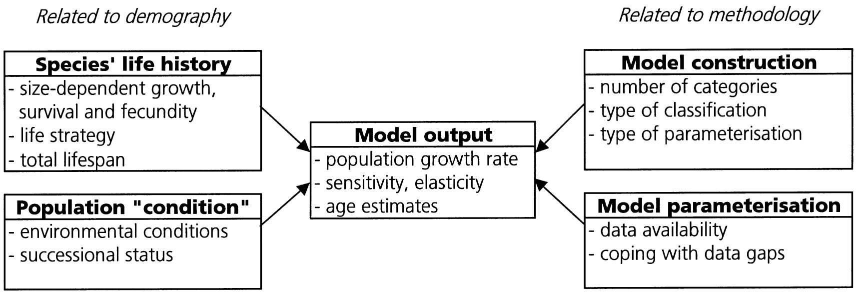


Figure 1
Schematic diagram of factors influencing the output of size-structured population matrix models. Factors are grouped into four categories: the life history of the species, the environmental conditions experienced by the study population, factors related to the construction of the model and those related to the parameterisation of the model. Each of the four categories may influence the model output.

among-individual variation in demographic rates influences population growth rate and output from elasticity analysis (Mills *et al.* 1999, Wisdom *et al.* 2000, Chapter 6). Thus, it is becoming increasingly clear that the output generated by matrix models is codetermined by the construction and parameterisation of the model (Figure 1). However, model results are generally interpreted as a reflection of the life history of the study species or the environmental conditions experienced by the studied population.

The influence of methodology on model output is probably generic and to some extent applicable to every species. However, it may be especially important for models of long-lived plant species for several reasons. Models of these plants are constructed in very different ways: the number of size categories in which populations have been divided varies widely (compare *e.g. Nothofagus* in Enright & Ogden 1979, *Bertholletia* in Chapter 2); the method of parameterisation of the transition matrix differs between studies (compare *e.g.* Batista *et al.* 1998, Hoffmann 1999); and data constraints are often encountered in demographic field studies.

In this paper we investigate the effect of model construction and parameterisation on output of stage-based (Lefkovitch 1965) matrix models developed for 35 woody species. We choose to analyse models for woody species, as these are generally long-lived, are the largest group of long-lived plants for which models have been generated, and yield comparable model output in terms of elasticities (Silvertown *et al.* 1993). Specifically, we consider the influence of population classification, calculation of transition elements and data constraints. Apart from reviewing published matrices, we modify matrix models of two long-lived tropical trees (*Bertholletia excelsa* and *Chlorocardium rodiei*) by greatly increasing the number of categories, thus considerably shortening average stage duration. Subsequently, we analyse changes in model output resulting from this model modification. Finally, using the results of these analyses, we formulate recommendations for the application of matrix models to long-lived species.

Methods

Review of matrix models for woody species

Matrix models for 35 woody species (7 shrubs, 17 trees and 11 palms) published in 27 studies were reviewed in this paper (Table 1). Part of these studies were previously reviewed by Silvertown and co-workers (Silvertown *et al.* 1993, 1996, Franco & Silvertown 1996) for different purposes. When several transition matrices of the same species were presented in one publication, only one model was used, preferably a pooled or mean matrix or a transition matrix for 'normal' conditions (*e.g.* regular climatic conditions, no exploitation, mean density). For two palm species (*Euterpe precatoria* and *Iriartea deltoidea*), two matrices were included as these were based on studies in different areas or habitats.

For each of the reviewed matrices we inventoried factors related to the methodology used in terms of model construction and parameterisation, and related these to model output (see Figure 1). The following parameters related to model construction were recorded: number of stages used, number of adult stages, criteria used for classification (*e.g.* related to the biology of the species, or considerations of minimisation of distribution and sampling errors as proposed by Vandermeer [1978] and Moloney [1986]). Information related to the parameterisation of the matrices was also obtained: type of parameterisation (directly observed transitions, calculated transitions based on observed growth rates or calculated stage durations), total number of individuals used to construct the matrix, number of adult individuals used to construct the matrix, duration of the study, and whether problems with the estimation of adult mortality were mentioned. Finally, elements a_{ij} in the transition matrix were grouped according to the type of transition they represent: P are elements that represent the probability of surviving and remaining in a stage (stasis; along diagonal of transition matrix), G are probabilities of surviving and growing to a stage with larger individuals (progression; in lower diagonals), R are probabilities related to surviving and going back to a category with smaller individuals (retrogression; in upper diagonals), and F are values of the number of offspring produced (fecundity; usually on first row).

The reviewed models were run to obtain the asymptotic population growth rate and the elasticity matrix (de Kroon *et al.* 1986). In addition to regular elasticity analysis (henceforth referred to as element elasticity), elasticity

Table 1
List of 35 woody species of which matrix models are reviewed. Size refers to matrix dimension; λ is the finite population growth rate.

Species	Life form	Size	λ	Reference
Aesculus turbinata[1]	tree	7	1.0287	Kaneko *et al*. 1999
Alnus incana[6]	shrub	5	1.0062	Huenneke & Marks 1987
Araucaria cunninghamii	tree	11	1.0205	Enright & Ogden 1979
Araucaria hunsteini[7]	tree	7	0.9867	Enright 1982
Ardisia escallonioides[8]	shrub	8	1.5889	Pascarella & Horvitz 1999
Astrocaryum mexicanum[9]	palm	14	1.0114	Piñero *et al*. 1984
Bertholletia excelsa[3,10]	tree	17	1.0071	Chapter 2
Brosium alicastrum	tree	11	1.0666	Peters 1990a
Cecropia obtusifolia[1,11]	tree	8	1.0124	Alvarez-Buylla 1994
Chlorocardium rodiei [2]	tree	15	0.9978	Zagt 1997
Cocothrinax readii	palm	9	1.0549	Olmsted & Alvarez-Buylla 1995
Duguetia neglecta[2]	tree	12	1.0061	Zagt 1997
Dycimbe altsonii[2]	tree	15	1.0279	Zagt 1997
Euterpe edulis[1,12]	palm	7	1.2582	Silva Matos *et al*. 1999
Euterpe precatoria - flooded	palm	7	0.9969	Peña-Claros & Zuidema 1999
Euterpe precatoria - unflooded[3]	palm	11	0.9769	Chapter 3
Fagus grandifolia[5,13]	tree	9	0.9834	Batista *et al*. 1998
Fumana procumbens[14]	shrub	6	1.0446	Bengtsson 1993
Geonoma deversa[3,15]	palm	9	1.0591	Chapter 4
Grias peruviana	tree	9	1.0196	Peters 1990b
Iriartea deltoidea - Brazil[1]	palm	6	1.0091	Pinard 1993
Iriartea deltoidea - Ecuador	palm	8	0.9792	Svenning & Balslev 1997
Lindera benzoin[16]	shrub	5	1.0027	Cipollini *et al*. 1994
Miconia albicans[4]	shrub	13	1.1854	Hoffmann 1999
Myrsine guianensis[4]	tree	15	1.1014	Hoffmann 1999
Nothofagus fusca[17]	tree	4	1.0095	Enright & Ogden 1979
Pentaclethra macroloba	tree	15	1.0017	Hartshorn 1975
Periandra mediterranea[4]	shrub	8	1.0706	Hoffmann 1999
Phytelephas seemannii[1]	palm	6	1.0589	Bernal 1998
Pinus palustris[5,18]	tree	8	1.0117	Platt *et al*. 1988
Podococcus barteri	palm	7	1.0125	Bullock 1980
Rhopalostylis sapida[19]	palm	8	1.0059	Enright & Watson 1992
Roupala montana[4]	tree	14	1.0534	Hoffmann 1999
Rourea induta[4]	shrub	14	0.9895	Hoffmann 1999
Sequoia sempervirens[20]	tree	5	0.9922	Namkoong & Roberds 1974
Thrinax radiata[21]	palm	9	1.1493	Olmsted & Alvarez-Buylla 1995
Vochysia ferruginea	tree	5	1.1548	Boucher & Mallona 1997

[1] Pooled matrix; [2] Undisturbed plot; [3] Normal year; [4] Unburn matrix; [5] Matrix starts at 2 cm DBH; [6] Product matrix over 3 yrs for Divide Swamp; [7] Plot 15A; [8] Plot F; [9] Plot AA; [10] El Sena; [11] Homogeneous environment; [12] Density independent; [13] Closed canopy phase; [14] 1987-1988; [15] Genets; [16] Understorey, females only; [17] Middle stand, seedling age = 20 yr; [18] Fertility calculated from Fig 4; [19] Frond scar matrix; [20] Moderate mortality and no cutting; [21] Venadito

values were also calculated for lower level parameters (vital rates) that are used to derive transitions: survival (σ), positive growth (γ), negative growth (ρ) and reproductive output (*f*), following Caswell (1989, p. 135; henceforth referred to as vital rate elasticity). These values were calculated per stage. To facilitate comparison with element elasticity values, vital rate elasticities were standardised to sum to unity.

Using the algorithms presented by Cochran and Ellner (1992), several age estimates were obtained: conditional age at entering a category (τ, for each category, equations 9 and 10 in Cochran & Ellner 1992), mean age of residence (S, for each category, eq. 29-30) and three values for generation time (*T*; Â: eq. 26; μ: eq. 27-28). Species life span was estimated by the mean age (S) for individuals in the last category. A measure of stage duration in a category *i* was obtained by subtracting the conditional age for category *i*+1 from that of category *i*. For the last category, it was approximated by subtracting mean age (S) from conditional age (τ). In case two newborn types were present in the transition matrix (*e.g.* seeds and seedlings), age estimates were only calculated for the smallest newborn type.

Increasing the number of categories in two matrix models

In the second part of the study, the number of stages used in transition matrices for two long-lived Neotropical trees, *Bertholletia excelsa* and *Chlorocardium rodiei*, was greatly increased (by a factor of 4.5 and 7, respectively). Previous studies that considered the influence of matrix dimension have done so by reducing the number of stages (Enright *et al.* 1995, Boucher 1997), as increasing was not possible due to data limitations. This problem was not present for the two transition matrices used here, as they were parameterised using overall size-dependent patterns (regressions or averages over several categories) for survival, growth and reproductive output (Zagt 1997, Chapter 2).

For *Bertholletia excelsa* (the Brazil nut tree), a matrix model for a population in moist tropical forest located in Northern Bolivia (site El Sena) was used (Chapter 2). This matrix was constructed with data from a year with normal precipitation. The population was divided into 17 size categories: four for seedlings (classified by stem length), seven for juveniles and six for reproductive individuals (both classified by diameter at breast height, DBH). Transitions among seedling categories were based on growth in stem height (using linear regression of growth *vs.* size); those for juvenile and adult categories on diameter growth (using a Hossfeld IV equation, Zeide 1993). Survival was constant within categories 1-4, 5-7, 8-11 and 12-17, as no size-dependent patterns were found. Production of new seedlings was calculated from information on fruit production and density of seedlings.

For *Chlorocardium rodiei* ('Greenheart', yielding valuable timber) a model for an undisturbed population in evergreen rain forest in central Guyana was used, containing data collected in 1991-1995 (Zagt 1997). The population was divided into 15 size categories: one for seeds, six for seedlings (classified by stem length and number of leaves/dm stemlength), four for juveniles and four for reproductive individuals (both classified by DBH). Progression, retrogression and stasis transitions for seedlings were calculated using observed transition frequencies. Transitions for juveniles and adults were determined using non-linear regression equations for size-dependent DBH increment (Hossfeld IV equation) and for survival (double logistic regression, Zagt 1997). Seed production was calculated as the density of current year's seeds divided by density of adult trees.

Category width was modified for juvenile and adult individuals of 1-100 cm DBH for *Chlorocardium* and 1-180 cm DBH for *Bertholletia*. In the original matrices, transitions of individuals >1 cm DBH included only 1-step progression and stasis. Thus, only these elements were changed by increasing the number of categories. No modifications were applied to seed and seedling categories (the first four in *Bertholletia* and first seven in *Chlorocardium*) as transitions among these categories were based on observed transitions (*Chlorocardium*) and stage duration was generally short (*Bertholletia*). The category width (expressed as cm DBH) was chosen such that it was broader than the maximum observed growth rate, so as to guarantee that individuals do not skip a category in one time step. The resulting matrices (hereafter referred to as expanded matrices) had a category width of 1 cm DBH in *Chlorocardium* and 2.5 cm in *Bertholletia*, resulting in 106 and 76 categories, respectively.

As with the species compared in the first part of the study, population growth, element elasticity, vital rate elasticity and age estimates (conditional age, mean age of residence and generation time) were calculated and compared to those values obtained from the original matrices.

Results

Model construction and parameterisation

Matrix models for the 35 woody species differed widely with respect to model construction and parameterisation. Table 2 provides some characteristics of the reviewed models. The number of categories used in the transition matrix ranged from 4 to 17. Along with the variation in estimated life span (ranging from 18 to 566 yr), this gave rise to a large variation in stage duration among the reviewed models (Table 2). The stage duration for the reviewed models

Table 2

Characteristics of matrix models for 35 woody species related to model construction and parameterisation. For samples sizes, median values of the reviewed models are shown. For stage duration and survival probability, median values were calculated for each matrix model and then averaged over all models.

Parameter		Mean or median	(SD)	Min	Max	*n*
Matrix dimension		9.4	(3.6)	4	17	*37*
Median stage duration	[yr]	12.2	(11.1)	1.6	42.3	*36*
Median survival - all categories	[yr^{-1}]	0.939	(0.122)	0.308	1.000	*37*
Median survival - adult categories	[yr^{-1}]	0.973	(0.029)	0.907	1.000	*37*
Maximum survival probability	[yr^{-1}]	0.991	(0.013)	0.958	1.001	*37*
Sample size - all categories		768		102	6905	*33*
Sample size - adults		126		20	668	*22*
Sample size - proportion adults	[%]	20	(15)	1.3	50	*21*
Study period	[yr]	3.2	(2.6)	0.2	14	*36*

was considerably higher than that for 34 herbaceous species reviewed in Enright *et al.* (1995), which amounted to 2.5 ± 1.4 yr (mean ± SD). The number of stages used to construct the transition matrix increases with life span (Figure 2a), but this was not sufficient to maintain a constant stage duration (Figure 2b). Thus, in general, few stages were used to describe population dynamics and stage durations in very long-lived species were longer than in shorter-lived species.

A consequence of long stage durations is that stasis probabilities were generally high, as can be seen in Figure 3a: 50% of all stasis elements in the reviewed models have a value >0.85, and for 20% this is >0.95. High stasis values may result in very long stage duration as shown in Figure 3a, *e.g.* with a stasis probability of 0.99, 60% of the individuals stay for 50 yr in that category,

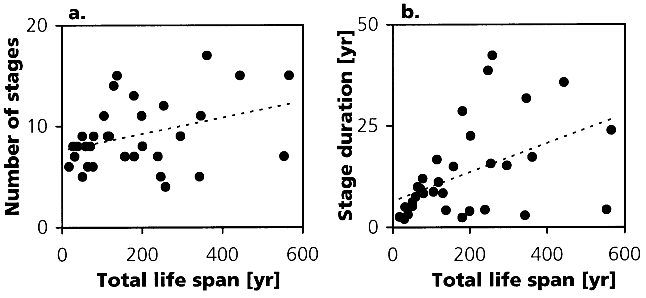


Figure 2

Model construction in relation to life span of study species for 35 woody species. (a) the relation between number of stages used and total life span (Pearson correlation: r=0.36, p<0.05, n=33). (b) the relation between median stage duration and life span (r=0.47, p<0.01, n=33). *Astrocaryum mexicanum* was left out as the estimated life span for this species was unrealistically high.

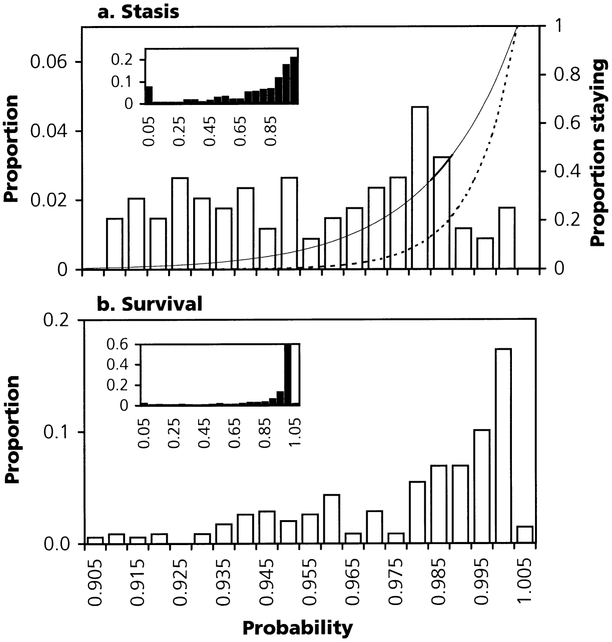


Figure 3

Distribution of stasis (a) and survival (b) probabilities in population matrix models for 37 matrix models for woody species. Proportion of the total number of stasis elements in the reviewed models (n=342) is shown in (a); that of the total number of categories (n=347; the sum of all matrix sizes in Table 1) in (b). Insets show the distribution of values over the complete range; main Figures only show values >0.90. For (a), all stasis elements of the review models were pooled to obtain a histogram. Similarly, for (b), all survival probabilities were pooled. Note that survival rate exceeded 1.00 in several cases. Lines in (a) denote the proportion of individuals (scale on right y-axis) that stay in a category for 50 yr (continuous line) or 100 yr (dashed line) for the range of stasis probability plotted along the x-axis.

and over 35% stay for 100 yr. In particular, such high values may strongly influence model output when they are found in the last matrix category.

The long life spans of the woody species included in this analysis were a consequence of high survival probabilities in the transition matrices (Table 2), reflected also in the skewed distribution of survival rates towards high values (Figure 3b). Almost 60% of the categories in the reviewed matrix models had survival probabilities >0.95. For 43 of the 347 categories (12%) in the reviewed models survival equalled 1.00, implying no mortality. Five categories had erroneous survival rates of >1 (but always < 1.001), probably due to averaging annual transition probabilities. Low mortality rates make precise quantification of survival difficult. In 15 of the 37 reviewed model studies (41%) problems with quantification of survival rates in certain categories were mentioned, due to complete absence or insufficient observations of deaths. In 12 of these studies, survival values for one or more categories were estimated using a best guess (2 cases), confidence intervals or other data sources (4), or an arbitrary value (6). In the latter case, widely different figures were used, ranging from 0.92 to 0.999.

Classification of populations in size categories was done using biological criteria in most cases (84%), with many populations being categorised using ‘simple’ category limits (*e.g.* 10-cm diameter intervals). Only in two studies were category boundaries entirely determined using numerical the classification methods of Vandermeer (1978) and Moloney (1986). The remaining 11% of the models applied a combination of numerical and biological considerations for classification.

A variety of ways to parameterise transition matrices was applied in these studies. (a) The largest share (54%) of the reviewed models used observed transition frequencies to determine transitions among categories. (b) A smaller proportion of the models (11%) started from the assumption of a fixed stage duration to obtain transition probabilities (following Crouse *et al.* 1987, Caswell 1989a), using population structure, growth rings or leaf scars to obtain estimates for stage-dependent survival and growth. (c) A few studies (5%) used an approach similar to the first by adding mean observed growth rate to each individual in a category, and determining in this way which individuals would be found in the next category in the following time interval. (d) In the remaining 30% of the models transitions among categories were calculated using average values of observed rates of survival, growth and reproduction.

In the majority of the reviewed studies (78%), transition values for each category were calculated irrespective of the demographic rates in other categories, *i.e.* no overall patterns of size-dependent growth, survival or reproduction were used to obtain transition values. Studies that used such overall patterns, applied different techniques (linear, non-linear and logistic regression).

Sample size used to parameterise the reviewed transition matrices equalled 768 (median value), but varied by a factor of 70 between the smallest and the largest sample (Table 2). Only a small proportion (on average 20%) of the total sample size was accounted for by adult individuals, and median adult sample size (126) was rather low. The study duration averaged 3 yr, with some studies based on instantaneous measures such as population structure or annual growth rings.

Model output - Population growth

Population growth rate of the reviewed models was mostly close to 1: in 65% of the cases λ was within the range 0.97-1.03 (Table 3). Extreme values occurred especially for growing populations ($\lambda > 1$): in six studies λ was >1.1 (implying a doubling time of < 7 yr) with an extraordinarily high rate (1.58) for *Ardisia*.

Table 3

Characteristics of matrix models for 35 woody species related to model output. Elasticities are sums over categories, and in the case of element elasticity in adult categories they include all different types of elements. Vital rate elasticities are adjusted to sum to 1. The median value for λ equals 1.012.

Parameter	Average	(SD)	Min	Max	*n*
Population growth rate (λ)	1.052	(0.109)	0.977	1.589	*37*
Population growth rate - zero reproduction (λ_{ZR})	0.968	(0.032)	0.888	1.000	*37*
Element elasticity - *P*	0.83	(0.15)	0.29	1.00	*36*
Element elasticity - *G*	0.15	(0.13)	0.00	0.58	*36*
Element elasticity - *F*	0.03	(0.03)	0.00	0.13	*36*
Element elasticity - in adult categories	0.60	(0.23)	0.13	1.00	*37*
Vital rate elasticity - σ	0.92	(0.07)	0.65	1.00	*36*
Vital rate elasticity - σ in adult categories	0.50	(0.21)	0.12	1.00	*35*
Vital rate elasticity - λ	0.06	(0.05)	0.00	0.26	*36*
Vital rate elasticity - ρ	0.004	(0.007)	0.00	0.04	*36*
Vital rate elasticity - *f*	0.02	(0.02)	0.00	0.08	*36*

Population growth rate was related to model construction and parameterisation in two ways. Firstly, λ tended to decrease with increasing stage duration (Spearman correlation of λ and median stage duration r=-0.43, p<0.01, n=36). Although this result might be explained by a greater stability (*i.e.* $\lambda \approx 1$) for long-lived species, no correlation was found between λ and life span (Spearman: p=0.97, n=33). Secondly, λ was positively correlated with the maximum survival rate used in the model (Figure 4a), especially when

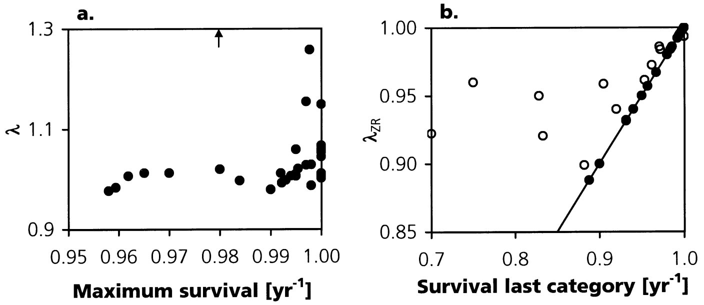


Figure 4

Relation between survival probability and population growth rate (λ) for matrix models of 35 woody species. (a) the relation between λ and the maximum survival in any category of the model; one outlier (arrow; survival=0.98, λ=1.58) for the *Ardisia* model is outside the borders of the graph (Spearman rank correlation: r=0.41, p<0.05, n=37; without outlier: r=0.49, p<0.01). (b) a similar relation for λ of a model with zero fecundity (λ_{ZR}) against survival in last category (Spearman r=0.95, p<0.001, n=37). Filled dots in (b) denote those models for which λ_{ZR} equals the survival rate in the last category; these lie on the line y=x .

maximum survival exceeded 0.90. Other parameters related to survival probability (median survival rate in adult or all categories, maximum survival in adult categories) were not correlated with λ (Spearman: $p>0.05$).

In addition to the calculation of population growth rate, λ was also determined for a model without reproduction (*i.e.* all fecundity elements were set equal to zero). Reducing reproduction in matrix models is regularly used to simulate impact of fruit or seed harvest (Peters 1990a, b, 1996, Bernal 1998). The sustainable harvest level is then determined as the proportion of seeds or fruits removed in the model such that $\lambda=1$. (Obviously, the prerequisite of this method is that $\lambda>1$ for the unmodified model.) The population growth with zero reproduction (λ_{ZR}) was generally high, averaging 0.97 (Table 3). Furthermore it was found that λ_{ZR} was equal to the survival probability in the last category in 24 (65%) of the reviewed matrix models (Figure 4b). This was the case if the last category has the highest or close to the highest survival rate in the transition matrix. In this situation, all individuals in the population are eventually contained in the last category (*i.e.* the stable stage structure has value 0 for all but the last category). In case survival rate in previous categories is considerably higher, individuals may accumulate in other than the last category and a different λ_{ZR} is obtained. As a consequence, in matrix models with a high survival probability in the last category (either the result of the species' life history or of a poor estimation) population growth without reproduction remains close to 1, thus suggesting more scope for sustainable seed extraction than in models with a lower survival rate. However, a high survival rate in the last category does not necessarily imply a high tolerance to seed extraction.

Model output - Elasticity analysis

Elasticities for matrix elements were generally large for stasis elements (*P*), intermediate for progression elements (*G*) and very low for fecundity (*F*, Table 3). This placed almost all reviewed species in the lower-right part (high *P*-low *F*) of the demographic triangle (Figure 5a). The demographic triangle, originally introduced by Silvertown *et al.* (1992,1993), positions species (or in fact models of species) by the summed elasticities for different types of matrix elements: stasis, growth and fecundity. Reviews of matrix models for plant species (Silvertown *et al.* 1993, 1996, Franco & Silvertown 1996) showed that woody species are generally found in the lower-right corner of the triangle, a result that is confirmed here for a larger number of woody species.

Apart from a species' life history, other factors influenced the values for *P*, *G* and *F* elasticity, and thus the position of a species in the demographic triangle. Firstly, the species' life span codetermined the stasis elasticity as is shown in Figure 6a. This may be intuitively interpreted as the result of its life

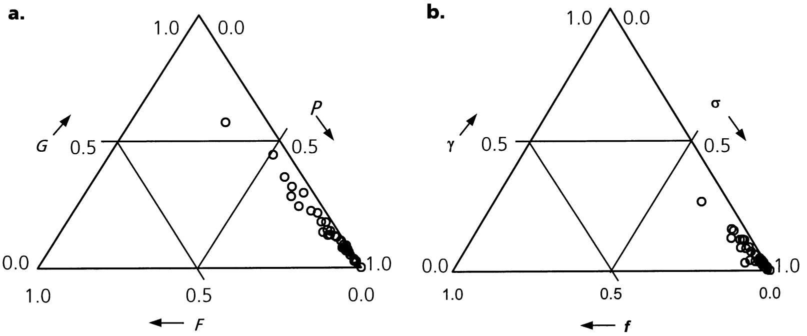


Figure 5

Triangular ordination of 35 woody species using elasticity values. Two types of elasticities were used: elasticities of matrix elements (a) and of vital rates (b). For (a) the approach introduced by Silvertown *et al.* (1992, 1993) was used: elasticities for stasis (including retrogression) were summed over all categories to obtain the value of *P*; similarly those for progression (including multi-step transitions) were used to calculate *G* and those for fecundity to calculate *F*. In analogy, elasticity values for vital rates were also summed over categories: survival (σ), positive growth (including multi-step progressions, γ) and reproductive output (*f*). These values were then adjusted to sum to 1. As the proportion of negative growth elasticity (ρ) was very low (see Table 3), this parameter was not included in the triangle, nor was it combined with other vital rates.

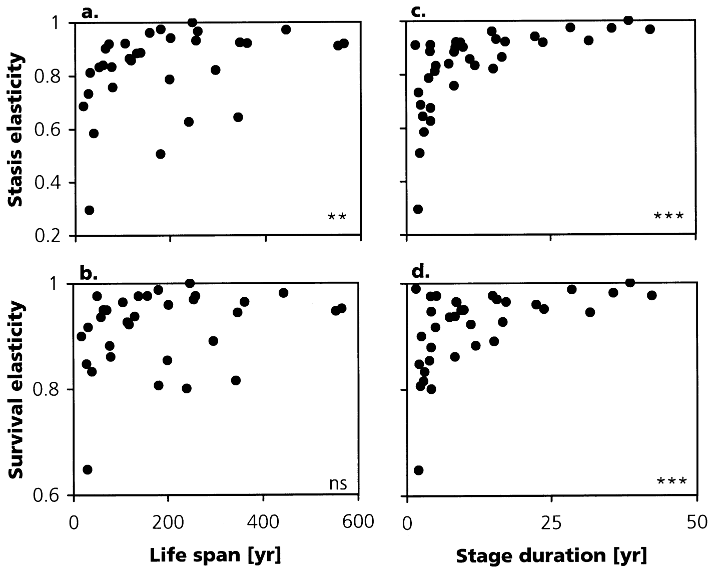


Figure 6

Influence of life span and stage duration on elasticity values for 35 woody species. Upper panels show the relation of total stasis elasticity with species life span (a) and median stage duration (b). Lower panels show the relations of total survival elasticity with these two parameters (c and d). Note the different scaling of *y*-axis for top and bottom panels. See Methods for calculation of life span and stage duration. Results of Spearman rank correlations (significance indication shown in each panel) presented as *r*, *p*, *n*: (a) 0.50, <0.01, 32; (b) not significant; (c) 0.80, <0.001, 34; (d) 0.59, <0.001, 34.

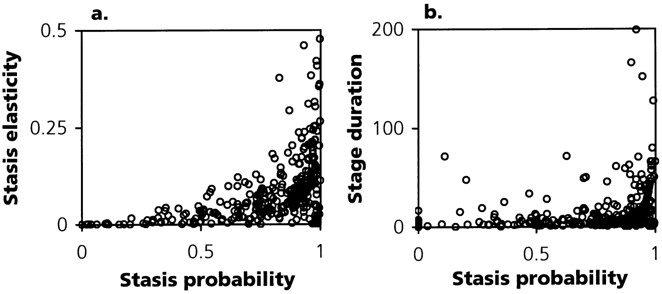


Figure 7

Influence of stasis probability in transition matrix on stasis elasticity (a) and stage duration (b) for 342 stasis elements of matrix models constructed for 35 woody species. One point (*x*=0.9922, *y*=1) is located outside the borders of panel (a); in (b) this is the case for five points with stage durations of 216-999 yr and stasis values > 0.84. Results of Spearman rank correlations presented as *r*, *p*, *n*: (a) 0.69, <0.001, 342; (b) 0.46, <0.001, 326.

history: 'persistence' is perhaps more important than growth for population maintenance in very long-lived species. However, models for species with long life spans also tended to have large median stage duration (see Figure 2). As a result, the values of stasis elements for these species is higher, resulting in higher stasis elasticities (Figure 7a). In this way, stasis elasticity was increased by stage duration (Figure 6c). Secondly, there was a relation between the value of λ and the distribution of elasticities over types of matrix elements (Figure 8a). Stasis elasticity decreased with λ, whereas both progression and fecundity elasticity increased with λ.

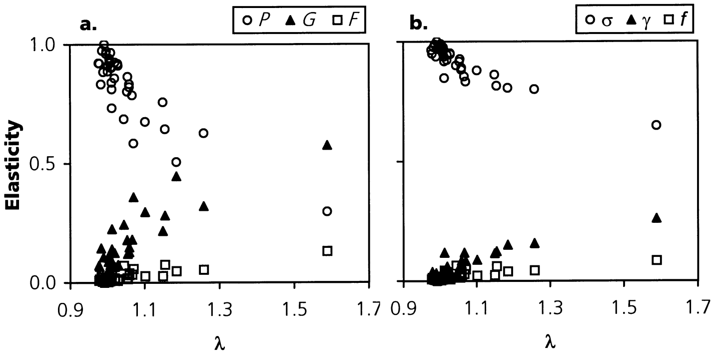


Figure 8

Relation of population growth rate and elasticity values in matrix models constructed for 35 woody species based on matrix elements (a) and based on vital rates (b). For the left panel (a), elasticities were summed over categories for stasis and retrogression elements (*P*), for progression elements (*G*) and for fecundity elements (*F*). For the right panel, elasticities were summed over categories for survival (σ), positive growth (γ) and reproductive output (*f*). Results of Spearman correlations (*r*; for all: *p*<0.001, *n*=36): (a) *G*: -0.78; *P*: 0.77; *F*=0.77; (b) σ: -0.86; γ: 0.82; *f*: 0.78.

In addition to element elasticities, elasticities for vital rates were also calculated. When summed over categories, these elasticity values were by far highest for survival (σ, on average 92%), followed by much lower values of positive growth (γ) and reproductive output (*f*) (Table 3). Furthermore, adult survival contributed with 50% of the total vital rate elasticity (Table 3). Using elasticities for the three main vital rates (σ, γ and *f*), a second demographic triangle can be constructed (Figure 5b), analogous to that for element elasticities (Figure 5a). This triangle positions species (or in fact models) based on the relative importance of their vital rates (survival, growth and reproductive output), as observed in the field. The interpretation of this triangle differs from the original one in that the values are not *contributions* to the value of λ as is the case for matrix elements, but they are proportions of the total vital rate elasticity (which does not sum to 1, but was scaled to do so; Caswell 1989a). In the vital rate triangle, species were strongly confined to the corner with high σ, low γ and very low *f* values. Considering the long life span of many of the reviewed species, this position in the triangle intuitively makes sense, as survival of individuals is crucial for population maintenance. Comparing the two triangles, it can be seen that in the vital rate graph, points are less scattered than in the original triangle (Figure 5).

Vital rate elasticities were influenced by several factors, in a similar way as element elasticities. Survival elasticity increased with species life span and median stage duration (Figure 6b & d), and decreased with λ (Figure 8b). Elasticity of positive growth (γ) and reproductive output (*f*) were both positively correlated to λ (Figure 8b). In spite of the similar relations found for element elasticities and vital rate elasticities, the changes in the latter were smaller, as shown by the more clumped distribution of points in the demographic triangle (Figure 5), and the relatively small variation of elasticity values with varying λ (Figure 8b). Nevertheless, in both cases it was clear that other parameters – apart from life history – covary with the relative importance of demographic processes to λ.

Model output - Age estimates

Stage duration generally increased with the value of stasis elements in the transition matrix (Figure 7b). For high stasis values, a very small increase in stasis probability resulted in extraordinarily long stage durations. Survival probability in the last category had a strong influence on various age estimates. Total life span increased steeply for survival rates of >0.98 (Figure 9a), amounting to the extremely high value of 1110 yr for the undergrowth palm *Astrocaryum* for which more direct and precise age calculations result in maximum life spans that are one order of magnitude smaller (Piñero *et al.* 1984). Similarly, one of the three measures of generation time presented by

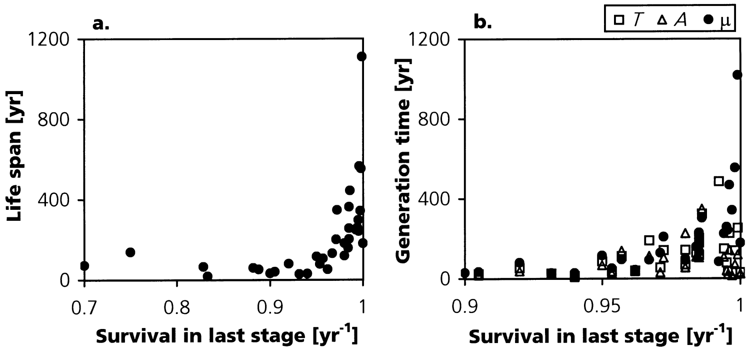


Figure 9

Influence of survival in the last category on age estimates in matrix models constructed for 35 woody species. (a) three estimates of generation time (following Cochran & Ellner 1992) and (b) an estimate of life span (mean age of residence in last category - S_1). For clarity, the left panel (a) only shows generation times for survival ≥ 0.90.

Cochran & Ellner (1992), μ, appeared to be very sensitive to high survival in the last categories, whereas the other two measures responded less strongly (Figure 9b). In several cases estimates for life span and generation time could not be derived as stasis (*Lindera*) or survival (stasis plus retrogression in *Roupala* and *Myrsine*) in the last category equalled 1.00.

Increasing matrix dimension

The increase in matrix dimension in the models for *Bertholletia* and *Chlorocardium* considerably reduced stasis probability and increased progression probability (Table 4). As a result, stage duration was strongly reduced (by 60% for *Bertholletia* and 86% for *Chlorocardium*). Secondly, element elasticities changed after increasing the number of categories. For both species, elasticity of stasis elements (*P*) decreased, whereas that of progression (*G*) increased (Table 4). Consequently, the position of the models in the element-based demographic triangle was shifted (Figure 10). Thirdly, age estimates increased substantially for the modified models, while their variability decreased (Table 4). Other model output parameters – λ and vital rate elasticity – remained the same after increasing matrix dimension (Table 4).

Discussion

The significance of stage duration

Matrix models for woody species use very matrix dimensions, causing a wide variation in stage durations (Table 2). Matrices for longer-lived species, tend to use a larger number of categories, but not sufficiently large to make

Table 4

Comparing output of original and expanded matrices for *Bertholletia* and *Chlorocardium*. Bold figures identify elasticities that differ by an absolute value >0.05. Vital rate elasticities are adjusted to sum to 1.

Parameter	*Bertholletia*		*Chlorocardium*	
	original	expanded	original	expanded
Number of categories	17	76	15	106
Median value stasis elements (*P*)	0.95	0.82	0.98	0.86
Median value progression elements (*G*)	0.18	0.05	0.13	0.01
Median stage duration [yr]	17	7	36	5
Population growth rate (λ)	1.007	1.005	0.998	0.998
Element elasticity - *P*	**0.92**	**0.78**	**0.97**	**0.90**
Element elasticity - *G*	**0.07**	**0.22**	**0.03**	**0.10**
Element elasticity - *F*	0.006	0.005	0.003	0.002
Element elasticity - in adult categories	0.37	0.36	**0.34**	**0.29**
Vital rate elasticity - σ	0.96	0.98	0.98	0.98
Vital rate elasticity - σ in adult categories	0.37	0.36	0.33	0.29
Vital rate elasticity -	0.03	0.02	0.01	0.01
Vital rate elasticity - ρ			0.003	0.003
Vital rate elasticity - *f*	0.005	0.005	0.003	0.002
Total life span [yr]	362	637	444	822
CV of mean age per category	45	29	49	16
Average generation time [yr]	228	245	302	380
CV of generation time	43	38	45	29

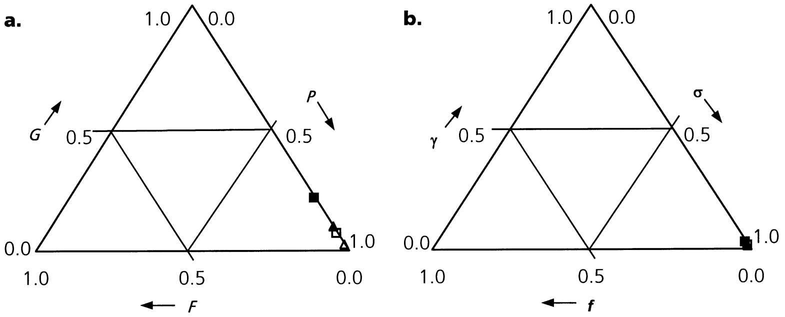


Figure 10

Triangular ordination of two matrix models that were modified to increase the number of categories. The influence of increasing category number is shown for elasticities based on matrix elements (a) and based on vital rates (b). Calculations and axes labels as in Figure 5. Triangles identify *Chlorocardium* models and squares *Bertholletia* models; open symbols denote the output from original matrix models and closed symbols that of the modified models. In (b) all four symbols are clumped.

stage duration comparable to that of shorter lived woody species or herbs (Figure 2, Enright *et al.* 1995). By applying a low number of categories, model output was influenced in several ways. Firstly, the contribution of stasis elements to population growth (stasis elasticity, Figures 6 and 7) was increased. This was demonstrated clearly by the considerable changes in elasticities caused by decreasing stage duration in two of the reviewed models (Figure 10). Similar changes in position in the demographic triangle have been found by Enright *et al.* (1995) for several tree species. Mathematical explanations of such shifts are provided by de Matos & Silva Matos (1998) for a common type of transition matrices. This effect of model construction on elasticity values hinders a straightforward interpretation of a species' position in the demographic triangle (*GPF* space) as an expression of its life history. This position is also codetermined by factors related to methodology and not directly to species' life history.

We presented an alternative demographic triangle based on vital rate elasticities (as opposed to element elasticities, Figure 5b). The distribution of total elasticity among vital rates seems to be less dependent on stage duration than is the case for element elasticities: a large reduction in stage duration had almost no impact on vital rate elasticities (Figure 10b). This may make this triangle more suitable to be used for comparative demography or interpretation of individual model results.

There is, however, another factor that complicates the interpretation of the position in demographic triangles: the population growth rate (λ). In both types of triangles, the position of models is strongly correlated with the value of λ, and the largest part of the spread of points in the triangles can probably be attributed to variation in λ. The magnitude of changes in elasticities, however, appears to be smaller for vital rate elasticities (Figure 8). Similar correlations of λ with element elasticities were found by Silvertown *et al.* (1993), using a set of 66 herbaceous and woody plant species. In our dataset, λ generally decreased from the top of the triangle towards the lower-right corner (Figure 5; *cf.* Oostermeijer *et al.* 1996, Silvertown *et al.* 1996, Valverde & Silvertown 1998). This relation can be explained by the notion that a growing population necessarily depends on reproduction (*F*) and on growth (*G*) to reproductive sizes; in contrast, in a non-growing (*e.g.* non-reproducing) population, stasis elasticity (*P*) will have a dominating contribution to the value of λ (see Figure 4b; de Kroon *et al.* 2000). Thus, in cases where λ deviates much from the value of 1, the position in the triangle reflects the performance a particular population (either growing or declining rapidly), rather than the species' life history (Oostermeijer *et al.* 1996, Silvertown *et al.* 1996). Clearly, as several factors influence elasticities, the position of in the demographic triangle should be interpreted carefully (*cf.* Shea *et al.* 1994).

Problems with the influence of stage duration on model output may be overcome using a recently developed modelling technique named the *integral projection model* (Easterling *et al.* 2000). As the model does not use categories, but rather applies continuous size-dependent patterns of vital rates, there is no influence of categorisation. The model is developed such that it yields output (population growth rate, sensitivity, elasticity, stable population structure) compatible with matrix model output. However, the recent development of this model and the statistical (curve-fitting) procedures that should be conducted prior to model construction, implies mean that it is not yet a complete substitute of matrix models. Furthermore, in its present state, the integral projection model requires that there is a single size-related parameter that can be used as an independent variable to fit all demographic rates. For many woody plants, this may be difficult to implement, *e.g.* diameter cannot be recorded for small seedlings and height measurements are inaccurate (and often uninformative) for large adults.

Age estimates were influenced by model construction in two different ways. Firstly, stage duration increased with stasis probability, with small changes in high stasis probabilities having a great impact on stage duration. Since very high stasis values imply a high survival probability, and this is generally hard to determine with precision, uncertainty in estimation of adult survival rates may have a considerable influence on stage duration and age estimates (*cf.* Caswell 1989a).

Secondly, age estimates were greatly increased in the expanded matrix models for two tree species. This phenomenon is complex and probably results from the intrinsic characteristics of matrix models. Part of the difference in age can be explained by the fact that each extra category adds one year to the minimum value of the species' life span (that is if only one-step progressions are coded in the matrix). Even if categories with 1.00 probability for progression and 0.00 for stasis would be inserted, life span would increase by one year. Nevertheless, this difference explains only a small part of the increase in estimated age: *e.g.* in the *Bertholletia* model, 59 categories were added whereas the estimate for life span increased by 275 yr; in the *Chlorocardium* model this was 91 and 378 yr, respectively. Another explication may be that in small matrices, the value of the total life span is to a large extend determined by individuals that pass rapidly through the whole life cycle, as those that stay for a long time 'accumulate' probability to die, with the risk of never reaching the next (and thus also the last) category. By increasing the number of categories, the 'maximum speed' to pass through the matrix is considerably reduced, which may lead to longer life spans (but see Zagt 1997 for an example of shorte life span in an expanded matrix). Clearly, additional simulations and mathematical analysis of matrix-derived age estimates are needed to understand the consequences of matrix dimension for age estimates.

Thirdly, the increase in age estimates in the expanded matrices was accompanied by a decrease in variation in these parameters. A similar result was obtained by Boucher (1997) who showed that within-stage age distributions are more sharply peaked as the number of categories increases. The decrease in variability of age estimates in expanded matrices may be explained by the fact that in these matrices the variation in stage duration in each category is relatively small, so that individuals are 'forced' to pass through the matrix in a certain way. In smaller matrices of long-lived species, which typically have high stasis values, individuals may either stay one or many years in a category (see Figure 3a), causing high variability in stage durations.

Model Parameterisation and data limitations

Parameterisation of matrix models for woody species has been carried out in many ways. Inevitably, this has had an impact on model output. In most models, the transitions among categories strongly depend on the distribution of sampled individuals among and within categories. Unintended differences in sample size among categories may therefore affect the values of the transition matrix and thus the model output. As woody species are generally long-lived, this approach may cause problems with the calculation of growth transitions and survival rates. In several cases, the value of progression elements was guessed as no progressions were observed. Similarly, mortality was frequently not observed, especially in adult categories, and in that case often a value of 1.00 was used, which is probably unrealistic for many categories. In this way, survival could amount to 1.00 in one category, whereas it was considerably lower in neighbouring categories. Such strong and 'abrupt' changes in survival or growth rates over categories is not likely to reflect the overall patterns of vital rates for the species. By analysing size-dependent patterns in vital rates over the complete (or even partial) size range of a species, such problems may be overcome (see below).

The use of observed transition probabilities implies that care should be taken with respect to the number of individuals in a category. Vandermeer (1978) and Moloney (1986) developed algorithms to determine category size for transition matrices, based on considerations of sample size and differences among categories. Surprisingly, these algorithms were hardly used in the models reviewed.

In some studies, different parameterisation techniques were combined in one transition model (*e.g.* Zagt 1997, Chapters 3 and 4). In cases like this, observed transitions were usually employed for seedling stages (often with retrogressions to previous size categories), and calculated transitions using size-dependent patterns in vital rates were employed over several categories of juveniles and adults. This approach is useful when two clearly different demographic patterns can be observed within a species, as is the case in tropical forest species. Usually, the demography of seedlings is characterised by high mortality, and by unpredictable, generally low and occasionally negative, growth, as a result of low light availability, low resistance to drought, herbivore attack, etc. Adults, on the other hand, typically experience low mortality combined with a continuous and more deterministic growth rate, as they are well-established and face less constraining factors.

The importance of adult categories

Adult categories contribute importantly to population growth in the reviewed woody species: they account for 60% of total element elasticity, survival in adult categories accounts for 50% of the total vital rate elasticity and the category with the highest elasticity is in most cases (81%) an adult stage. In contrast with this importance is the low sampling effort and sample size for adult categories (only 20% of total sample size). This is obviously a consequence of the monotonic decrease of plant density with size. The small sample sizes in adult categories are likely to result in problems of parameter estimation. In addition, the typically high survival (>0.97) in adult categories requires an increased sample effort for these categories. Indeed, many authors mentioned the quantification of adult survival as a problem of model parameterisation.

Our review shows that for high survival (and stasis) probabilities, a small change in these parameters yields considerable changes in population growth, elasticity values and age estimates. This, combined with a low precision of survival estimates in adult categories, leads to a large degree of uncertainty in model output. To illustrate this, we calculated confidence intervals for adult survival, based on the median number of adults sampled in the reviewed studies and their average survival (Table 2). The binomial standard deviation for the average survival probability of 0.973 equals 0.015; the resulting 95% confidence interval for survival is 0.926–0.991. This wide range of survival probabilities has important implications for values of λ, elasticities and age estimates (see Figures 4, 7 and 9). This example shows that it is important to consider the implications of problems in model parameterisation. Similarly, care should be taken with the use of unrealistically high survival rates when mortality cannot be quantified. In this case, employing a larger sample size by combining individuals from several categories and assigning the same survival probability to all of them may be a practical solution.

Recommendations for model construction

The foregoing shows that model construction and parameterisation may have an important influence on the output of matrix models (see Figure 1).

This has implications for the interpretation of results of individual models, and for the comparison of model output of different studies. Based on the result of our review, we have formulated several recommendations that may overcome some of the observed problems, or prevent misinterpretation of model results.

Firstly, we argue that for long-lived species, the use of overall size-dependent patterns to parameterise transition matrices yields more reliable model output than the use of observed transition frequencies. In the latter case, the transition matrix depends very much on distribution of individuals among and within categories, especially when sample sizes are small. Therefore, 'methodology' may have considerable influence on model output, thus hampering the interpretation of model results as an expression of the species' life history or the population's present status (see Figure 1). Several simple statistical methods can be used to analyse size-dependent relations in growth (linear regressions, non-linear regressions, see Zeide 1993 for equations commonly used in forestry), survival (logistic or double-logistic regressions; Gompertz or Weibull distributions) and reproduction (logistic regression and/or linear regression). In case no significant patterns can be found, using an average value for a number of categories is preferred over using stage-specific rates that fluctuate more or less randomly among categories. In our opinion, a model with less detail (vital rates averaged over categories), but with more robust values and a more straightforward interpretation, is advantageous over a model with more, but shaky, detail.

Secondly, the review shows the need to increase sample size of adults in demographic field studies. In particular, difficulties in determining adult survival ask for more intense sampling, perhaps over longer periods of time. As it was shown that unrealistically high values for survival or stasis have considerable impact on model output, care should be taken when using uncertain estimates or substituting missing values. Often, values of neighbouring categories can be adopted. Also, in certain cases, confidence intervals can be calculated (*e.g.* when no mortality is observed) to assist the selection of a realistic value. In addition, different values of an uncertain or unknown parameter can be used to analyse their impact on model output, before a definite value is chosen. In cases where confidence intervals can be quantified, the impact of parameter uncertainty can be assessed using the approach presented in Chapter 6.

Thirdly, we feel that it is useful in many cases to pool demographic information of various sites or observation periods, when no differences are found between such datasets. Differences in vital rates can be readily detected using simple statistics (see *e.g.* Chapters 2 & 4). When no significant differences are found, pooling information from various years or populations may yield a matrix model which is based on more or more reliable information (more individuals, longer observation period, fewer problems with parameter estimation or measurement errors). Most probably, such a model provides a better representation of the species' life history than several matrices based on incomplete subsets of data.

Fourthly, we encourage the use of elasticities for vital rates as an additional tool for demographic analysis. They have the advantage of being less sensitive to matrix dimension, provide a more direct idea of the dependency of lambda to changes in certain measured parameters, and are therefore perhaps more easily interpreted in terms of life history. However, also for this type of elasticity, care should be taken with its covariation with λ.

Finally, in our view, less focus should be given to the exact value of λ when interpreting matrix model output. As λ gives the population growth rate when time goes to infinity (assuming conditions to remain unchanged), it may not always be the most appropriate parameter to assess the population status with respect to population management, or gradual environmental changes (Doak & Morris 1999). Furthermore, wide confidence intervals are frequently found for λ, which often include the value of 1 (Alvarez-Buylla & Slatkin 1994, Silva Matos *et al*. 1999, but see Batista *et al*. 1999). Studies that have looked backwards in time, have shown that predictions of population development by λ do not always hold (Bierzychudek 1999, Ehrlen 2000). Therefore, one should be careful not to be base conclusions (about *e.g.* sustainable harvesting or population response to succession) on the value of λ alone.

Acknowledgements

We thank Miguel Franco for providing us with several transition matrices and a template to calculate vital rate elasticities. Heinjo During, Miguel Franco and Marinus Werger gave valuable comments on a draft version of the paper. Part of this study was financed by grant BO009701 from the Netherlands Development Assistance.

Manupare river, Bolivian Amazon.

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

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.

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

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 understorey 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

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 understorey specialist, completing its entire life cycle under the dark understorey 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 Sourthern 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 (λ) as a the 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

Methods to assess sustainability

	1	2	3
Using:	Population growth rate (λ)	Absolute population size	Relative population size
Type of dynamics:	Asymptotic ($t \rightarrow \infty$)	Transient (t<100 yr)	Transient (t<100 yr)
Used for:	Fruits, seeds	Whole individuals	Individuals, leaves
Advantage:	Simple Straightforward	No dependence on λ Flexible	No dependence on λ Also if pop. shrinks Flexible
Disadvantage:	λ should be >1 Relies on value λ	Pop. should grow	

Figure 1
Three methods to assess sustainability of extraction of plant parts. See text for further explanation.

can be harvested, without affecting the stability of the population. Sustainability is thus assured when a harvested population is stable or grows (λ≥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 λ=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 (λ–1) (Usher 1966, 1969) or by ([λ-1]/λ) (Enright & Ogden 1979). An important disadvantage of this method is that it requires λ to be larger than 1, otherwise no extraction is possible. A second disadvantage is that the method relies heavily on the value of λ, which is often uncertain. For instance, for population models which predict a growing population (λ>1), the value of λ 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 λ close to one (65% of models for woody plants have λ 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 λ, 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

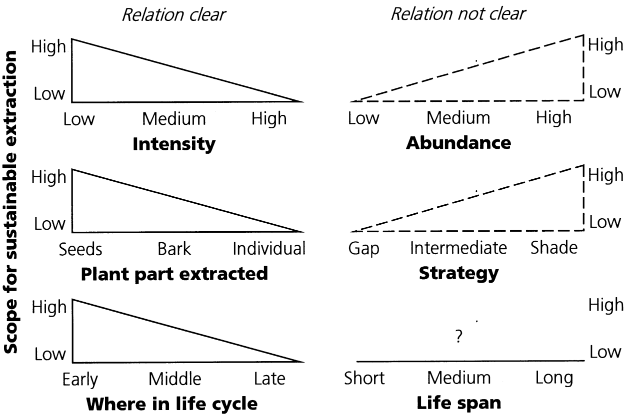


Figure 2

Scope for sustainable extraction in relation to (demographic) characteristics of woody species. Broken lines indicate uncertain relations, the question mark for life span indicates that no general relation is expected. Note that these relations are generalised, and do not apply to all cases. "Intensity" refers to harvest intensity; "where in life cycle" refers to where extraction is taking place in the species' life cycle; "strategy" refers to regeneration strategy ("gap" = gap dependent; "shade" = shade tolerant). In "plant part extracted", fruits and in certain cases - latex and leaves - can be added to the "seeds" category, and roots to the "bark" category. See text for further explanation.

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.

Acknowledgements

I thank Rene Boot, Marielos Peña, Marinus Werger, Floris Zuidema and Corien van Zweden for valuable comments on a draft version of this chapter.

Resumen ejecutivo

Aprovechamiento de productos no-maderables

Los bosques tropicales de la región Amazónica han sido utilizados por miles de años por sus inhabitantes. Solamente desde hace 150 años, el uso se ha convertido en una explotación comercial en grande escala, en algunas regiones. En la segunda mitad del siglo 19 y la primera parte del siglo 20 se aprovechaban en grande escala productos como la quinina y la goma. La extracción de madera se intensifico en las últimas décadas del siglo 20. El daño causado por la tala de árboles para madera, la deforestación tropical debido a otras razones, y la perdida de biodiversidad de bosques tropicales causó una preocupación ambiental a nivel mundial en los años '80. Al mismo tiempo, se admitía el valor de los productos no-maderables proveniente de bosques tropicales (Myers 1984, de Beer & McDermott 1989, Peters *et al*. 1989b). Se argumentó que para estos productos (denominados productos forestales no-maderables, PFNM), es más factible reconciliar el uso con la conservación de bosques tropicales que en el caso de la extracción maderera. La estructura y el funcionamiento del bosque no son afectados por el aprovechamiento de PFNM y, en la mayoría de los casos, la extracción del producto no causa la muerte de la planta (nótese que no se considera animales en este texto). Los productos no-maderables son importantes para millones de hogares en los países en vías de desarrollo (FAO 1997a), y contribuyen substancialmente a la economía local y regional (Homma 1992, FAO 1997a). Además, se usa una variedad enorme de productos, algunos con un mercado importante al nivel internacional (FAO 1997a), y otros con un potencial de ser vendido en gran escala.

Los productos no-maderables que se aprovechan en gran escala, puede ser susceptibles a la sobre-explotación, así como es el caso de la extracción maderera. En estos casos, se necesitan regulaciones para prevenir el declinio de la disponibilidad del recurso o la extinción de la especie (FAO 1997a). Para otros productos, existen perspectivas buenas para un uso sostenible, y en estos casos se podría certificar el sistema de extracción. En ambos casos, es necesario contar con información sobre el impacto de la explotación en la disponibilidad futura del recurso. Esta información se puede obtener en estudios ecológicos en los cuales se evalúa la sostenibilidad del aprovechamiento.

Sostenibilidad del aprovechamiento de productos no-maderables

La sostenibilidad ecológica del aprovechamiento de un producto puede ser evaluada a tres niveles: a nivel del individuo, de la población y del ecosistema entero. Al nivel del individuo, hace una diferencia si el aprovechamiento causa la muerte de individuo o si solamente algunas hojas de la planta son cosechadas. Al nivel de la población, el aprovechamiento puede ser considerado sostenible si la población no desaparece o si la productividad de la población (en términos de la disponibilidad del recurso aprovechado) no disminuye. Al nivel del ecosistema, la sostenibilidad será lograda si – en términos generales – el aprovechamiento no cambia el funcionamiento del ecosistema. El foco de este tesis es el impacto del aprovechamiento de productos no-maderables a nivel de la población. En este nivel se puede obtener información sobre cómo la producción del recurso puede ser mantenido por un periodo prolongado. Esta información es importante para diseñar regulaciones para el aprovechamiento de los PFNM, y para justificar la certificación de sistemas de aprovechamiento.

El aprovechamiento de PFNM siempre influye en la dinámica de la población: por ejemplo, el recojo de frutos disminuirá la regeneración, la colecta de hojas disminuirá el crecimiento, y la colecta de goma probablemente incrementará la mortalidad. Por lo tanto, es posible obtener conocimiento sobre el impacto del aprovechamiento, tomando en cuenta la dinámica de los individuos y las poblaciones (Hall & Bawa 1993, Peters 1996b). Para hacer un análisis de este tipo, se necesita dos tipos de información. Primeramente, se necesita una comprensión de la demografía de la especie sin perturbar. Esto incluye respuestas a preguntas como: ¿cuales son las tasas de sobrevivencia, crecimiento y reproducción de individuos de diferentes tamaños?; ¿que es el tamaño mínimo de reproducción?; ¿cuales son las fases cruciales en el ciclo de la vida?, etc. Seguidamente, se necesita información sobre cómo las tasas demográficas están siendas afectadas por el aprovechamiento. Estos dos tipos de información pueden ser analizados usando modelos demográficos.

Una grande variedad de modelos demográficos son aplicados en la ecología (forestal) (por ejemplo Vanclay 1995, Peng 2000). Estos pueden ser agrupados según su unidad de modelaje: si esta es la planta individual, los modelos son "modelos de base individual" (*individual-based models*, DeAngelis *et al*. 1992). En cambio, si esta es una categoría de individuos agrupados por edad o tamaño, los modelos se llaman "modelos de poblaciones estructuradas" (*structured-population models*, Tuljapurkar & Caswell 1997). El primer tipo de modelos es más complejo en el sentido de que se usan las tasas demográficas de individuos para analizar la dinámica al nivel de la población, sin agrupar a los individuos. Como consecuencia, estos modelos son más complicadas de construir. En el segundo tipo de modelos, los individuos están agrupados en categorías y se toma estos grupos como unidad de modelaje. Consecuentemente, se "pierde" a los individuos mismos en el proceso de modelaje.

Los modelos de matrices son los más populares del segundo tipo de modelos (Caswell 1989a, ver Enright & Hartshorn 1981, y Peña-Claros & Zuidema 1999 para una introducción técnica en español), y son los que se utiliza en esta tesis. Estos modelos son aplicados frecuentemente para analizar la sostenibilidad de sistemas de aprovechamiento de productos no-maderables (Capítulos 2, 3 y 5, Pinard & Putz 1992, Peña-Claros & Zuidema 1999).

Como hay muchas diferentes partes de plantas que se aprovechan como productos no-maderables, existen varias maneras en que la extracción de estas partes influye en la dinámica de la población. Para analizar el impacto del aprovechamiento, primeramente se necesita responder a las siguientes preguntas: (1) ¿cuáles categorías están afectadas por el aprovechamiento?, y (2) ¿cuáles tasas demográficas están afectadas por el aprovechamiento? La respuestas a estas preguntas son importantes para diseñar estudios en el campo y para construir el modelo demográfico. La Figura 1 muestra con algunas ejemplos como el aprovechamiento de PFNM pueden influenciar la dinámica de la población. Como se puede apreciar en la Figura 1, el aprovechamiento de semillas o palmito tiene un impacto directo en una o varias flechas del ciclo de vida, mientras que el impacto de la extracción de hojas y goma es indirecto. En el primer caso, se extrae individuos, semillas o frutos de la población, y el aprovechamiento puede ser "traducido" directamente en un cambio en las transiciones entre categorías (indicadas como flechas). Por ejemplo, si se colecta 25% de las semillas, resulta en una reducción del 25% en la transición reproductiva. También, este tipo de aprovechamiento puede ser simulado por una reducción en la abundancia de ciertas categorías en la estructura poblacional: por ejemplo si se extrae 50% de los adultos en una población para obtener palmito se reduce la abundancia de estos individuos con un 50%. Sin embargo, si el impacto del aprovechamiento no puede ser traducido directamente en un cambio en una o más transiciones, es necesario ejecutar experimentos para determinar el impacto de la extracción en las tasas demográficas. Por ejemplo, se puede ejecutar una extracción experimental en

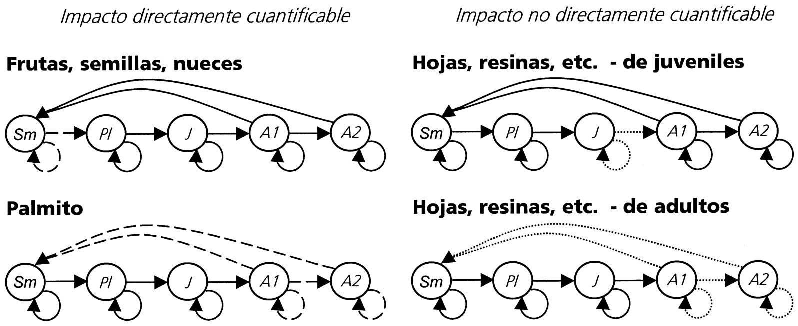


Figura 1
La influencia de diferencias que tiene la parte extraída de plantas en la dinámica poblacional de un árbol imaginaria. Un ciclo de vida generalizado está mostrado, que consiste de cinco categorías: semillas (Sm), plantines (Pl), juveniles (J), adultos pequeños (A1) y adultos largos (A2). Las flechas indican transiciones entre categorías: flechas hacia la derecha se refieren a crecimiento, las que conectan a la misma categoría se refieren a permanencia en la misma categoría y las de categorías de adultos a la categoría de semillas indican reproducción. Las flechas no interrumpidas no son afectadas por la extracción; las flechas interrumpidas indican transiciones que son afectadas por la extracción y que pueden ser cuantificadas en base a la intensidad de la extracción; las flechas punteadas se refieren a transiciones que pueden ser afectadas por la extracción, pero que necesitan ser cuantificadas en un estudio de aprovechamiento. Una suposición de esta figura es que no hay cambios en tasas demograficas debido a cambios en el medio ambiente que resultan del aprovechamiento (por ejemplo una disponibilidad de luz más alta).

parte de la población estudiada (ver Capítulo 5). Luego, se determina el impacto del aprovechamiento en la dinámica de la población, comparando o combinando modelos de poblaciones sin perturbar con los de poblaciones aprovechadas (ver por ejemplo Capítulo 5, Zagt 1997).

Contexto de este estudio

Este estudio forma parte del Programa Manejo de Bosques de la Amazonía Boliviana (PROMAB), que es un proyecto de investigación, extensión y educación del Instituto para el Hombre, Agricultura y Ecología (IPHAE, Riberalta, Bolivia), la Carrera de Ingeniería Forestal de la Universidad Técnica del Beni (CIF/UTB, Riberalta, Bolivia) y la Universidad de Utrecht (Holanda). Desde 1995, las actividades de PROMAB han sido: estudios ecológico-forestales y socio-económicas, asistencia técnica y entrenamiento de los usuarios de los bosques de la región (con énfasis en agricultores y comunidades rurales), educación a estudiantes de forestería, y la diseminación de conocimiento e información a usuarios del bosque e instituciones gubernamentales responsables para la implementación de la Ley Forestal. El objetivo del Programa es contribuir al mejoramiento de la calidad de vida de los habitantes de la región a través del uso sostenible y la conservación de los bosques y sus recursos.

Objetivos del estudio

Los objetivos de este estudio fueron:

1. analizar la demografía de varias especies de árboles de la Amazonía Boliviana, que se utilizan para extraer productos no-maderables;
2. evaluar el impacto y la sostenibilidad de la explotación de productos no-maderables de varias especies de árboles de la Amazonía Boliviana; y
3. examinar la aplicación de modelos de matrices para analizar la demografía de árboles y para evaluar la sostenibilidad ecológica de la extracción de productos no-maderables.

Comparando la historia de vida de las especies estudiadas

En esta tesis de doctorado, la demografía de tres especies de árboles fueron estudiadas: un árbol emergente (*Bertholletia excelsa*, Capítulo 2) y dos palmeras (*Euterpe precatoria*, Capítulo 3; y *Geonoma deversa*, Capítulos 4 & 5). Resultados de un estudio demográfico de una cuarta especie, la palmera *Attalea butyracaea* ('palla') de la cual también se usa las hojas para techos, serán publicados en una otra oportunidad. Las tres especies estudiadas son aprovechadas para la obtención productos no-maderables: castaña (o almendra, nuez de Brasil) es colectada de *Bertholletia*, palmito de *Euterpe*, y hojas para techos de alta calidad de *Geonoma*. Las especies son similares en algunas características y diferentes en otras características relacionadas a su demografía, el impacto del aprovechamiento y sus perspectivas para manejo sostenible. En la Tabla 1, las especies estudiadas son comparadas. El siguiente texto explica la información en esta Tabla.

Las especies estudiadas son notablemente diferentes en relación al tamaño de los adultos y la distribución espacial: *Bertholletia* es un árbol emergente que ocurre con una baja densidad; *Euterpe* es una palmera del (sub)dosel que se encuentra en densidades altas; y *Geonoma* es una palmera del sotobosque que forma rodales con una alta densidad de plantas. La estrategía reproductiva de las especies también es diferente: *Geonoma* se reproduce tanto de manera vegetativa como por semillas, *Euterpe* y *Bertholletia* se reproducen solamente por semillas. En la última especie, la dispersión de semillas depende mayormente de roedores (*Dasyprocta* spp.) que pueden abrir los frutos

Tabla 1

Una comparación de las tres especies estudiadas en esta tesis. Notese que se presenta solamente valores promedios y que algunos parametros son muy variables. Las densidades están presentadas para las parcelas de estudio y son generalmente inferiores si calculadas en áreas más extensas; la distribución espacial se refiere a áreas más grandes. Plantines incluyen plantines pequeños en la primera categoría de tamaño; adultos incluyen individuos desde la primera categoría con un porcentaje alto de individuos reproductivos. La sobrevivencia presentada es un año con precipitación normal. Para *Geonoma* la información incluida se refiere a los macollos (individuos genéticos). La importancia de las categorías y las tasas demográficas están basadas en el análisis de sensibilidad de los modelos de matrices. La importancia de sobrevivencia es el porcentaje de la elasticidad total de tasas vitales que se debe a la sobrevivencia (ver métodos en Capítulo 6). Cantidades de los productos obtenidos son representados como nueces, palmitos y hojas, respectivamente. *a.* = aproximadamente.

Parámetro			Especie	
		Bertholletia	*Euterpe*	*Geonoma*
- Características generales				
Forma de vida		Árbol emergente	Palmera del (sub)dosel	Palmera del sotobosque
Altura de adultos	[m]	35-45	15-25	1-4
Típo de reproducción		Semillas	Semillas	Semillas & clonal
Densidad de adultos	[ha^{-1}]	*a.* 1-3	*a.* 25	*a.* 1,000
Densidad de plantines	[ha^{-1}]	*a.* 25-45	*a.* 200	*a.* 14,000
Distribución espacial		Heterogéneo	Homogéneo	Muy heterogéneo
- Dinámica de población				
Sobrevivencia de plantines	[% año^{-1}]	*a.*55	*a.*70	*a.* 55
Sobrevivencia de adultos	[% año^{-1}]	*a.*99	*a.* 97	> 99
Crecimiento de plantines		Bajo	Bajo, frecuentemente negativo	Bajo, frecuentemente negativo
Categorías más importantes		Reproductivas - temprano	Reproductivas - tarde	Reproductivas - temprano
Tasa demográfica más importante		Sobrevivencia	Sobrevivencia	Sobrevivencia
Importancia de sobrevivencia	[%]	97	96	89
Estrategía de regeneración		Dependiente de claros	Intermediario?	Tolerante a sombra
Duración de vida	[año]	*a.* 360	*a.* 110	*a.* 300
Edad al alcanzar tamaño reproductivo	[año]	*a.* 125	*a.* 70	*a.* 25
- Aprovechamiento				
Parte extraída		Semillas	Meristema apical	Hojas
Producto obtenido		Castaña o almendra	Palmito	Material para techos
Abundancia de individuos aprovechados	[ha^{-1}]	*a.* 1-3	*a.* 25	*a.* 1,000
Abundancia del producto	[ha^{-1}]	*a.* 2,000-4,000	*a.* 25	*a.* 35,000
Impacto del aprovechamiento		Bajo	Alto	Intermediario
Capacidad de recuperación		Probablemente alta	Baja	Alta
Tiempo de recuperación		-	Largo (>50 años)	Corto (<5 años)
Persepectivas para uso sostenible		Buenas	Malas	Buenas

(Capítulo 2). Para todas las especies, la abundancia de plantines relativa a la abundancia de adultos fue alta, y las estructuras de población fueron similares (con forma de una J invertida).

En cuanto a la dinámica de la población, la sobrevivencia de plantines fue baja, contrastando con una (muy) alta tasa de sobrevivencia de adultos en las tres especies. Se ha encontrado frecuentemente que plantines de árboles tropicales tienen un alta mortalidad. Esto puede ser atribuido a la baja intensidad de luz en el sotobosque (Capítulos 2 & 3), a la vulnerabilidad para herbivoría y predación de semillas (Capítulo 2), y a la vulnerabilidad a ser dañado o totalmente cubierto por hojas o ramas (Capítulo 4). Además, la variabilidad climatológica influyó en la sobrevivencia de los plantines (Capítulos 2,3 & 4). En las tres especies, la probabilidad de sobrevivir incrementó rápidamente de plantines pequeños hasta plantines más grandes o brinzales.

La tasa de crecimiento de plantines fue en general baja, y se observó frecuentemente un crecimiento negativo. Aparentemente, los plantines de *Bertholletia* sufren menos con las condiciones desfavorable del sotobosque, probablemente como pueden utilizar la reserva de su cotiledón (Zuidema *et al*. 1999). En cambio, la tasa de crecimiento de juveniles (individuos no-reproductivos con un tallo visible o un diámetro medible a 1.3 m altura) fue generalmente alta. Para *Bertholletia* y *Euterpe*, la tasa de crecimiento incrementó rápidamente a partir de juveniles pequeños, y alcanzó su valor máximo con los individuos pre-reproductivos. Los adultos de estas especies generalmente tienen tasas de crecimiento bajas. Este padrón no linear entre crecimiento y tamaño de la planta es típico para árboles tropicales (por ejemplo: Zagt 1997, Clark & Clark 1999, Alder & Silva 2000, Silvie-Gourlet & Houillier 2000). El estado reproductivo (es decir si la planta es reproductivo o no) estuvo íntimamente relacionado al tamaño de la planta en las tres especies, y estubo relacionada con la disponibilidad de luz en el caso de *Bertholletia* y *Euterpe*.

La estrategia de regeneración varía entre las especies estudiadas: *Bertholletia* es considerada como una especie que depende fuertemente de claros en el dosel (Mori & Prance 1990), lo cual se confirma por la alta tasa de crecimiento que tiene la especie en condiciones de alta luz (Capítulo 2, Kainer *et al*. 1998, Poorter 1999, M.Peña-Claros *comunicación personal*). *Euterpe* probablemente depende menos de claros para su regeneración natural: en este estudio plantines de esta especie respondieron menos fuertemente a un incremento de intensidad de luz, aunque en otros estudios se ha observado una tasa de crecimiento más elevada en alta luz (Peña-Claros 1996, Poorter 1999). Por último, *Geonoma* es una especialista del sotobosque, que crece en condiciones de poca luz (<7% apertura del dosel) en el sotobosque (Capítulo 4).

A pesar de las diferencias en el tamaño de adultos y en la estrategia de regeneración, existen correspondencias importantes en las historias de vida de las tres especies: todas tienen una duración de vida larga (con excepción de los caules individuales de *Geonoma*, que viven por 37 años aproximadamente) y tienen poblaciones estables (es decir, tasa de crecimiento poblacional cercana a 1). En todas las especies, categorías con individuos reproductivos contribuyen en la mayor medida a la tasa de crecimiento poblacional, y sobrevivencia es la tasa demográfica más importante.

Impacto del aprovechamiento y sostenibilidad

El impacto del aprovechamiento varió considerablemente entre las especies estudiadas: para *Euterpe* se encontró un fuerte impacto de la extracción debido a que los individuos que se cortan para extraer palmito contribuyen mucho a la tasa de crecimiento poblacional. Para *Geonoma*, la extracción de hojas tuvo una influencia marcada en la tasa de crecimiento de las plantas y en la reproducción, pero no influyó en la tasa de mortalidad. En los primeros años después de la colecta de hojas, la reproducción sexual y vegetativa fueron reducidas considerablemente (por 40-70%), mientras que las tasas de crecimiento y producción de hojas fueron menos afectadas (por 30-40% y 10-15%, respectivamente). Para *Bertholletia*, no se observó indicaciones de una explotación insostenible en dos bosques donde se ha aprovechado castaña por un tiempo largo: en ambos poblaciones se observó regeneración natural de la especie, y ambas poblaciones tienen un tamaño estable. Además, no se esperaría un impacto negativo del aprovechamiento en por lo menos 125 años, el tiempo estimado hasta que un plantín alcance el tamaño reproductivo en un bosque primario.

El tiempo necesario de recuperación después del aprovechamiento es corto en el caso de la recolección de hojas de *Geonoma*: 36% y 68% del número de hojas colectadas fueron recuperadas después de un y dos años, respectivamente. Se puede esperar la recuperación completa del área de hojas en tres años; después de este periodo es posible que las tasas de crecimiento y reproducción retornen a niveles de una situación sin aprovechamiento. Sin embargo, para la extracción de palmito de *Euterpe* el tiempo de recuperación es largo, ya que los individuos extraídos pueden solamente ser reemplazados por semillas, un proceso que toma casi 100 años. Para *Bertholletia*, es difícil estimar el tiempo de recuperación, ya que no se encontró un impacto claro del aprovechamiento en la regeneración de las poblaciones estudiadas.

Los factores antemencionados - el impacto del aprovechamiento y la habilidad de recuperación - determinan si un cierto producto puede ser extraído de manera sostenible. Para *Bertholletia*, el análisis demográfico demuestra que hay buenas perspectivas para una producción sostenible, no obstante la alta intensidad del aprovechamiento (casi el 90% de las semillas son colectadas): existe una regeneración continua de plantines, no existen vacíos en la estructura poblacional, el modelo demográfico no predice un declinio en el tamaño de la población, y la producción de semillas es el proceso demográfico menos importante para el crecimiento de la población. La actividad no intencionada de 'sembrar' semillas de *Bertholletia* que realizan los colectores de castaña, y la cacería de los dispersadores de la especie (roedores) en áreas aprovechadas podrían contribuir a la regeneración continua de la especie, a pesar del aprovechamiento que se realiza. Sin embargo, estas relaciones son altamente especulativas, ya que no existen evidencias que estos factores jueguen realmente un papel importante. Aun así, hay buenas perspectivas de un uso sostenible de castaña, proporcionando de esta manera oportunidades para la certificación como un producto "verde". Iniciativas de certificación de castaña en Bolivia ya han sido asumidas (CFV 1999).

La situación para *Euterpe* es claramente diferente. Los individuos cortados para la extracción de palmito son viejos y su muerte tiene un impacto fuerte en el crecimiento de la población y la disponibilidad futura de palmito. Simulaciones de modelos demográficos demostraron que intensidades altas de extracción (75-100% de los adultos cosechados) combinadas con ciclos de extracción cortos (4-8 años), causan un deterioro rápido del tamaño de la población y la abundancia de adultos. Sin embargo, también con regímenes de extracción menos intensivos - extrayendo 25% de los individuos reproductivos cada 32 años - la disponibilidad de palmito disminuye continuamente, cuando comparado con la situación sin perturbar. Estos resultados están confirmados por un estudio demográfico similar en poblaciones en bosque inundado en el departamento de Santa Cruz, Bolivia (Peña-Claros 1996, Peña-Claros & Zuidema 1999). Además, estudios de *Euterpe edulis*, una palmera similar que se explota para palmito en Argentina y el Sur-Este de Brasil, indican la misma tendencia (Galetti & Fernandez 1998). Ajustes en la intensidad o frecuencia del aprovechamiento de palmito de *Euterpe precatoria* no son considerados como una opción económicamente viable, ya que haría que la extracción no sea lucrativa. Las conclusiones de los dos estudios en Bolivia han resultado en la formulación de normas técnicas para el aprovechamiento de palmito a nivel nacional. Una fuente alternativa de palmito son plantaciones de la palmera clonal *Bactris gasipaes* que tiene un crecimiento rápido. Pruebas con esta especie en Bolivia y Brasil han tenido éxito, y han demostrado que se puede obtener cosechas considerables en un tiempo corto (PROMAB 1998). En conclusión, es evidente que las limitaciones demográficas de la especies descartan un sistema de aprovechamiento de palmito de *Euterpe precatoria* que sea económicamente viable y ecológicamente sostenible. El aprovechamiento de esta especie es un caso típico de expansión y declinio rápido (*boom and bust*) el cual también ha sido encontrado para otros productos no-maderables (Homma 1992).

Las perspectivas de un aprovechamiento sostenible de la colección de hojas de *Geonoma* son buenas. Aunque se observó una disminución considerable en las tasas de crecimiento y reproducción, la sobrevivencia de plantas explotadas no fue afectada y el área foliar colectada fue recuperado rápidamente. Resultados similares han sido obtenidos para otras especies de palmeras de sotobosque (Mendoza *et al*. 1987, Oyama & Mendoza 1990, Chazdon 1991), indicando que estas plantas son muy tolerantes a la remoción de hojas. Simulaciones de extracción de hojas demostraron que poblaciones aprovechadas recuperan bien después de la cosecha: se puede mantener la disponibilidad de hojas inicial al nivel de la población con cosechas repetidas. Sin embargo, es necesario tener cuidado con cosechas frecuentes: probablemente se puede asegurar la disponibilidad sostenible de hojas cuando se colecta hojas una vez cada 10-15 años. Las buenas perspectivas para un uso sostenible en combinación con la alta densidad local de la especie y la alta calidad de sus hojas, sugieren que hay oportunidades para realizar un aprovechamiento más intensivo de este producto. En este momento, las hojas de *Geonoma* son vendidas solamente en cantidades bajas y a nivel nacional, pero la diseminación de información sobre la calidad de este producto, y la certificación de su sistema de aprovechamiento puede incrementar el interés en el mismo.

La construcción de modelos de matrices

En este estudio, modelos de matrices fueron utilizados para analizar la dinámica de población de las especies investigadas. Sin entrar en demasiados detalles técnicos, los siguientes párrafos tratan del uso (como construir, como tratar variación) y la utilidad (para el análisis de demografía, para la evaluación de sostenibilidad) de los modelos de matrices.

Los modelos de matrices tienen una forma estandarizada que puede ser adaptada dependiendo de la especie de interés o de los deseos del investigador. Para la construcción de modelos de matrices, toda la población de la especie es dividida en categorías de tamaño (categorías de edad se usa muy poco para plantas; por lo tanto, el siguiente texto se limita a categorías de tamaño). La información básica que el modelo requiere son las probabilidades de transiciones entre las categorías, las cuales están organizadas en una matriz de transición (una matriz cuadrada de dimensión $m \times m$, en que m significa el número de categorías). Para la construcción de esta matriz de transición, se necesita tomar varias decisiones: (1) ¿Cuales parámetros se aplica para la categorisación de la población? (2) ¿Cómo se determina los límites de las categorías? (3) ¿Cómo se cuantifican las probabilidades de las transiciones?

Con respecto al parámetro usado para la categorisación (1), es importante que este parámetro tenga una relación con el crecimiento, sobrevivencia y reproducción de los individuos. Aunque en general solamente un parámetro de clasificación está disponible (por ejemplo: diámetro del tallo), existen casos en que varios parámetros pueden ser utilizados (por ejemplo en el caso de plantines: número, tipo o tamaño de hojas). En este caso, se recomienda el uso de un parámetro que tenga la relación más fuerte con las tasas demográficas que se usa en el modelo. En esta tesis, la clasificación de plantines fue basada en altura (*Bertholletia*), número de hojas (*Geonoma*) y longitud de la hoja (*Euterpe*). Juveniles y adultos fueron clasificados por diámetro del tallo (*Bertholletia*) y altura del tallo (otras especies).

La determinación de los límites de las categorías (2) puede ser hecho de dos maneras: por criterios biológicos o por criterios de tamaño de muestra. En ambos casos, el objetivo es de maximizar las diferencias en tasas demográficas entre las categorías y minimizar la variación de estas tasas dentro de una categoría. La segunda manera de categorizar parte del concepto que existen dos tipos de errores contrastantes que influyen en la solidez de las tasas de transiciones entre categorías: el error de la muestra (que incrementa cuando se disminuye el tamaño de la muestra y, por lo tanto, con categorías angostas) y el error de distribución debido a la variación demográfica dentro de una categoría (que incrementa con el ancho de la categoría). Varios métodos fueron diseñados para determinar los límites de categorías tratando de minimizar de estos dos tipos de errores (Vandermeer 1978, Moloney 1986), pero estos casi nunca se aplican en estudios de plantas arbóreas (Capítulo 7). El primer tipo de clasificación, basado en criterios biológicos, es el más popular. Este método fue también utilizado en esta tesis. Si se aplica esta técnica, es importante elegir límites de categorías de manera que las diferencias en sobrevivencia, crecimiento y reproducción sean maximizados entre las categorías. Por ejemplo, el límite de categorías no-reproductivos y reproductivos tiene que ser elegido de manera que se maximice la diferencia en la producción de semillas entre categorías. Además, se tiene que tomar en cuenta que el uso de categorías muy anchas tiene como efecto que individuos pueden quedarse por mucho tiempo en una categoría, lo que puede tener un impacto importante y poco realista en los resultados del modelo (Capítulo 7). Finalmente, a pesar de la existencia de algunas reglas, la determinación del número de categorías y sus límites sigue siendo un proceso muy subjetivo.

La decisión de como se cuantifica el valor de las transiciones (3) también puede tener implicaciones importantes para los resultados del modelo. El método más popular para calcular valores de transiciones entre categorías es de usar frecuencias de transiciones observadas (Capítulo 7). Usando este método, cada individuo es asignado a una categoría en el tiempo *t*, y esto se repite en el tiempo *t*+1. Luego, la frecuencia de transiciones es calculada como la proporción del número de individuos inicial en la categoría que se encuentra en una otra categoría o en la misma categoría, después de un año. En caso de que el número de individuos en una categoría sea pequeño, si la categoría es ancha o si la tasa de crecimiento es baja, puede ser difícil de cuantificar adecuadamente los valores de las transiciones. En este caso, puede ser que no se observe ciertas transiciones.

Las probabilidades de transiciones también pueden ser calculadas de manera diferente, usando las tasas demográficas (o *tasas vitales*: sobrevivencia, crecimiento y reproducción) que forman parte de las probabilidades en la matriz de transiciones. Este método ha sido aplicada en los estudios de esta tesis y en algunos otros estudios (por ejemplo Zagt 1997, Batista *et al*. 1998), y es más adecuada para especies de larga vida como plantas leñosas (Capítulo 7). Las tasas vitales usadas en este método pueden ser medidas directamente en el campo (tasas de sobrevivencia, de crecimiento y producción de semillas). Luego, estas tasas pueden ser relacionadas al tamaño de la planta para obtener padrones de tasas vitales para todo el rango de tamaños. Este se puede hacer usando análisis de regresión, o en el caso de no encontrar padrones de tasas vitales dependientes del tamaño de la planta, se puede calcular el valor promedio de varias categorías. Seguidamente, se puede obtener una estimación de una tasa vital para cada categoría usando la ecuación de regresión. Los detalles técnicos de este método se encuentran en los Capítulos 2, 3 y 4.

Los dos métodos de parametrización pueden ser combinados en un modelo (por ejemplo Capítulos 3 & 4, Zagt 1997). Esta combinación es útil cuando se puede distinguir dos tipos de demografía dentro de una especie: por un lado la demografía de plantines con una alta tasa de mortalidad y una tasa de crecimiento muy variable, y por otro lado, la demografía de adultos con baja mortalidad y crecimiento continuo y predecible. En este caso (que es común en árboles tropicales), la demografía de plantines es descrita adecuadamente usando frecuencias de transiciones observadas (especialmente cuando el tamaño de la muestra es grande) y demografía de adultos usando transiciones calculadas en base a padrones de tasas vitales dependiente del tamaño de la planta.

Resumiendo, existen diferentes maneras de construir y parametrizar modelos de matrices, que pueden resultar en diferentes matrices de transición. Una selección cuidadosa del método para determinar el tamaño y contenido de la matriz de transición es importante, ya que diferencias en metodología pueden tener implicaciones significativas para los resultados del modelo (Capítulo 7).

Incorporando variación en tasas demográficas en modelos de matrices

Los modelos de matrices asumen que las tasas demográficas de individuos (sobrevivencia, crecimiento y reproducción) en una cierta categoría de tamaño (o de edad) son descritas adecuadamente por el valor del promedio. Es claro que esta suposición no es valida en el caso de que ciertas tasas demográficas varíen mucho. Esta variabilidad puede ser causada (1) por variación natural entre los individuos en una categoría debido a diferencias en tamaño o en edad, variación genética, variación espacial y variación temporal; y (2) por la incertidumbre en la estimación de parámetros. En los estudios incluidos en esta tesis, ambos tipos de variación fueron importantes. El primer tipo de variación fue bastante importante para el crecimiento de plantines en las tres especies estudiadas, y para el crecimiento de juveniles de *Bertholletia* y *Euterpe*. Esta variación se debe por parte a las diferencias en la disponibilidad de luz entre individuos de este tamaño. Árboles adultos, por el contrario, se encuentran generalmente en condiciones similares en relación a la disponibilidad de luz. Una alta variación en tasas de crecimiento de plantines y juveniles ha sido observado frecuentemente en árboles tropicales (por ejemplo: Zagt 1997, Clark & Clark 1999). En el caso de *Bertholletia*, el fuerte aumento de crecimiento en condiciones con más luz también contribuyó a la variabilidad de este parámetro. Un otro parámetro que demostró una alta variación es la producción de semillas en *Bertholletia* (Capítulo 2). Para las otras especies la producción de semillas no fue determinada, pero es probable que también sea bastante variable entre individuos y años (Janzen 1978).

Con respecto al segundo tipo de variación, se encontró dificultades en la estimación de las tasas de sobrevivencia en dos de las tres especies (*Bertholletia* y *Geonoma*). Este problema parece ser común: en un compendio de 37 modelos de matrices para plantas leñosas (Capítulo 7) se mencionó este problema en >40% de los estudios. En este capítulo, también se demostró que esta inseguridad puede tener una influencia considerable en los resultados del modelo (en la tasa de crecimiento poblacional, estimaciones de edades, análisis de sensibilidad), especialmente en el caso de que la sobrevivencia está muy alta.

En el Capítulo 6, se presenta un método para incorporar la variación de parámetros demográficos en el análisis de sensibilidad de modelos de matrices. Los tipos de análisis de sensibilidad regulares (también denominados “análisis de perturbación") examinan la importancia de una cierta tasa demográfica, aplicando un cambio infinitamente pequeño y absoluto ("sensibilidad", Caswell 1978) o infinitamente pequeño y proporcional al valor de la tasa en consideración ("elasticidad", de Kroon *et al*. 1986). Por lo tanto, estas técnicas no toman en cuenta que ciertas tasas demográficas demuestran una variación más grande que otras, y que un cierto cambio en una tasa demográfica es más probable en un parámetro variable que en un parámetro constante. El método de perturbación usado en Capítulo 6 toma en cuenta la variabilidad de tasas demográficas, simulando los cambios en la tasas de crecimiento poblacional que resultan de cambios 'probables' en tasas demográficas dentro el modelo. Este método fue aplicado a seis especies de plantas para determinar la influencia de la variabilidad demográfica en las tasas de crecimiento poblacional. Los resultados de las simulaciones demuestran que la variación demográfica puede influenciar las tasas de crecimiento de manera considerable. Por ejemplo, la alta variación del crecimiento individual de juveniles de *Bertholletia* y *Euterpe* tiene un impacto importante en la tasa de crecimiento poblacional.

Incorporando variación temporal en modelos de matrices

En su forma básica, los modelos de matrices no varían temporalmente, es decir, asuman que las condiciones de la población estudiada continúan por siempre. En los estudios reportadas en esta tesis, la demografía fue afectada por dos tipos de variación temporal: variación climatológica (en precipitación; para las tres especies) y el efecto del aprovechamiento (en el caso de *Geonoma*).

La variación climatológica fue causada por una reducción grande en la precipitación del fin de '97 hasta medianos del '98, con una precipitación promedio de <100 mm por mes en un año, mientras que este promedio es normalmente 143 mm. Este periodo coincidió con una época de 'El Niño', pero no se encontró un padrón consistente de poca precipitación en años con 'El Niño'. Datos de precipitación de 50 años demuestran que años secos similares ocurren regularmente en la región: en promedio un año seco en cada ocho años. Variación en precipitación entre años también ha sido observada en otros lugares en los Neotrópicos (ver por ejemplo, Ropelewski & Halpert 1996). El año seco afectó significativamente la demografía de las tres especies estudiadas: el reclutamiento de nuevas plantines fue afectado fuertemente (una reducción de 70-80% en las tres especies). También se observó un efecto en la sobrevivencia (0-20%) y en el crecimiento de plantines (0-20%). Sin embargo, la sobrevivencia y el crecimiento de juveniles y adultos fue menos afectado.

La variación temporal causada por efecto del aprovechamiento puede ocurrir en caso de que los individuos aprovechados se recuperen gradualmente después de la explotación, como se observó en *Geonoma* después del corte de hojas (Capítulo 5). Este tipo de variación temporal también puede darse si las condiciones de la población cambian gradualmente después del aprovechamiento (por ejemplo, Peña-Claros 1996, Zagt 1997), después de un cambio súbito del ambiente (por ejemplo, después de un huracán, Pascarella & Horvitz 1999), o en el transcurso de la sucesión de una vegetación (por ejemplo, en bosques tropicales, Alvarez-Buylla 1994).

Existen diferentes modificaciones del modelo de matriz básico que permiten incorporar variación temporal. Estos modelos con variación temporal (*time-varying models*) pueden ser clasificados en modelos determinísticos y modelos estocásticos (Caswell 1989a). Modelos determinísticos asumen que diferentes tipos de años siguen una secuencia fija, por ejemplo siempre un año seco después de siete años normales. En cambio, en los modelos estocásticos los años están seleccionados al azar, aunque la probabilidad de ocurrencia de diferentes tipos de años es fija: por ejemplo, la probabilidad de un año seco es 1/8.

Ambos tipos de modelos (determinísticos y estocásticos) fueron aplicados en esta tesis. En el estudio de *Geonoma*, se encontró que la secuencia de años secos y normales - sea fija o al azar - tiene un impacto muy pequeño en la tasa de crecimiento poblacional a largo plazo, probablemente por las pequeñas diferencias en las tasas demográficas más importantes entre un año normal y un año seco. Para *Bertholletia* se aplicó un modelo estocástico para incorporar la variación temporal. Para simulaciones del aprovechamiento de hojas de *Geonoma*, se usó un modelo determinístico ya que el objetivo fue proyectar la dinámica de la población, usando varios regímenes de extracción con un ciclo de corta fijo (cortando hojas cada 4, 8, o 16 años). En este caso, se requiere una secuencia fija de tipos de años. Un método afín fue aplicado para *Euterpe*. Como se asumó que la extracción de adultos no tenía un efecto en la dinámica de la población remanente, se aplicó el mismo modelo de matriz para las poblaciones sin perturbar y las que fueron aprovechadas. La extracción del palmito fue simulado mediante la remoción de un porcentaje de adultos la estructura de la población al comienzo de cada ciclo de corta (ver también Olmsted & Alvarez-Buylla 1995).

El uso de modelos de matrices para analizar la demografía de plantas

Se han publicado modelos de matrices para aproximadamente unas 140 especies de plantas (M. Franco, *comunicación personal*), de las cuales por lo menos 35 son especies leñosas (Capítulo 7). Por lo tanto, estos modelos pueden ser considerados como un instrumento popular para el análisis demográfico.

Se han sido aplicado modelos de matrices para asistir en la conservación de especies raras o en peligro (por ejemplo Silvertown *et al*. 1996, Heppell *et al*. 2000, Sæther & Bakke 2000), y para evaluar la sostenibilidad de sistemas de aprovechamiento de plantas, como en esta tesis (Pinard & Putz 1992, Peters1996b, Peña-Claros & Zuidema 1999).

Los modelos de matrices han sido aplicados más que cualquier otro tipo de modelo para el análisis demográfico de plantas. Se presenta posteriormente una breve sobrevista de las fortalezas y defectos de los modelos de matrices.

Las fortalezas de los modelos de matrices incluyen que estos pueden ser construidos con relativa facilidad, que usan una estructura simple y estandarizada, que generan resultados que pueden ser comparados fácilmente, que pueden ser construidos con pocos datos, que su método de trabajo está claramente descrito en libros de texto, y que pueden ser implementados usando software relativamente simple (por ejemplo RAMAS-Stage, Applied Biomathematics, Setauket, New York) inclusive con programas de hoja de cálculo. La mayoría de otros modelos demográficos tienen requerimientos más rigurosos en relación a la disponibilidad de datos, requieren más capacidad de computación y tienen una estructura mucho más compleja.

La sencillez de los modelos de matrices también es su principal defecto, ya que implica que deben hacerse varias suposiciones. Algunos de estas suposiciones pueden ser pocas realistas. Primeramente, como antemencionado, los modelos de matrices estándares asumen que la dinámica de la población no cambiará en el tiempo, una suposición que puede ser poca realista debido a la variación temporal en condiciones ambientales. Además, los modelos de matrices asumen que las tasas demográficas de individuos son adecuadamente descritas por el valor promedio. Esto no puede ser realista para especies que dependen de claros en el dosel del bosque para su regeneración y que demuestran un crecimiento muy elevado en condiciones de alta luz (ver Capítulo 2). También esto puede ser poco realista cuando la variabilidad en tasas demográficas es grande. Terceramemte, en modelos de matrices, la demografía de individuos en una categoría es solamente determinada por su estado presente, es decir que los individuos "se olvidan de su pasado". Esto implica que un individuo que pasa rápidamente por algunas categorías de tamaño, puede repentinamente dejar de crecer y quedarse por un tiempo largo en una sola categoría. Además, individuos se pueden quedar por periodos muy extensos en una categoría que tiene una baja probabilidad de progresión a la siguiente categoría (Capítulo 7). Puesto que en la realidad las tasas demográficas de un individuo en el pasado frecuentemente tienen una correlación con las tasas futuras, la suposición que la demografía solamente depende del estado presente de un individuo no es realista frecuentemente (por ejemplo Ehrlen 2000).

Considerando las fortalezas y defectos antemencionados, los modelos de matrices pueden aún así ser considerados como una herramienta muy útil en el análisis demográfico de plantas. Son especialmente útiles cuando (1) los datos son escasos, (2) el investigador tiene poco conocimiento de modelaje, (3) están construidos tomando en cuenta sus suposiciones y su sensibilidad para limitaciones de datos, y (4) cuando se interpreta sus resultados con cuidado. En relación al último punto, se necesita tomar en cuenta que los resultados de los modelos de matrices están influidos no solamente por factores relacionados a la historia de vida y las condiciones ambientales de la población, sino también por factores relacionados a la construcción del modelo (Capítulo 7).

El uso de modelos de matrices para evaluar la sostenibilidad de aprovechamiento

Tres métodos han sido usados para evaluar la sostenibilidad del aprovechamiento de plantas con modelos de matrices (Figura 2). Las diferencias principales entre estos métodos es el tipo de dinámica aplicada: el primer método aplica la dinámica asimptótica, es decir después de un periodo muy extenso. Los dos otros métodos usan la dinámica de tiempo determinado (*transient dynamics*), es decir en un periodo relativamente corto. En este caso, el modelo de matriz proyecta cambios en el tamaño y la estructura de la población, empezando con la estructura poblacional inicial.

El primer método, que fue utilizado para evaluar la sostenibilidad de la extracción de frutos y madera, toma la tasa asimptótica de crecimiento de la población (λ) como criterio para evaluar sostenibilidad. Esta tasa de crecimiento es constante y se la alcanza a medida que el tiempo tiende al infinito. La lógica de este método es que el ‘excedente’ de individuos (frutos o árboles) producido cada año en una población creciente puede ser cosechada sin afectar la estabilidad de la población. Se asegura de este manera la sostenibilidad si la población aprovechada es estable o creciente ($\lambda \geq 1$). En el caso de extracción de frutos (Peters 1990a & b, Bernal 1998), el nivel de extracción máximo sostenible es determinado mediante incrementos en la extracción de semillas en el modelo hasta que el valor de λ llega a ser 1 (indicando una población estable). En el caso de la madera, este valor es determinado en una manera similar, como la porción de la población que es igual a (λ-1) (Usher 1966, 1969) o a ($[\lambda-1]/\lambda$) (Enright & Ogden 1979). Una desventaja importante de este método es que requiere que el valor de λ sea arriba de 1; ya que si no es el caso no se puede aprovechar la población. Una segunda desventaja es que el método depende fuertemente en el valor de λ, que frecuentemente no es muy seguro. Por ejemplo, para los modelos de matrices que proyectan que una población creciente ($\lambda > 1$), el valor de λ frecuentemente parece ser no significativamente diferente de 1 (por ejemplo, Alvarez-Buylla & Slatkin 1994). Esto implica que el tamaño de estas poblaciones también puede ser estables o disminuyendo. Este incertidumbre es especialmente importante ya que en un gran porcentaje de los modelos de matrices para especies arbóreas el valor de λ es cerca a uno (el 65% de los modelos de estas especies obtienen un λ entre 0.97 y 1.03, Capítulo 7). Terceramente, la tasa asimptótica de crecimiento de la población es calculada para una población en que la distribución de individuos en las categorías de tamaño es estable, es decir no cambiará durante el tiempo. Frecuentemente, en los modelos de matrices, la estructura poblacional observada difiere importantemente de la estructura estable, lo que implica que el matriz de transición no refleja adecuadamente la demografía de la especie, o que la estructura de la población está cambiando (por ejemplo, por sucesión de la vegetación).

Algunos de los problemas mencionados pueden ser eliminados cuando se usa un método basado en la dinámica de tiempo determinado. El segundo método en Figura 2, aplica los cambios absolutos en el tamaño de la población (o cambios en la abundancia de una cierta categoría, por ejemplo la de adultos) para evaluar la sostenibilidad. Si este tamaño no llega abajo de un nivel determinado, o abajo de una proporción de su valor inicial, se puede considerar la extracción como sostenible (por ejemplo Olmsted & Alvarez-Buylla 1995, Zagt 1997). Este método es más flexible que el anterior, ya que se lo puede aplicar para diferentes regímenes de aprovechamiento con diferentes frecuencias e intensidades de extracción. Esto es más difícil o imposible de hacer usando el primer método. Esta técnica no depende del valor de λ, pero aún requiere que la población crezca (o que sea estable) durante el periodo de la simulación. Si la población está disminuyendo, no existen perspectivas para una extracción sostenible.

El tercer método en Figura 2 es similar al segundo, con la diferencia que no requiere que la población crezca. En cambio, considera los cambios en el tamaño de la población (o categoría) aprovechada relativamente al tamaño en una situación sin perturbar. Si la proporción de estos tamaños disminuye abajo de un cierto nivel, se considera que el sistema de aprovechamiento no es sostenible (por ejemplo Capítulo 3, Peña-Claros 1996). Este "nivel de sostenibilidad" puede variar en función a cuan importante es que el aprovechamiento sea sostenible, y en función a cuanto riesgo de tener una población en declinio se puede aceptar. Ya que esta técnica no requiere que la población crezca (en periodos cortos o largos), es más flexible que los demás métodos.

Métodos para evaluar sostenibilidad

	1	2	3
Usando:	Tasa de crecimiento de la población (λ)	Tamaño absoluto de la población	Tamaño relativo de la población
Tipo de dinámica:	Asimptótico ($t \to \infty$)	Tiempo determinado ($t<100$ años)	Tiempo determinado ($t<100$ años)
Utilizado para:	Frutas, semillas	Individuos completos	Individuos, hojas
Ventaja:	Simple Fácil	No depende de λ Flexible	No depende de λ También si pob. no crece Flexible
Desventaja:	λ debe ser >1 Cuenta con valor λ	Pob. debe crecer	

Figura 2
Tres métodos para evaluar la sostenibilidad de la extracción de partes de plantas. Ver el texto para explicación.

En el estudio de *Bertholletia* se aplicó un cuarto método para evaluar la sostenibilidad de sistemas de extracción, de una manera indirecta. Como no fue posible estudiar la demografía de una población sin perturbar, no se podía comparar una población no perturbada con una aprovechada. En este caso, varios parámetros indirectos fueron aplicados para evaluar la sostenibilidad: si se encontró regeneración natural de la especie, si la población estaba creciendo o estable, la edad mínima de reproductiva y el periodo reproductivo de los árboles adultos. Usando estas medidas, también se puede hacer una evaluación de la sostenibilidad, en el caso de que no se pueda hacer una comparación entre situaciones aprovechadas y no perturbadas.

En conclusión, los modelos de matrices han demostrado ser una herramienta útil para evaluar la sostenibilidad de sistemas de aprovechamiento de productos no-maderables. Además, proveen un mejor entendimiento de la demografía de la especie aprovechada, el cual puede ser aplicado para diseñar tratamientos silviculturales con el objetivo de incrementar el potencial del aprovechamiento, o para proveer información necesaria para el cultivo de las especies de interés.

¿Podemos derivar reglas simples para evaluar la sostenibilidad de sistemas de aprovechamiento?

Obviamente, no es posible construir modelos de matrices para todas las especies que son aprovechadas para la obtención de productos forestales no-maderables (PFNM). Por lo tanto, la pregunta es si se puede desarrollar reglas simples o de fácil implementación para evaluar la sostenibilidad de las sistemas de aprovechamiento. ¿Bajo que condiciones hay perspectivas de un manejo sostenible y bajo cuales no? Peters (1996b) evaluó el manejo potencial de especies arbóreas usadas para la extracción de PFNM. Seguidamente se hace un análisis similar en base a los resultados de esta tesis.

La perspectiva para sostenibilidad de un sistema de extracción depende tanto de la demografía de la especie explotada como del impacto de la extracción en la demografía. Para generar reglas simples, por lo tanto, se necesita información sobre ambos asuntos. En cuanto a la demografía, se puede derivar algunas generalizaciones en base a la comparación de las especies estudiadas (Tabla 1) y en base al compendio de modelos de matrices para especies leñosas (Capítulo 7): la estructura poblacional contiene típicamente muchos más individuos pequeños que grandes; la sobrevivencia es mucho más importante que el crecimiento y la reproducción para la tasa de crecimiento poblacional; las categorías reproductivas contribuyen importantemente al crecimiento poblacional; las especies leñosas tienen generalmente una vida larga; y el tamaño de sus poblaciones es estable frecuentemente.

En cuanto al impacto del aprovechamiento, dependerá de la parte de la planta extraída así como de la intensidad y frecuencia de la extracción. La capacidad de individuos aprovechados de recuperarse después de la cosecha y el tiempo requerido para la recuperación son factores importantes. En caso de que la recuperación no sea posible (si el individuo está matado debido al aprovechamiento), existen todavía perspectivas para un uso sostenible, si la población puede recuperarse de la pérdida de individuos. Si los individuos matados son cruciales para el mantenimiento del tamaño de la población o si la recuperación toma mucho tiempo, hay pocas perspectivas para sostenibilidad.

Combinando los padrones generales en demografía de especies leñosas con el impacto de la extracción, las perspectivas para un uso sostenible pueden ser relacionadas a información sobre la demografía y la extracción de la especie (Figura 3). Tres relaciones relativamente inequívocas puede ser establecidas (paneles al lado izquierdo en Figura 3). Una intensidad de extracción alta limita las perspectivas para un uso sostenible: existen ejemplos bien documentados de sobre-explotación de productos no-maderables. En cuanto a la parte extraída de la planta, el aprovechamiento del individuo completo claramente disminuye las perspectivas para uso sostenible, aunque esta relación depende también de la intensidad de la extracción y de la importancia de los individuos matados para la población en total. La categoría afectada por la extracción es importante ya que un dado impacto negativo en la demografía de adultos tiene un efecto mucho más grande en la dinámica de la población que un impacto equivalente en plantines.

Las otras relaciones representados en la Figura 3 (paneles al lado derecho), son menos claras como dependen de otros factores. Se ha argumentado que

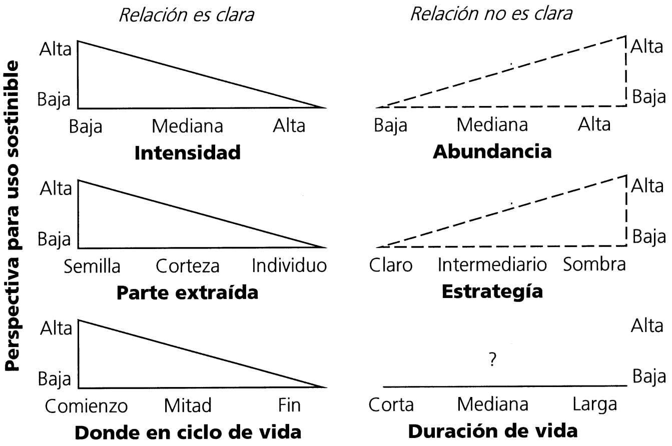


Figura 3
Perspectivas para uso sostenible en relación a características (demográficas) de especies arbóreas. Líneas interrumpidas indican relaciones inseguras, el signo de interrogación para duración de vida indica que no se esperaría una relación. Notese que estas relaciones son generalizados, y que no ser válidos en todos casos. "Intensidad" se refiere a la intensidad del aprovechamiento; "Donde en ciclo de vida " se refiere a donde la extracción es localizada en el ciclo de vida de la planta; "Estrategía" se refiere a la estrategía de regeneración ("Claro" = dependiente de claros; "Sombra" = tolerante a la sombra). En "Parte extraída", frutos y en ciertos casos resinas y hojas pueden ser añadidos a la categoría de "Semillas", y raices a la categoría de "Corteza". Ver el texto para explicación.

una abundancia alta de la especie aprovechada provee más perspectivas para un manejo sostenible, ya que en especies raras existe una probabilidad más alta de sobre-explotación (Boot 1997, Peters 1996b). Sin embargo, existen varios ejemplos de disminución severa en la disponibilidad de productos no-maderables en bosques con alta densidad de especies aprovechables (por ejemplo, Vasques & Gentry 1989). Evidentemente, el valor del producto también juega un role importante, ya que también el riesgo de sobre-explotación es más grande para productos con un alto valor económico. En segundo lugar, las perspectivas para uso sostenible han sido relacionadas con la estrategia de regeneración: se ha considerado que árboles tolerantes a la sombra tienen mayores expectativas de un uso sostenible ya que pueden regenerarse en un bosque primario, es decir no necesitan condiciones ambientales especiales (Peters 1996b). Sin embargo, la alta tasa de crecimiento potencial de plantas que depende de claros podría se aprovechada en sistemas silviculturales para incrementar la productividad. Además, la duración de vida larga de árboles tolerantes a la sombra pueden causar un uso no-sostenible en caso de que los individuos sean severamente dañados o matados por la extracción. Finalmente, no existe una relación clara entre la duración de vida y las perspectivas para un uso sostenible. Por ejemplo, en especies de larga vida, la extracción de semillas puede ser sostenido por periodos largos sin causar un declinio en la producción del recurso. Sin embargo, la extracción de semillas en plantas de vida corta probablemente tiene un impacto mucho más fuerte, ya que para estas especies la tasa de crecimiento poblacional depende fuertemente de la regeneración. En contraste, si se extrae (o mata) individuos completos para el aprovechamiento, las perspectivas son mejores para especies de corta vida. Por lo tanto, en este caso, no se puede establecer una relación clara.

En conclusión, es difícil generar reglas simples para evaluar la sostenibilidad de sistemas de aprovechamiento de productos no-maderables. La sostenibilidad de un sistema extractivo depende de la interacción de la demografía de la especie y del impacto del aprovechamiento, y requiere información sobre ambos asuntos. Sin embargo, se puede hacer una primera evaluación aproximada usando información limitada sobre la historia de vida de la especie, así como información sobre el impacto de la extracción, y las relaciones mostradas en Figura 3.

Agradecimientos

Agradezco Marielos Peña por su asistencia valiosa en la traducción de este texto. El texto original fue comentado por ella, Rene Boot, Marinus Werger, Floris Zuidema y Corien van Zweden.

Samenvatting

Achtergrond

De tropische regenwouden van het Amazonegebied worden al duizenden jaren op kleine schaal gebruikt door de inheemse bevolking. De laatste 150 jaar bestaat er naast dit kleinschalige gebruik ook grootschalige exploitatie van het regenwoud gericht op de (inter-)nationale markt van produkten uit tropische bossen. In het midden van de 19de eeuw begon men met het verzamelen van kinine, die verhandeld werd naar Europa. De rubbertapperij kwam in opkomst rond 1880 en groeide in een paar decennia uit tot 'booming business'. Pas sinds de jaren '70-'80 heeft de exploitatie van hardhout een hoge vlucht genomen. Sinds die tijd worden tropische bossen wereldwijd aangetast door de toenemende bevolkingsdruk en grootschalige houtkap. Naarmate meer kennis beschikbaar is gekomen over de grote soortenrijkdom in tropisch regenwouden en hun complexe ecologische interacties, is de roep om bescherming en duurzaam gebruik van deze ecosystemen groter geworden. Sinds de jaren '80 wordt in natuurbeschermingskringen steeds vaker de aandacht gevestigd op niet-houtige bos-produkten, als een voorbeeld van hoe bosbescherming en bosgebruik samen kunnen gaan.

Omdat bij het verzamelen van produkten zoals noten, vruchten en latex, veel minder schade aan het bos wordt toegebracht dan bij de exploitatie van hout, lijkt duurzaam gebruik op deze manier makkelijker te realiseren. In sommige gevallen blijkt echter dat ook bij het verzamelen van niet-houtige produkten door een te hoge exploitatie druk of door verkeerde oogsttechnieken grote schade aan het bos wordt toegebracht. In dat geval dienen normen opgesteld te worden om een duurzame exploitatie te garanderen. Wanneer de duurzaamheid van de exploitatie kan worden gewaarborgd, is het mogelijk de exploitatie te voorzien van een certificaat voor een 'groene' produktie. Zowel voor het opstellen van oogstbeperkende normen als voor de beslissing tot certificering van een exploitatie systeem, is het van belang te weten in hoeverre de exploitatie invloed heeft op het voortbestaan van de soort en op de toekomstige beschikbaarheid van het geoogste produkt. Deze informatie kan worden verkregen in demografische studies zoals werden uitgevoerd voor dit proefschrift.

Uitvoering

Het onderzoek is uitgevoerd in de tropische bossen van Noord Bolivia. Het gebied, dat tot het Amazonische deel van Bolivia behoort, heeft een lange historie van gebruik van niet-houtige bosprodukten, waarvan rubber, paranoten en palmhart de belangrijkste voorbeelden zijn. De doelstellingen van dit onderzoek waren (1) om de demografie van een aantal geëxploiteerde boomsoorten in het Boliviaanse Amazonegebied te onderzoeken; (2) om de invloed van exploitatie op de populatie dynamiek te bepalen, en na te gaan of deze exploitatie duurzaam is; en (3) om de bruikbaarheid vast te stellen van een bepaald soort demografische modellen (matrix modellen) die gebruikt worden voor het analyseren van de demografie van bomen, en het bepalen van duurzaamheid van exploitatie systemen.

Dit onderzoek werd uitgevoerd in het kader van PROMAB (Programa Manejo de Bosques de la Amazonía Boliviana), een internationaal projekt voor onderzoek, onderwijs en voorlichting op het gebied van duurzaam bosbeheer in Noord-Bolivia. Drie boomsoorten werden onderzocht: de emergente boom *Bertholletia excelsa* waarvan de zaden (paranoten) worden geoogst (Hoofdstuk 2); de palm *Euterpe precatoria* die wordt geëxploiteerd voor palmhart (Hoofdstuk 3), en de kleine ondergroei palm *Geonoma deversa* waarvan de bladeren worden gebruikt voor zeer duurzame dakbedekking (Hoofdstukken 4 & 5). Daarnaast werd een nieuw type gevoeligheidsanalyse voor demografische modellen (matrix modellen) geïntroduceerd en toegepast op een aantal soorten (Hoofdstuk 6). Als laatste werd het gebruik en de bruikbaarheid van deze modellen voor het analyseren van de demografie en de exploitatie van houtige soorten geëvalueerd (Hoofdstukken 7 & 8).

Resultaten

De resultaten van het onderzoek aan de drie geëxploiteerde soorten, laten veel overeenkomsten zien wat betreft hun demografie. Zo is voor alle soorten de overlevingskans van kleine kiemplanten beduidend lager dan die van grotere, gevestigde individuen; is de groei van kiemplanten laag en zeer variabel; en kunnen reproducerende individuen van alle onderzochte soorten een hoge leeftijd behalen (variërend van 100 tot 350 jaar). In twee van de drie soorten (*Bertholletia* en *Euterpe*) werd een groeipatroon gevonden waarbij de hoogste groeisnelheden werden waargenomen voor juveniele individuen en geringe groei voor kiemplanten en volwassen bomen.

De drie soorten verschillen echter met betrekking tot hun regeneratie strategie: de kleine palm *Geonoma* is een schaduw-specialist die zijn gehele levenscyclus volbrengt in de donkere ondergroei van het bos. Voor *Bertholletia* is de groei tot volwassen individuen waarschijnlijk sterk afhankelijk van de verhoogde lichtbeschikbaarheid op plekken waar gaten in het kronendak zijn ontstaan. De palm *Euterpe* neemt ten opzichte van de andere twee soorten een intermediaire positie in, omdat deze soort minder sterk afhankelijk lijkt van een hoge lichtbeschikbaarheid.

De demografische modellen laten zien dat de onderzochte populaties van drie soorten redelijk stabiel zijn in grootte, en dat de groei en handhaving van de populaties sterk afhankelijk is van de overleving van individuen, en in veel mindere mate van hun groei en reproduktie. Volwassen individuen zijn veel belangrijker voor de handhaving van populaties dan kiemplanten en juveniele individuen.

Er zijn grote onderlinge verschillen tussen de drie onderzochte soorten voor wat betreft de invloed van exploitatie. Zo blijkt het oogsten van paranoten van *Bertholletia excelsa* geen duidelijke invloed te hebben op de verjonging van de soort. In twee populaties waar vermoedelijk al langer dan 50 jaar noten worden geraapt, werd gedurende twee jaar een redelijk aantal nieuwe kiemplanten gevonden, en waren kiemplanten en kleine bomen van alle groottes aanwezig. Het demografische model voorspelt dat het oogsten van noten weinig invloed heeft op de handhaving van de populatie. Daarnaast is berekend dat het zo'n 125 jaar duurt voordat bomen volwassen worden en dat de totale levensduur van deze bomen ongeveer 350 jaar bedraagt. Beide resultaten suggereren dat de oogst van paranoten gedurende een aantal decennia op het huidige nivo kan blijven, zonder dat de populatie zal worden aangetast, en dat de exploitatie waarschijnlijk ook op de langere termijn duurzaam zal blijken te zijn.

Voor palmhart verkregen van *Euterpe precatoria* is duurzaam gebruik een probleem. De oogst van palmhart betekent de dood van een volwassen boom. De vervanging van deze individuen duurt lang, aangezien deze palm alleen reproduceert via zaden, d.w.z. geen vegetatieve uitlopers maakt. Een demografisch model laat zien dat de gekapte volwassen palmen ten minste 70 jaar zijn en gemiddeld genomen waarschijnlijk ouder dan 90 jaar. Ook blijkt uit dit model dat de groei en handhaving van de populaties sterk afhangt van juist die individuen die worden gekapt voor palmhart. Simulaties van verschillende exploitatie regimes laten zien dat de huidige oogstpraktijk waarbij zo'n 90% van de volwassen palmen wordt gekapt, geen mogelijkheid voor duurzaam gebruik biedt. Zelfs bij een veel lager percentage en een lange oogst cyclus zijn de perspektieven voor duurzaam gebruik gering. Bovendien moet worden bedacht dat voor palmhart een zeer lage prijs wordt betaald, hetgeen de vermindering van de oogstdruk economisch onrendabel maakt.

De oogst van bladeren van de palm *Geonoma deversa* biedt goede perspektieven voor duurzame exploitatie. Hoewel palmen waarvan de bladeren zijn geoogst minder groeien en een sterk verlaagde produktie van vruchten en vegetatieve uitlopers laten zien, veroorzaakt bladkap geen verhoogde mortaliteit en worden de gekapte bladeren snel vervangen. Twee jaar nadat alle bladeren zijn verwijderd, is zo'n 65% van het oorspronkelijke aantal bladeren opnieuw aanwezig. Uit de demografische modellen blijkt dat de groei van de populatie na bladkap niet sterk afneemt. Simulaties met oogstcycli van verschillende lengte laten zien dat na herhaalde bladkap de hoeveelheid beschikbare bladeren zich goed herstelt. Duurzame en rendabele exploitatie van deze palm is goed mogelijk vanwege de hoge dichtheid waarin de soort voorkomt, de goede kwaliteit van de bladeren voor dakbedekking en het goede herstel na bladkap.

Voor de studies in dit proefschrift werd gebruik gemaakt van populatie matrix modellen. Deze modellen hebben het grote voordeel dat ze eenvoudig te construeren zijn, geen hoge eisen stellen aan de beschikbaarheid van gegevens en resultaten opleveren die goed zijn te vergelijken met die van modellen voor andere soorten. De gevoeligheidsanalyse van dit soort modellen is een belangrijk middel om het belang van verschillende stadia en processen in de levenscyclus van soorten te bepalen. In dit proefschrift wordt een type gevoeligheidsanalyse geïntroduceerd waarin rekening wordt gehouden met de variabiliteit van de demografische parameters die worden gebruikt voor het opstellen van matrix modellen. Ook wordt een overzicht gegeven van het gebruik van matrix modellen voor bomen, palmen en struiken. Uit dit overzicht blijkt dat verschillen in de manier van opstellen van matrix modellen en het omgaan met onzekerheden in de beschikbare gegevens grote invloed kan hebben op de uitkomsten van het model. Het is daarom belangrijk om zorgvuldigheid te betrachten, zowel in het construeren van modellen als in het interpreteren van model uitkomsten.

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Acknowledgements

In analogy with the life cycle that is frequently used in this thesis to describe the demography of plants, one can also construct a life cycle for the production of a PhD thesis. This cycle starts with the initiation of a research project, continues with field work, data entry, data analysis, modeling and writing of the manuscript, and ends with the preparation for the thesis' publication. During each of these phases in the "thesis life cycle", many people have supported me in many different ways.

During the initiation of the project my promotor Marinus Werger and my co-promotor René Boot have been very cooperative in finding the right scope for the thesis. With regards to the practical decisions on the setup of the research also my colleagues Marielos Peña and Lourens Poorter have been of great help in taking important decisions concerning study sites and parameters to be measured.

The field work for this study was carried out in Northern Bolivia during three years. In a demographic study one tries to include as many individuals as possible, remeasure all of these each year and make sure that measured plants don't get lost. This implies the demarcation of numerous hectares and many more (sub-)subplots; searching large areas for individuals that occur at low densities; tagging and painting very small to very tall individuals; and counting seeds, fruits, seedlings, leaves and leaflets. This is an impossible task for one person. Many people have supported me with the field work, in particular the four field assistants at PROMAB.

El trabajo de campo de un estudio demográfico no se puede hacer sólo. Ha sido un trabajo de muchas personas. Agradezco muchissimo a todos que han contribuido a este trabajo: primeramente a los cuatro del equipo de campo de PROMAB: Luis Apaza, Rene Aramayo, Miguel Cuadiay y Don Nico Divico que han hecho la mayoría del trabajo. Además agradezco a Alejandro Hayashida, James Joffrey, Santiago Mamani, Nazareno Martinez, Marielos Peña, Thomas Stockman, Corien van Zweden, "Oso" y "Tigre" de El Turi, y "Tatú" de El Sena. También quisiera agradecer a las familias de don Santiago en La Reserva y de don Walter en El Sena, y los habitantes de El Turi para su hospitalidad durante el trabajo de campo.

In the PROMAB office, the cooperation with my colleagues has been very helpful and stimulating, as well as the atmosphere. I would like to thank colleagues and students, from Bolivia, the Netherlands and elsewhere for their contributions to this thesis. *Quisiera agradecer a todas las personas de la oficina de PROMAB por su apoyo incondicional y por el atmosfera que crearon: Margarita Apuri, Marcos Arredondo, René y Carmen Boot, Alan Bojanic, Yaskara Hayashida, Ariènne Henkemans, Kira Kawano, Jhon Leigue Gómez, Nelson Marriaga, Marielos Peña, Lourens Poorter, Doña Adelia Portillo, Claribel Sandóval y Dietmar Stoian. También quisiera agradecer a las demas personas involucradas en PROMAB por su asistencia y cooperación: Oscar Llanque, Luis Medina, Guido Pardo, Edgardo Ribert, Armelinda Zonta y estudiantes de la Carrera de Ingeniería Forestal y de otros institutos.*

Apart from the forest, the work and my colleagues, other things and persons have been important during my stay in Riberalta. I am grateful to René and Carmen Boot for introducing me to the town of Riberalta and to the project, and for their continuous support in organising my work and private life in this new environment. I sincerely thank those who have made this period a very special experience. *Agradezco de todo mi corazón a las personas que han convertido el periodo en Riberalta en una experiencia muy especial. Aparte de mis compañeros de trabajo fueron: Karen Coesmans y Roger Heemskerk, Doña Rosa Córtez y su familia, Susy Guardia, Peter y Johanni Lange, Rik Overmars,*

Ivonne Venema y Guus Meeuwsen, y en La Paz: Matthias y Carmen Preiswerk y sus hijas. I am also grateful to friends and relatives who visited us in Riberalta, allowing us to show and share a bit of our Bolivian life: Aleid and Floris Zuidema, Noud Drewes and Lieneke de Vries, Ineke van Zweden, Enno Zuidema and Myrabelle Heeroma, Hanna Bok, Victor Zuidema and Simcha Knip.

After three years I arrived in Utrecht with field forms and spread sheets filled with thousands of numbers. Cas Kruitwagen, Maria Schipper and Paul Westers gave valuable advice on the statistical analysis. René Boot, Heinjo During, Marielos Peña, Lourens Poorter and Marinus Werger helped me in the inevitable dilemmas that arise during the analysis of data. Hans de Kroon and Jan van Groenendael have provided very helpful advice in the field of matrix models. I am very grateful to Miguel Franco for providing the opportunity to work at his department at the UNAM in Mexico and at the Open University in the UK. I thank him also for his interest in my ideas, for the close cooperation and for his hospitality.

During the writing phase, the guidance of my promotor Marinus Werger has been very important. I am grateful for his direct and constructive comments on my -often technical- manuscripts, for teaching me to always keep asking questions, to write clearly and to refrain from stating the obvious. The contents of the thesis has also been shaped by the co-authors and the persons who commented on manuscripts: Niels Anten, René Boot, Heinjo During, Graham Floater, Miguel Franco, Jan van Groenendael, Hans de Kroon, Xavier Pico, Marielos Peña, Lourens Poorter, Josef Stuefer, Marinus Werger and Roderick Zagt. I thank them for their interest and cooperation. During the writing phase at the Plant Ecology group in Utrecht, I have enjoyed the friendly atmosphere at the department. In particular I would like to thank those also involved in tropical forest ecology for their interest and open attitude towards the work of each others: Zeng Bo, Wim Dijkman, Mark van Nieuwstadt, Marielos Peña, Lourens Poorter, Simmone Rose, Hans ter Steege and Roderick Zagt. The department's support staff is acknowledged for their assistance and Bor Duplica for his coffee and the pleasant atmosphere he creates. The last phase - the layout of the contents and the design of the cover - has been the work of Marjolein Kortbeek-Smithuis and Emy Franck, whom I would like to thank for their dedication and creativity.

Some people have provided indispensable support during the entire "thesis cycle". René Boot has assisted me greatly throughout the project in globally shaping the research, discussing details on sampling schemes and in shaping the thesis chapters. His continuous stream of ideas, energy and enthusiasm have been of great help to me. My close colleagues and office mates Marielos Peña and Wim Dijkman have stimulated me throughout the project, always being interested in personal and work-related developments. I am very grateful to Floris and Aleid Zuidema, Kees and Ineke van Zweden, Enno and Myrabelle, Victor and Simcha, and Hanneke, and close friends that have maintained contact with us in Bolivia through numerous letters and faxes and have always provided hospitality and support during our home leaves and after returning to the Netherlands. I am much indebted to Corien for joining me to Bolivia, and for her continuous and unconditional support in all possible ways during the past years. Finally, this thesis and the period during which it was produced will always remain connected in a special way to the birth of my daughters Lisa and Sara.

Utrecht, August 2000

Pieter Zuidema

Curriculum vitae

Pieter Alle Zuidema was born in the Zuidelijke IJsselmeerpolders, The Netherlands, on 16th of April 1970. He graduated from high school (Atheneum) at the "Scholengemeenschap de Rietlanden", Lelystad, in 1988. In the same year he started to study Biology at Utrecht University. During this study, Pieter focussed on plant ecology in general and on tropical ecology and population biology in particular.

Two thesis studies were carried out for his MSc degree, both at the Department of Plant Ecology and Eolutionary Biology in Utrecht. The first study dealt with changes in the vegetation of Dutch lowland streams due to organic pollution. The second study focused on the population biology and seedling growth of the Brazil nut tree in the Bolivian Amazon. This study included a 4-month field work period in Bolivia, in cooperation with a local university.

During the last year of his study, Pieter followed the 12-months post-graduate course "Rural and land ecology survey" at the International Institute for Aerospace Survey and Earth Sciences (ITC) in Enschede. The course focused on the application of remote sensing, GIS, and surveys of land cover and land use, and included a mapping study in Eastern Kenya.

After he obtained his MSc degree in Biology in 1994, Pieter worked as a staff member at ITC in Enschede. He wrote a software manual for an internationally-used land use database system.

In the same period he started working on a voluntary basis at the Department of Plant Ecology and Evolutionary Biology in Utrecht to prepare a proposal for WOTRO (the Dutch Foundation for the Advancement of Research in the Tropics). This proposal dealt with the impact of rain forest fragmentation on seed dispersal and tree regeneration in Sumatra, Indonesia. To prepare the field study and seek cooperation with Indonesian partners, a mission to Indonesia was conducted in 1995. The proposal was granted in 1995.

In 1996, Pieter took up the position of junior researcher at the Department of Plant Ecology and Evolutionary Biology in Utrecht, working at PROMAB (Programa Manejo de Bosques de la Amazonía Boliviana), a research, training and extension project in Bolivia. From early 1996 until early 1999 he lived and worked in Riberalta, Northern Bolivia, where he carried out field research on the demography of exploited tree species. During this period he also collaborated with Bolivian researchers in forest-ecologial studies, supervised Bolivian and Dutch BSc and MSc students, took part in the education at the local university, and assisted in the (logistic) management of the project. The information obtained in one of his field studies contributed to the formulation of governmental norms regulating the use of an (over-exploited palm. The results of the demographic field studies carried out in Bolivia are presented in this PhD thesis.

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