

Demography of *Bursera glabrifolia*, a tropical tree used for folk woodcrafting in Southern Mexico: An evaluation of its management plan

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Abstract

Tropical dry forest in Mesoamerica has long been disturbed by the extraction of different forest products by local inhabitants. *Bursera glabrifolia* (white “copalillo”) is a dry tropical forest tree extensively used in several communities of the State of Oaxaca, Mexico, for the elaboration of folk-art woodcarvings called “alebrijes”. Historically, the extraction of *B. glabrifolia* had not been regulated; however, in October 2002, the first management plan for this species was implemented in San Juan Bautista Jayacatlán, based on abundance, distribution and economic data. However, no demographic information is available on which to base a sounder management plan that would guarantee the ecological sustainability of this extractive activity. Thus, we studied the population dynamics of this species over a 2-year period in Jayacatlán, where no tree extraction had taken place since 1998. We used stem expansion rates and observations on survival and fecundity to build size-based population projection matrices. The projected population growth rate values (λ) were 1.14 and 1.04 for the 2001–2002 and the 2002–2003 periods, respectively. These values suggest that the *B. glabrifolia* population at Jayacatlán shows a growing trend. Several harvesting scenarios were simulated to theoretically assess the impact on population dynamics of harvesting whole trees and, in particular, to ascertain whether the extraction regime recommended by the management plan (8 trees/ha/yr) is sustainable. For this purpose, we used an average population matrix where specific entries were modified to simulate different extraction levels. The results suggest that the harvesting regimes established in the management plan for *B. glabrifolia* are sustainable. However, resource managers should not exceed the amounts recommended by the management plan and should avoid extrapolating our results to other regions of the country where no demographic studies have been carried out. The need for long-term demographic studies and their incorporation in ‘adaptive management plans’ is discussed.

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1. Introduction

Tropical forests are an important source of natural resources for local inhabitants all over the world (Challenger, 1998). In particular, tropical dry forests in Mesoamerica have been intensively exploited by local communities since Pre-Columbian times (Murphy and Lugo, 1995; Janzen, 1988; Maass, 1995). This recurrent and growing disturbance pressure associated to human activities has posed a severe threat to tropical dry forests (Janzen, 1988; Murphy and Lugo, 1995;

Gentry, 1995; Trejo and Dirzo, 2000). In the Mexican state of Oaxaca, one of the products obtained from tropical dry forests is the wood of *Bursera glabrifolia*, which is used for folk woodcrafting. The success and sustainability of this extractive activity depends on the application of management plans based on sound demographic information, which is now lacking. In this study, we present a 2-year demographic analysis of a population of *B. glabrifolia* on which management guidelines may be based in the future.

Tropical dry forests (also called seasonally dry tropical forests) represent 42% of all tropical forests of the world (Murphy and Lugo, 1986). A wide array of plant communities that share a number of structural and physiognomic features are generally regarded as examples of this vegetation type.

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Some of these common features are a high diversity of life forms and a marked phenological response of most woody elements to the drought season, typically lasting for several months (Kalacska et al., 2004). In Mesoamerican tropical dry forests, the canopy is usually composed of deciduous trees of short stature (ranging from 5 to 15 m tall) as well as thorny shrubs and a number of xerophytic elements. These forests are associated with subtropical areas with a highly seasonal climate in relation to rainfall, i.e. the dry season may last for 7–9 months, while the rainy season (during which ca. 70% of the yearly precipitation falls) is generally shorter (3–5 months—Bullock et al., 1995). Tropical dry forests occupy an important proportion of the Mexican territory (11%); which house a large part of the biodiversity of the country and show high floristic endemism (ca. 40%—Rzedowski, 1991; Trejo and Dirzo, 2000; Ceccon et al., 2003). This vegetation type is rapidly declining worldwide. In Mesoamerica, the deforestation of these ecosystems has been taking place since pre-Columbian times and continues today (Bye, 1995; Maass, 1995; Murphy and Lugo, 1986, 1995; Janzen, 1988). The main cause of this decline has been land-use change towards cattle ranching and agriculture. However, it has also been recognized that selective timber extraction and harvesting of non-timber forest products has played an important role in this respect, especially in the last decades (Bye, 1995; Challenger, 1998).

Only a few studies have evaluated the effects of harvesting on the population dynamics of dry tropical forest trees. Among them, the information available for *Amphipterygium adstringens*, *Bursera aloexilon*, *Croton* sp., *Crescentia* sp., *Guaiacum* sp., *Hermiagium excelsum*, *Leucena* sp., and *Swietenia macrophylla*, have shown that natural populations have been dramatically affected by extraction (Bye, 1995; Gullison et al., 1996; Hughes, 1998; Grow and Schwartzman, 2001; Hersch Martínez et al., 2004). The trees of the genus *Bursera* have been the targets of different extraction practices. In the central valleys of the Mexican state of Oaxaca, three *Bursera* species (*B. glabrifolia*, *B. submoniliformis*, and *B. aloexilon*) are exploited by local inhabitants who fell whole trees and use the wood to produce woodcarvings called “alebrijes” (Fig. 1). These alebrijes usually evoke small fantasy animals and are sold very successfully in local,



Fig. 1. An example of an alebrije, a fantasy animal hand-carved using *B. glabrifolia* wood.

national, and even international markets as an example of Mexican folk-art (Chibnik, 2003). Of the three *Bursera* species mentioned, *B. glabrifolia* (locally known as white “copalillo” or “copal blanco”) is by far the most frequently used for alebrije elaboration. Local artisans report that this preference is related to its softer and lighter wood, compared to that of the other species (Purata et al., 2004).

Alebrijes are a relatively new folk-art product (Chibnik, 2003). Originally (ca. 40 years ago), these figures were made by people from the villages of Arrazola and Tilcayete, near the city of Oaxaca (Fig. 2). The wood was extracted from the tropical dry forests surrounding these villages. However, in the last 30 years the commercialization of alebrijes has expanded dramatically and people from many villages are now involved in their production. As the demand increased, *B. glabrifolia* populations have declined noticeably around Arrazola and Tilcayete and now trees are being extracted from forest areas as far as 100 km from these villages (Peters et al., 2003). So far, these extractive activities have not been regulated or designed through appropriate management plans. In recent years, Mexican government agencies are requiring resource managers to elaborate management plans for the forest products being extracted in different parts of the country. The lack of such management plans for *B. glabrifolia* (and in fact for most of the products harvested from tropical forests in Mexico) implies that current extraction is being carried out illegally (Peters et al., 2003).

A management plan for *B. glabrifolia* was devised in 2000 by professional ecologists, based on abundance, distribution and dasonomic data obtained in the region of Jayacatlán, in Oaxaca (Fig. 2—Brosi et al., 2000). A complete description of the ecological data used for the elaboration of this management plan may be found in Peters et al. (2003) and Purata et al. (2004). The management plan is assumed to be sustainable; however, no demographic information is available in which to support this assumption. A sounder management plan based on a deeper knowledge of the population dynamics of this species has still to emerge.

Population projection matrices have been used by plant ecologist to address different ecological matters, from life-history evolution to issues in conservation biology and resource management (de Kroon et al., 1986; Pinard, 1993; Silvertown et al., 1993). In the last decade, these models have been successfully applied to ponder over different resource management strategies in several plant species. The consequences of extractive activities may be evaluated through the analysis of the numerical changes that take place within populations, and the identification of the most vulnerable life-cycle stages of the target population (Olmsted and Alvarez-Buylla, 1995; Anderson and Putz, 2002; Ticktin, 2002). The advantages of population projection matrices for resource management are now widely recognized and management plans for some plant species have been based on this type of models (Soehartono and Newton, 2001; Anderson and Putz, 2002; Ticktin, 2002; Zuidema and Boot, 2002). In this paper, we present the results of a demographic study of a population of *B. glabrifolia* in which we used population projection matrices to address

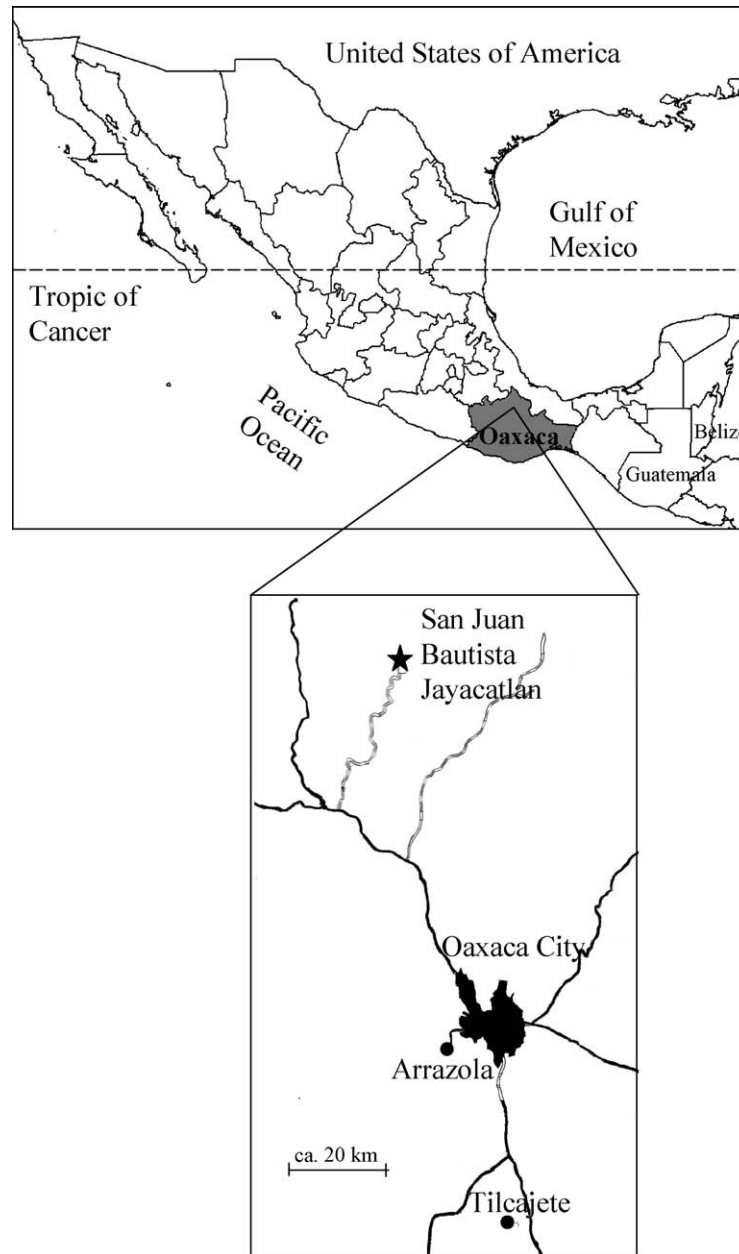


Fig. 2. Location of the study site within the Mexican state of Oaxaca.

different ecological and management issues. In particular, our aims were: (a) to describe the demographic behavior of a population of *B. glabrifolia* in Jayacatlán to evaluate its current status; (b) to identify the most vulnerable life-cycle stages on which to prevent extraction; (c) to use the matrix model to theoretically evaluate the sustainability of the harvesting regime recommended by the management plan by simulating different intensities of tree extraction.

2. Methods

2.1. The studied species

In Mexico, *B. glabrifolia* trees are known as white copalillo (copal or copalillo blanco). This species belongs to the

Burseraceae family and is a dioecious tree that in the adult stage may reach between 5 and 12 m in height. Its bark is persistent, which characterizes the Section *Bullockia* within the Burseraceae, and is smooth, gray or gray-reddish in color (Rzedowski et al., 2004). Leaves are composite and have a whitish aspect due to the presence of pubescence on the abaxial surface; they are shed during the dry season, which in the study area (see below) spans from November to May. Inflorescences are paniculate, reaching a length of up to 10 cm and bearing four-merous unisexual flowers. Fruits are bivalve drupes with an ovate shape (Toledo, 1982; Rzedowski et al., 2004). Each fruit generally contains a single seed (occasionally two).

The distribution range of *B. glabrifolia* includes south-central Mexico and Central America. In Mexico, it is found at altitudes of 500–2000 m, in tropical dry forests and dry

temperate deciduous forest (Toledo, 1982). In our study site (Jayacatlán, Oaxaca—see below), this species occupies an altitudinal range that spans from 500 to 1250 m; it is one of the dominant tree species of the tropical dry forests present in this area (Brosi et al., 2000).

2.2. The study site

This study was carried out near the village of Jayacatlán (17°25'24"N, 96°49'19"W), in the Mexican state of Oaxaca. This area has a warm and seasonally dry climate with a mean annual temperature of 21.7° C and an annual precipitation of 616 mm (García, 1988). The summer rainy season spans from June to September, during which 78% of the yearly precipitation falls. Soils are generally shallow, calcareous and of diverse origin. This area is set within the southern Sierra Madre, which is a complex mountain range with a high ecological and floristic diversity. Some vegetation types that are well represented in the area are tropical dry forests, dry temperate forests, temperate deciduous forests, temperate evergreen forests, and anthropogenic grasslands and agrosystems. Our study was carried out in the tropical dry forest, which in this municipality covers an area of ca. 5000 ha; in this ecosystem the vegetation is dominated by trees of medium height (ca. 6–12 m), with a high representation of the Burseraceae and Leguminosae, as well as other conspicuous tree species such as *Amphyterigium adstringens*. Some columnar cacti are also present (e.g. *Pachycereus weberi*, *Myrtillocactus geometrizans*, *Eschontia chiotilla*, *Stenocactus rectispinus* Schmoll.), as well as a number of thorny shrubs (*Acacia* sp., *Mimosa* sp.), herbs, epiphytes (*Tillandsia* sp., *Bromelia* sp.) and vines (lianas).

During the 1990s the tropical dry forest of Jayacatlán was affected by the unrestricted extraction of *B. glabrifolia*. In 1998 the extraction was stopped because local people became concerned in relation to the sustainability of this practice. They were interested in developing a management plan based on

biological information on which to design sustainable extractive regimes. This management plan was developed by ecologists and forest managers (Brosi et al., 2000; Peters et al., 2003), based on tree growth rates and other biological attributes; it recommends a maximum extraction rate of 8 trees/ha/yr (i.e. two trees in the 10–20 cm DBH category, four trees in the 20–30 cm category, and two trees in the >30 cm category), which adds up to 4.3 m³ of woodcarving material per hectare. According to the data gathered by the management planners, these are the amounts that may be naturally regenerated by the population, thus maintaining population structure and abundance relatively unaltered.

2.3. Field work

This study was carried out from the summer of 2001 to the summer of 2003. First, a sample of *B. glabrifolia* individuals was selected which would be marked and monitored for 2 years. To select this sample, we analyzed the distribution data gathered by Brosi et al. (2000) and located five 0.5 ha plots (within the 5000 ha of dry tropical forest owned by the Jayacatlán municipality) with a high density of *B. glabrifolia*. These plots were separated from each other by a distance that ranged from 50 m to 5 km. All *B. glabrifolia* individuals located within these plots ($n = 816$) were marked, mapped and monitored for 2 years. Trees were classified in five categories based on both height and DBH (diameter at breast height—Table 1). For convenience, we used the same size categories defined in the management plan referred to above (Brosi et al., 2000). The height or DBH of each tree was measured in the summer of 2001–2003, using ordinary measuring tapes, and each year the death of previously recorded individuals was noted. From these data we described population structure and calculated size-specific survivorship from 1 year to the next. To calculate accurate growth rates, we performed a more detailed diameter measurement in a sample of 67 trees (40 in size-category 3; 20 in size-category 4; 7 in size-category 5 for

Table 1
Size categories used to describe the population dynamics of *B. glabrifolia*, and mean individual growth rate (average increase in diameter from 1 year to the next, in cm) \pm S.D. for each category, using different measuring techniques

Stage	Size intervals for categories	Size-category	Measuring technique		
			Caliper	Dye	Dendrometer
2001–2002					
Seedlings	<1	1	0.22 ± 0.28 (336)		
Juveniles	1–10	2	0.29 ± 0.42 (193)		
Adult 1	10–20	3		0.61 ± 0.49 (40)	0.06 ± 0.11 (33)
Adult 2	20–30	4		1.14 ± 0.70 (20)	0.06 ± 0.05 (18)
Adult 3	>30	5		1.33 ± 0.50 (7)	0.06 ± 0.07 (6)
2002–2003					
Seedlings	<1	1	0.20 ± 0.24 (225)		
Juveniles	1–10	2	0.26 ± 0.36 (206)		
Adult 1	10–20	3		1.16 ± 1.01 (37)	0.15 ± 0.18 (38)
Adult 2	20–30	4		1.08 ± 1.02 (23)	0.17 ± 0.09 (22)
Adult 3	>30	5		1.33 ± 1.13 (6)	0.18 ± 0.09 (5)

Sample sizes (the same trees were used for the dendrometer and dye techniques; the sample sizes were slightly different for each technique mainly as a result of the loss of a few dendrometers due to burglary, and because no dye could be injected to a few trees to which dendrometers were adjusted) are given in parenthesis beside average values. In the two smallest size categories, diameter was measured at the trunk base. For the three larger size categories, diameter values refer to DBH.

2001–2002; 38 in size-category 3; 23 in size-category 4; 6 in size-category 5 for 2002–2003) with the aid of dendrometers, i.e. stainless steel bands marked with a scale in which stem expansion from 1 year to the next could be measured. In August 2001, two dendrometers were fit to each tree, at 1.2 m and 1.3 m high. Given that these dendrometers were hand-made and were still in the process of calibration (i.e. for the first months the two dendrometers on each tree would not give exactly the same stem expansion data), an additional measurement technique was also used. This technique consisted in a dye injection performed to the same 67 trees in August 2001, as detailed by Logman (1981). A 1 cm deep perforation was made on the trunk of each individual at a height of 1.35 m. A syringe was used to inject the dye (gentian violet) to color the live cells of the cambium. One year later a bore sample was taken in the immediacy of the dyed area of each trunk and the length of the new (uncolored) wood tissue was measured to estimate stem expansion (Logman, 1981). Previous growth analyses performed on these species (e.g. Brosi et al., 2000) had been carried out with the use of dendrometers only, following the same procedure described above.

The two measuring techniques (i.e. dendrometer and dye) were applied yearly from 2001 to 2003, from which annual mean individual growth rates were calculated for each size-category. These data (along with size-specific survivorship) were used to estimate transition probabilities among size categories for the periods 2001–2002 and 2002–2003, which were incorporated in the two annual population projection matrices reported below. Fecundity entries for these matrices were calculated using information on seed production and seed germination, as described below.

2.4. Analytical methods

2.4.1. Matrix analysis

Population projection matrices are a useful tool to describe the demographic behavior of structured populations (Caswell, 1989). Each entry a_{ij} in the matrix represents the transition probability or mean contribution of an individual in category j to category i in one time step (usually 1 year). By multiplying the matrix (A) by a vector representing the number of individuals in each category at time t (n_t), one obtains a new vector in which each entry represents the number of individuals per category at time $t + 1$ (n_{t+1}):

$$An_t = n_{t+1} \quad (1)$$

Certain mathematical properties of matrix A correspond to the demographic characteristics of the population it represents: the dominant eigen-value, λ , represents the finite rate of population increase; the associated right eigen-vector, w , corresponds to the stable-size distribution; the left eigen-vector, v , expresses the size-specific reproductive values (Caswell, 1989).

Matrix entries were obtained from survival, growth and fecundity data for individuals in each size-category (Table 1). To build the *B. glabrifolia* matrices we calculated transition probabilities and contributions among size categories from 1

year to the next using the field data described in the previous section. Transition probabilities of small trees (categories 1 and 2) were calculated from the proportion of individuals in each category that moved to larger categories from 1 year to the next, multiplied by their survival probability. Transition probabilities for large trees (categories 3–5) were calculated from the estimates of stem growth rate obtained through the dye technique (but see Appendix A). It is worth noting here that the stem expansion rate obtained through the two techniques applied (i.e. dendrometers and dye) gave very different results (Table 1). According to the above considerations, we judged that the data obtained through the dye technique were more reliable; therefore, our matrix transitions were based on these results. Following Enright and Ogden's (1979) procedure, transition probabilities for trees in categories 3–5 were thus based on average stem expansion rate per category, from which we could estimate the time needed for a tree to move from one category to the next. As the average expansion rates were measured for the periods 2001–2002 and 2002–2003, we used the data of the corresponding year to calculate the transition probabilities of the relevant matrices, which were then multiplied by the survival probabilities. We also calculated matrix transitions based on the stem expansion data obtained through the dendrometer technique, to evaluate the impact of potential errors in the estimation of stem expansion rate on our overall results (see Appendix A and Section 4).

In addition to 'stasis' and transition elements (which represent growth and survival), projection matrices also include fecundity entries which in this case occupy the first row; these represent the contribution of adult individuals to the first size-category, in this case 'seedlings'. Note that although many demographic matrices include a first category corresponding to the seed stage, this is appropriate only if seeds remain viable in the soil for periods longer than the projection time step (i.e. 1 year—Caswell, 1989; Bierzychudek, 1999). In the case of *B. glabrifolia*, seeds are clearly an ephemeral stage, i.e. they are shed in late autumn and remain in the soil only until the following summer rainy season, when seed germination takes place (Hernández-Apolinar, unpublished data). Thus, the reproduction of adult trees in 1 year expresses in the form of emerging seedling the following year. Therefore, the *B. glabrifolia* population projection matrix does not include a seed stage and fecundity is given in 'seedling' units. Fecundity entries (F_x) were calculated as follows:

$$F_x = \frac{N_{xr} \times S_x \times P_g}{N_x} \quad (2)$$

where N_{xr} is the number of individuals in our sample that belong to category x which reproduced during the reproductive season; S_x the estimated number of seeds produced by an average reproductive individual in category x (obtained through direct observations from a sample of ca. 10 individuals per size-category); P_g the germination probability of seeds under natural conditions (obtained through field experiments with ca. 1000 seeds in different field conditions—results not shown); N_x is the total number of individuals in our sample that belong to category x .

For each matrix, population growth rate (λ), the stable size-class distribution (w) and the size-specific reproductive values (v) were obtained by iteration using an Excel worksheet. A λ value above unity represents a growing population, whereas when λ is below unity the population may be assumed to be declining; a λ of one implies a population in numerical equilibrium (Caswell, 1989). To statistically test whether the obtained λ values were significantly different from unity, we calculated their 95% confidence intervals using a Montecarlo technique, as proposed by Álvarez-Buylla and Slatkin (1993, 1994), with the aid of a computer program developed by Martínez-Ramos and Hoffman (2002).

An important tool derived from projection matrix analysis is elasticity analysis, which allows us to evaluate the relative importance of different matrix elements to population growth rate (λ) (de Kroon et al., 1986). Each entry in the elasticity matrix represents the proportional sensitivity of λ to proportional changes in matrix elements, a_{ij} , and may be calculated as follows:

$$e_{ij} = \frac{v_i w_j}{\langle w, v \rangle} \frac{a_{ij}}{\lambda} \quad (3)$$

where w and v represents the vectors corresponding to the stable size-class distribution and the size-specific reproductive values, respectively. Since the entries in an elasticity matrix sum up to unity, their value may be interpreted as the relative contribution of each matrix entry to λ (de Kroon et al., 1986; Caswell, 1989).

2.4.2. Effect of different extractive regimes

The population projection matrices were used to theoretically evaluate the sustainability of different extractive regimes for *B. glabrifolia*. This was carried out through numerical simulations, i.e. specific modifications exerted on the values of matrix entries, after which a new λ value may be obtained to theoretically evaluate the effect of such changes on population growth rate. This approach has been fruitfully used by several authors to address a host of different ecological questions (Olmsted and Alvarez-Buylla, 1995; Esparza-Olguín et al., 2002; Soehartono and Newton, 2001). In this case, we carried out two simulation series: (i) first, we simulated the extraction

of different *numbers* of adult trees based on the suggestions made by the management plan (Brosi et al., 2000), and both increasing and decreasing this extraction level; (ii) secondly, we simulated the extraction of different *percentages* of the standing trees in each category. A resulting λ value significantly above unity was taken to imply that the simulated extractive regime is sustainable (Peters, 1994). Simulations were carried out using an average matrix, which incorporated the data from both 2001–2002 and 2002–2003:

- (i) The management plan for the *B. glabrifolia* population at Jayacatlán allows the extraction of 8 trees/ha (two, four and two, of the third, fourth and fifth size-category, respectively). To theoretically test the effect of this extractive regime, we changed the value of the matrix entries referring to stasis and growth of categories 3–5, simulating the effects of tree extraction. To modify these elements we used the data on total tree density per hectare for each size-category and calculated in what proportion this number would decrease due to extraction; the stasis and growth elements of the original matrix were then reduced by this proportion (Table 2). In addition, we also carried out three other simulations by constructing three new matrices, one in which the recommended extraction level was reduced by half, another one in which it was increased 1.5 times, and another one in which it was doubled.
- (ii) We performed another series of simulations by gradually decreasing the survival probability of trees in categories 3–5 by different proportions, ranging from 5 to 75%. This was intended to simulate the harvesting of different percentages of the standing trees in each category to theoretically evaluate the ability of the *B. glabrifolia* population to withstand different harvesting regimes.

3. Results

3.1. Individual growth rate

Individual growth rates on which the demographic model was based were measured in terms of stem expansion rate.

Table 2
Example of the calculations used to simulate tree extraction according to the management plan, which suggest the extraction of 2, 4 and 2 trees/ha (of categories 3–5, respectively)

Category	Density (trees/ha)	No. of trees extracted ^a	Additional mortality rate simulated by tree extraction	Original values for entries of retrogression (R), stasis (S) and growth (G)	New values for entries of retrogression, stasis and growth
3	41	2	0.049	0.005 (R) 0.902 (S) 0.083 (G) 0.026 (R)	0.005 0.858 0.079 0.019
4	16	4	0.250	0.856 (S) 0.106 (G)	0.642 0.079
5	13	2	0.154	0.969 (S)	0.814

The original values of matrix entries correspond to the average matrix (Table 4(c)).

^a The amounts given in this column correspond to the suggestion of the management plant. The simulations reported in Fig. 4 were carried out modifying these values to incorporate different theoretical extraction regimes.

Thus, we were interested in determining the best way of measuring this variable, as well as describing the way it varies among size categories or between years. The three-way ANOVA performed to test the effect of year (2001–2002 and 2002–2003), category (3–5) and measuring technique (dendrometer and dye) on annual stem expansion rate, indicated that the effect of measuring technique was highly significant ($F = 64.58$; d.f. = 1, 248; $P < 0.001$), while the differences between years or categories were not ($F = 1.20$; d.f. = 1, 248; $P = 0.28$ and $F = 0.67$; d.f. = 1, 248; $P = 0.51$, respectively). Dendrometers detected only a slight increase in stem diameter, whereas the dye technique recorded considerably larger diameter increments (Table 1).

According to the results of the dendrometer technique, stem expansion rate was noticeably higher in 2002–2003 compared to 2001–2002. However, the results of the dye measurements gave, in general, similar values in both years (Table 1). We considered that the dye measurements were more realistic than dendrometer ones, because when we directly measured stem diameter increments in plants of categories 1 and 2 with the aid of a caliper, we also observed similar results in both years (Table 1). Yearly variation in dendrometer measurements could have been related to an adjustment period of steel bands around tree trunks.

According to the stem expansion rates measured in 2001–2002 with the dye technique, a tree with a DBH of 10 cm (size-category 3) would take approximately 18 years to reach a DBH of 20 cm; similarly, a tree with a DBH of 20 cm

(size-category 4) would take ca. 9 years to increase to 30 cm; a tree with 30 cm of DBH (size-category 5) would take approximately 32 years to reach the maximum observed DBH of 72 cm (at which point we assume that death follows). This information was used to construct the matrix model presented below.

3.2. Matrix analysis

The population projection matrices constructed for the 2001–2002 and the 2002–2003 periods are shown in Table 3(a) and (b), respectively. The population growth rate (λ) projected by both matrices was significantly above unity. The first period (2001–2002) yielded a significantly higher λ value than the second period (2002–2003) despite the fact that mortality, which was highest in the first size-category, was slightly higher in the former. However, fecundity values were 2–10 times higher in the first than in the second period. The higher fecundity values of 2001–2002 were given mainly by a higher fruit production observed this year compared to the following, since both germination probability and the proportion of reproductive trees per category were comparable between years (Table 4). The matrix entries representing stasis and growth were similar in both matrices, with stasis elements always reaching high values, indicating that most trees remain in the same size-category from 1 year to the next. Some trees (ca. 3%) even regressed to smaller size

Table 3

Population projection matrices of *B. glabrifolia* for: (a) the 2001–2002 period, (b) the 2002–2003 period, and (c) the average of the two periods

Category (n_{t+1})	Category (n_t)						
	1	2	3	4	5	w	v
(a) $\lambda = 1.136 \pm 0.039$							
1	0.163	0.085	41.451	24.458	62.203	0.831	0.001
2	0.038	0.927				0.150	0.028
3		0.020	0.935	0.025		0.015	0.299
4			0.056	0.839		0.003	0.267
5				0.111	0.968	0.002	0.404
q_x	0.799	0.054	0.010	0.025	0.032		
(b) $\lambda = 1.040 \pm 0.022$							
1	0.243	0.064	4.031	12.180	15.018	0.617	0.001
2	0.060	0.938	0.010			0.338	0.020
3		0.008	0.869	0.026		0.017	0.279
4			0.111	0.874		0.011	0.364
5				0.100	0.969	0.017	0.335
q_x	0.697	0.047	0.010	0.000	0.031		
(c) $\lambda = 1.096 \pm 0.032$							
1	0.203	0.074	22.741	18.319	38.610	0.751	0.001
2	0.049	0.932	0.005			0.223	0.024
3		0.014	0.902	0.026		0.016	0.282
4			0.083	0.856		0.005	0.303
5				0.106	0.968	0.005	0.391
q_x	0.748	0.050	0.010	0.013	0.032		

The λ values ($\pm 95\%$ confidence intervals) are shown above each matrix. Only positive entries are given. Entries in the main diagonal are in bold to facilitate reading. Matrix entries given in italics are combined contributions of fecundity and retrogression. q_x , size-specific mortality; w, stable size-category distribution; v, size-specific reproductive values.

Table 4
Size-specific fecundities for the *B. glabrifolia* population during 2001–2002 and 2002–2003

Category	2001–2002				2002–2003			
	N_{xt}	S_x (mean \pm S.E.)	N_x	F_x	N_{xt}	S_x (mean \pm S.E.)	N_x	F_x
2	3	56 \pm 12.34	205	0.08	7	26.71 \pm 10	256	0.06
3	32	1318.90 \pm 364.61	105	41.45	25	211.20 \pm 42.52	101	4.03
4	7	1355.27 \pm 214.68	40	24.46	16	375.19 \pm 108.69	38	12.18
5	8	2337.33 \pm 657.41	31	62.20	19	692.60 \pm 230.14	32	15.02

Seed production data were collected during October 2002 and November 2003, which corresponded to the maximum fruit production periods for each year. The mean number of seeds per tree (S_x) was obtained from a sample of ca. 10 individuals per size-category. S_x , N_{xt} , N_x and F_x correspond to the parameters of Eq. (1), used to calculate matrix fecundity entries (see Section 2). The germination probabilities used were 0.103 (2001–2002) and 0.077 (2002–2003), according to the results of field experiments (not shown).

categories, mainly due to the loss of one of the main trunks, in the cases in which more than one trunk was present (Table 3).

The matrix with the highest λ value (2001–2002) projected a stable size distribution in which 83% of the population would correspond to seedlings, whereas in the 2002–2003 matrix, this percentage was barely above 60% (column w in Table 3). These stable population structures differed significantly from the observed population structures (2001–2002: $G = 213.6$, d.f. = 4, $P < 0.001$; 2002–2003: $G = 114.3$, d.f. = 4, $P < 0.001$ —Fig. 3). In both periods, the stable population structure was characterized by a higher proportion of individuals in category 2 and a lower proportion in category 3 compared to the observed population structure. However, the proportion of seedlings was similar between the observed and stable population structures (Fig. 3). In both periods reproductive values were low for non-reproductive stages (size categories 1 and 2) and increased substantially in reproductive categories, with the largest category contributing 33–40% of total reproductive value (column v in Table 3); these high reproductive values were accounted for by the large seed production observed in category 5 individuals (Table 4).

The average matrix, which incorporates the demographic information of the two periods showed, as expected, an intermediate behavior between the other two matrices (Table 3(c)). The λ value was also significantly above unity (1.096 ± 0.022), which supports the suggestion that the *B. glabrifolia* population has a potential for growth at the study site.

The elasticity matrices show that the entries corresponding to the persistence (stasis) of individuals in categories 2 and 3 were the demographic processes that contributed mostly to population growth rate in the two study periods (Table 5); these two entries alone accounted for 44–64% of the value of λ . In the second year (2002–2003), in which the λ value was lower than in the previous one, the persistence of individuals in category 5 also showed a high elasticity (25% of total elasticity—Table 5(b)). Overall, all the stasis elements represented 76–86% of total elasticity. In contrast, the fecundity elements accounted for only 3–7% of the λ value, and the growth elements summed up to 11–17% of total elasticity. The average matrix showed an intermediate

pattern between the other two matrices, with the persistence of individuals in categories 2–5 achieving the highest values (Table 5(c)).

3.3. Effect of different extractive regimes

The numerical simulations presented in this section were carried out on the average matrix referred to above. These

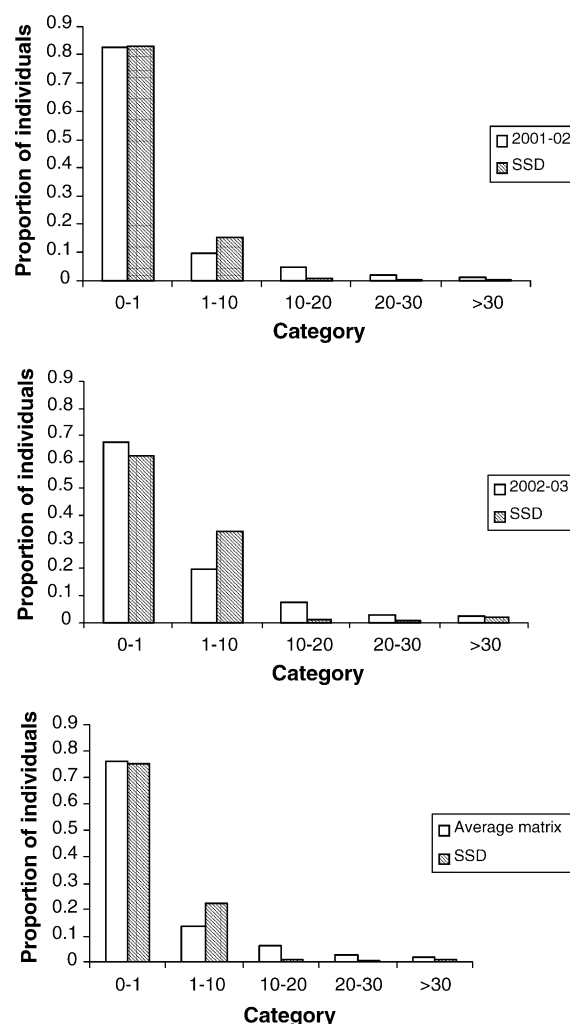


Fig. 3. Observed and stable population structures for periods: (a) 2001–2002; (b) 2002–2003; (c) 2001–2003.

Table 5

Elasticity matrices for the *B. glabrifolia* population studied corresponding to: (a) the 2001–2002 period, (b) the 2002–2003 period, and (c) the average matrix for the two periods

Category n_{t+1}	Category (n_t)				
	1	2	3	4	5
(a)					
1	0.012	0.001	0.053	0.006	0.011
2	0.071	0.313			
3		0.070	0.326	0.002	
4			0.017	0.048	
5				0.010	0.062
(b)					
1	0.009	0.001	0.003	0.006	0.024
2	0.031	0.269	0.000		
3		0.032	0.175	0.004	
4			0.029	0.159	
5				0.017	0.245
(c)					
1	0.013	0.001	0.030	0.008	0.016
2	0.055	0.313	0.000		
3		0.055	0.259	0.002	
4			0.026	0.090	
5				0.014	0.119

The highest elasticity values are highlighted in each matrix. Only positive entries are given; 0.000 entries indicate elasticity values <0.0001.

simulations were intended to test the potential effect of the management plan. The results indicate that under the extractive regime recommended, the *B. glabrifolia* population would show a 4% reduction in its population growth rate (Table 6(a)) compared to the unexploited conditions. The elasticity pattern of this ‘managed’ population reveal that 74% of the value of λ would rely on the persistence of trees in categories 2 and 3, whereas the persistence of trees in the largest category would

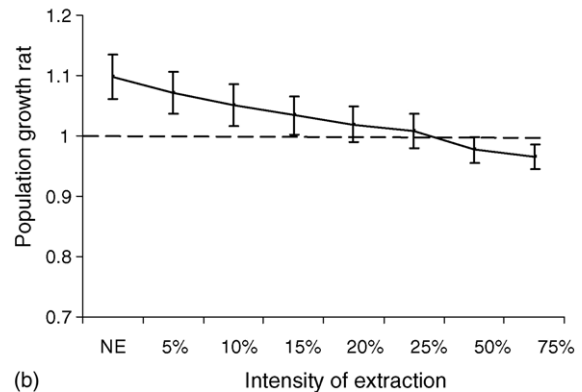
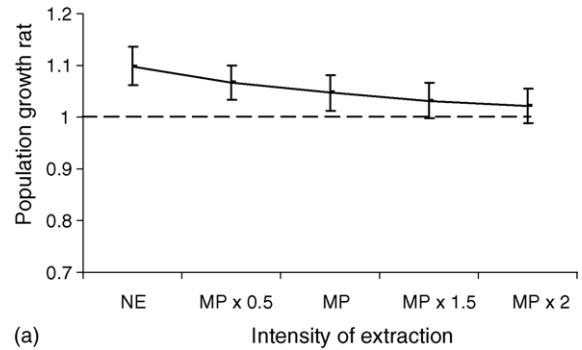


Fig. 4. Population growth rate values (λ) obtained through the simulation of different extraction regimes. (a) Theoretical effect of the extraction level recommended by the management plan and (b) theoretical effect of tree extraction through percentual reductions in the number of standing trees left per hectare.

decrease in importance compared to the original average matrix (Table 5(c)).

The results of the first simulation series suggest that if the tree extraction level recommended by the management plan

Table 6

(a) Population projection matrix incorporating tree extraction according to the suggestions of the management plan (see Table 3 for details) and (b) its corresponding elasticity matrix

Category n_{t+1}	Category (n_t)						
	1	2	3	4	5	w	v
(a) $\lambda = 1.054 \pm 0.034$							
1	<i>0.203</i>	0.074	22.741	18.319	38.610	0.695	0.002
2	0.049	<i>0.932</i>	0.005			0.280	0.042
3		0.014	<i>0.858</i>	0.019		0.020	0.366
4			0.079	<i>0.642</i>		0.004	0.200
5				0.079	<i>0.814</i>	0.001	0.390
q_x	0.748	0.050	0.058	0.263	0.199		
(b)							
1	<i>0.015</i>	0.002	0.047	0.007	0.005		
2	0.062	0.476	0.000				
3		0.060	0.267	0.001			
4			0.013	<i>0.021</i>			
5				0.005	<i>0.018</i>		

The λ value ($\pm 95\%$ confidence intervals) is given above the matrix. Only positive entries are shown; main diagonal entries are italicized to facilitate reading and the highest elasticity values are indicated in bold figures; 0.000 indicate an elasticity value <0.0001. Other symbols as in Table 4.

was to be doubled, λ would decrease so that its value would be indistinguishable from unity, i.e. the population would maintain itself without increasing (Fig. 4a). The second simulation series showed that λ would drop significantly below unity if 50% of standing trees were extracted every year (Fig. 4b).

4. Discussion

4.1. Demography

Although a number of studies have been published addressing different ecological aspects of dry tropical forest species (e.g. Arroyo-Mora et al., 2005; Quesada and Stoner, 2004; Grau, 2000; Shankar et al., 1998; Bullock, 1995; Bullock et al., 1995), the available information on the demography of dry tropical forest trees is still limited. In this sense, our study represents a relevant contribution to this field of knowledge. The demographic behavior of *B. glabrifolia* shows interesting patterns compared with other tree species. The λ values of the population studied were quite high for a tree species (Silvertown et al., 1993; Álvarez-Buylla et al., 1996; Golubov et al., 1999; Zuidema, 2000 and references there in). Only for pioneer tree species have such high λ values been reported (e.g. *Cecropia obtusifolia*, *Ardisia escallonioides*, *Acacia bilimekii*—Álvarez-Buylla et al., 1996; Pascarella and Horvitz, 1998; Jiménez-Lobato and Valverde, in press). Yet, *B. glabrifolia* does not conform completely to what would be expected of a pioneer species, since although it shows relatively high individual growth rates, it is mostly found in mature dry tropical forests and its regeneration is not particularly favored by canopy gaps (Peters et al., 2003; Hernández-Apolinar, unpublished). Other species in the same genus (i.e. *Bursera simaruba*) have been reported to behave in a similar manner (Ceccon et al., 2003), although the evidence in this respect is contradictory (see Macario Mendoza, 1991; Dickinson et al., 2000). The high λ values of our *B. glabrifolia* population may be associated with the fact that our study was carried out in a relatively undisturbed site. It remains to be empirically tested whether these λ values would also reflect a growing population in more disturbed conditions.

The λ values obtained were determined, in part, by the stem expansion rates on which our demographic model was based. However, different stem expansion rates were obtained depending on the measuring technique applied (i.e. dye or dendrometer); we considered that the dye measurements were more accurate and used these results to calculate transition probabilities. Our stem expansion rates obtained with the dye technique (ca. 1.1 cm yr⁻¹) are indeed comparable to those reported for other tropical trees. *S. macrophylla* and *B. simaruba* (which inhabit relatively more humid habitats) have been reported to reach values of ca. 1.1 and 0.8 cm yr⁻¹, respectively (Lamm, 1966; Snook, 1992; Gullison et al., 1996). For our study species other authors have reported a stem expansion rate of 0.19 cm yr⁻¹ using dendrometers (Peters

et al., 2003); we obtained similar values (in 2002–2003) using the same measuring technique (Table 1). Thus, it is possible that the stem expansion rates of ca. 1.1 cm yr⁻¹ obtained with the dye technique are somewhat overestimated. Nevertheless, dye results were trusted more since we considered that our hand-made dendrometers were not very precise, especially during the first year, since steel belts did not adjust perfectly to the irregularly shaped stems and, by accommodating to the growing stem, could have taken no notice of slight increases in trunk diameter.

In order to test to what extent our demographic results depended on the stem expansion rates used, we built an additional population projection matrix, this time based on the stem expansion rates obtained through the dendrometer technique (Appendix A). The analysis of this alternative matrix gave very similar results (i.e. λ value) compared to the original matrix (see Appendix A). This demonstrates that the results of the demographic model were not too sensitive to changes in stem expansion rate. This is not unexpected, since the main determinants of the λ value projected by a matrix are the gains and losses of individuals (i.e. fecundity and mortality), while the rate at which existing trees move from one category to the next is frequently not so critical (Enright et al., 1995; Zuidema, 2000). Thus, the λ values obtained, as well as the results of the simulations performed may be considered robust.

Many tree species that have been studied for periods of longer than 1 year have shown that demographic behavior vary between years, as is the case for *C. obtusifolia*, *Bellotia excelsa*, *Coccolrinax readii*, *Euterpe precatoria*, *Ireartea deltoidea*, *Prosopis gladiosa*, and *Trinax radiata* (Olmsted and Alvarez-Buylla, 1995; Golubov et al., 1999; Zuidema, 2000). The *B. glabrifolia* population studied also showed variation in its demographic behavior through time, possibly related to differences in environmental (i.e. weather) conditions between years. More detailed knowledge on the extent of this demographic variation and its causal factors would be fundamental, not only to understand the long-term numerical behavior of this population, but also to aid in its management strategies.

4.2. Consequences for management

The λ values obtained in the two study periods were significantly higher than unity, which suggests that the unexploited population of *B. glabrifolia* may show an overall increasing trend and would therefore be appropriate to consider tree extraction as a potentially adequate management strategy. However, as mentioned above, it would be necessary to evaluate population dynamics for a longer time period before concluding about the magnitude of this apparently increasing trend, since yearly variation in vital rates may cause long-term numerical fluctuations in population numbers (Valverde et al., 2004). Furthermore, considering that global environmental change is seemingly causing dry tropical forests in the Americas to become more arid (Villeres-Ruiz and Trejo-Vázquez, 1997), it is expected

that the long-term demographic behavior of *B. glabrifolia*, as well as that of other tropical dry forest species, will be negatively affected. Thus, resource managers should take into account both yearly demographic variation and long-term environmental change in their management guidelines. This could imply allowing a more intensive extraction during favorable periods but restricting management practices during unfavorable ones (Zuidema and Boot, 2002), as well as directing actions towards the protection of early life-cycle stages during adverse periods. Also, since the persistence of juveniles was found to be a demographic process with a high elasticity, management strategies should prevent juvenile mortality during extractive activities (e.g. these individuals should be protected from being crushed when trees are felled).

The theoretical evaluation of the potential sustainability of the management plan proposed for *B. glabrifolia*, suggest that the yearly harvest of 8 trees/ha is an amount that may be readily replenished by the natural regeneration of the population. Although these results appear optimistic suggesting that the management plan is indeed sustainable, it is important to take them with caution, since the study period apparently corresponded to a favorable one; thus, we cannot assume that long-term population dynamics may be adequately represented by the average matrix obtained. Also, because spatial variation in environmental conditions may result in dramatic differences in demography (Zuidema and Boot, 2002), we should be cautious to extrapolate these results to other regions of Mexico, where no management plans have been developed for this species, and where it is still being extracted illegally. Additionally, our simulation results showed that if the extraction level was increased, for instance to twice the amount recommended by the management plan, the population would not show an increasing trend (i.e. the projected λ value would not be significantly different from unity). Thus, forest managers must be careful not to exceed the extraction amount recommended by the management plan.

Selective extraction of forest products is considered one of the main factors causing tropical dry forest decline in Mexico (Bye, 1995; Challenger, 1998). Thus, government agencies are encouraging resource managers to elaborate management plans for these forest goods (CONAFOR, 2001). Once management plans are set in motion, it is important to corroborate whether they actually allow a sustainable extraction in the long term, an evaluation that has been referred to as validation. Yet, some time must elapse during which extraction is performed before we can carry out such validation on empirical grounds. In this paper, we have shown that a 'theoretical validation' is possible if robust demographic data are available, so that management plans may be set in motion with some security that sustainability may actually be achieved. Eventually, both theoretical and empirical information may be combined to arrive at an 'adaptive management plan' (*sensu* Boot and Gullison, 1995) to which new information may be incorporated in order to improve extraction guidelines.

5. Conclusions

The *B. glabrifolia* population at Jayacatlán shows an overall increasing trend. Under the current conditions in which almost no tree extraction has taken place in the last ca. 7 years, high fecundity and low mortality values appear to guarantee the persistence of the population. The elasticity analysis showed that the most vulnerable stages of the life cycle correspond to the juveniles and small adults; thus, management practices should protect these categories. Demographic variation between the two study years was apparent mainly in the fecundity values, which were lower in 2002–2003 compared to 2001–2002; this yielded a lower population growth rate in the second ($\lambda = 1.04$) than in the first year ($\lambda = 1.14$). These changes in the demographic behavior of the population were likely the result of weather conditions (i.e. 2001–2002 was rainier than 2002–2003).

The demographic model developed for the *B. glabrifolia* population was used to theoretically test the effect of different extraction regimes. The management plan proposed by Brosi et al. (2000) suggests the extraction of 8 trees/ha as a maximum sustainable harvesting regime. According to the results of our numerical simulations, this extractive regime is indeed sustainable, since the λ values of the matrix model were above unity when the recommended number of trees was theoretically harvested. However, more intensive harvesting regimes may undermine the long-term persistence of the population. Additional information on the long-term behavior of the population with and without extraction would be necessary in order to generate an 'adaptive management plan' which could be constantly tested and updated to optimize management guidelines.

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Appendix A

Population projection matrices of *B. glabrifolia* for the 2001–2002 and 2002–2003 periods is given in Table A.1.

Table A.1

Population projection matrices of *B. glabrifolia* for the 2001–2002 and 2002–2003 periods

Category (n_{t+1})	Category (n_t)						w	v
	1	2	3	4	5			
(a) $\lambda = 1.138 \pm 0.041$								
1	0.163	0.085	41.451	24.458	62.203	0.832	0.001	
2	0.038	<i>0.927</i>				0.149	0.031	
3		0.020	<i>0.985</i>	0.025		0.018	0.328	
4			0.006	<i>0.944</i>		0.001	0.205	
5			0.000	0.006	<i>0.968</i>	0.000	0.434	
q_x	0.799	0.054	0.010	0.025	0.032			
(b) $\lambda = 1.025 \pm 0.018$								
1	0.243	0.064	4.031	12.180	15.018	0.568	0.001	
2	0.060	<i>0.938</i>	0.010			0.369	0.015	
3		0.008	<i>0.966</i>	0.026		0.046	0.178	
4			0.015	<i>0.957</i>		0.011	0.409	
5				0.017	<i>0.969</i>	0.007	0.397	
q_x	0.697	0.047	0.010	0.000	0.031			

Demographic transition values were calculated using the dendrometer results for stem expansion. The λ values ($\pm 95\%$ confidence intervals) are shown above each matrix. Only positive entries are given. Entries in the main diagonal are italicized to facilitate reading. q_x , size-specific mortality; w , stable size-category distribution; v , size-specific reproductive values.

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