

## The population dynamics of *Astronium graveolens* Jacq. differ between topographically distinct areas in South Brazil

GABRIELA CORREIA ARAUJO DA CRUZ<sup>1</sup>, JOSÉ ANTONIO PIMENTA<sup>1</sup>, ELOÍSA DE SOUZA CARVALHO<sup>1</sup>, DANIEL CARATTI<sup>1</sup>, ANA PAULA PAVANELLI<sup>1</sup>, ANA VERGINIA L. MESSETTI<sup>2</sup> & EDMILSON BIANCHINI<sup>1\*</sup>

<sup>1</sup>*Departamento de Biologia Animal e Vegetal, Universidade Estadual de Londrina, Londrina, Paraná, Brazil, Caixa Postal 10011, 86057-970*

<sup>2</sup>*Departamento de Matemática Aplicada, Universidade Estadual de Londrina, Londrina, Paraná, Brazil, Caixa Postal 10011, 86057-970*

**Abstract:** The influence of slope on *Astronium graveolens* population dynamics in a Southern Brazilian Seasonal Semi-deciduous Forest was investigated by prospective (sensitivity and elasticity) and retrospective (LTRE-life-table-response-experiment) approaches. This study addressed the following questions: (i) Do vital rates (fecundity, mortality and growth) differ between slope (SA) and flat (FA) areas? (ii) Do population growth rates ( $\lambda$ ) differ between SA and FA? Demographic data were collected from 5,000 m<sup>2</sup> of FA and 5,000 m<sup>2</sup> of SA. All *A. graveolens* individuals within each plot were measured for height and grouped into five height classes to determine their transition probabilities. Five annual surveys (from 2007 to 2011) were conducted and demographic changes were described to total time interval (2007/2011) and to four annual intervals (2007/08, 08/09, 09/10 and 10/11), using the matrix model. In general, the probability of growth to taller height classes was higher in the SA, while the proportion of deaths and fecundity were higher in FA. The  $\lambda$  values differed between localities, although their values were always close to one. The  $\lambda$  values indicated that the *A. graveolens* population would remain stable or decrease in the FA, while the population would remain stable or increase in the SA. Therefore, the highest density of *A. graveolens* in the SA resulted from the higher probability of survival and height growth of individuals in this area. Regeneration was higher in the SA, probably due to environmental heterogeneity promoted by slope and associated factors.

**Key words:** Matrix analysis, population growth rate, slope, stochasticity, transition matrix, tropical forest, vital rates.

**Handling Editor:** Witness Mojeremane

### Introduction

Understanding the population dynamics of tropical tree species and how they respond to environmental changes or environmental heterogeneity are important goals in studies of population ecology (Bruna & Oli 2005).

Environmental heterogeneity is one of the main factors that determines the floristic composition and structure of tropical forests (Botrel *et al.* 2002; Durigan *et al.* 2000; Lindner 2011), through birth and death of individuals in these communities.

Tropical forests are highly heterogeneous ecosystems because of diverse biotic and abiotic

---

\*Corresponding Author; e-mail: bianchi@uel.br

factors that interact constantly with the species (Pulido *et al.* 2007). Topography has been highlighted as one of the environmental factors that influences the structures and dynamics of forest fragments (Cielo-Filho *et al.* 2007; Yamada *et al.* 2007) and in other kinds of vegetation (e.g. Srinivasan *et al.* 2015). Slope is a complex environmental gradient that include many factors (Takyu & Kitayama 2002) such as soil water availability (Becker *et al.* 1988; Daws *et al.* 2002), soil texture (Pavanelli *et al.* 2011) and light (Poorter *et al.* 1994; Tateno & Takeda 2003; Tsujino & Yumoto 2007; Yamada *et al.* 2007).

Various studies in tropical and subtropical forests have reported differences in tree species density across topographic gradients (Bunyavejchewin *et al.* 2003; Tsujino & Yumoto 2007; Yamada *et al.* 2006; Zuidema *et al.* 2010). For example, among seven Dipterocarpaceae canopy species growing in steeper areas, the highest density was recorded in *Hopea odorata* Roxb., and *Vatica cinerea* King. (Bunyavejchewin *et al.* 2003). Twelve tree species, among 17, showed different densities in a topographical gradient in Japan (Tsujino & Yumoto 2007), despite the random or homogeneous distribution of seeds in the study area. The differences in tree species distribution could be attributed to anthropogenic activities, the effect of competitors or other biological enemies and habitat specialization (Harms *et al.* 2001).

Whether niche differentiation occurs, species growing in sites they are bests adapted are expected to occur at higher density, while their density will be lower in 'niche margins', and may reach zero in poor sites (Yamada *et al.* 2007). Population traits that can affect tree density are: fecundity (number of seedlings produced per reproductive individual), survival of individuals and growth to the final life stages.

A higher density of *Astronium graveolens* Jacq., was recorded in sloppy areas in a seasonal semideciduous forest (SSF) remnant of Southern Brazil (Bianchini *et al.* 2010). The higher density of *A. graveolens* in SSF occurred probably due to favourable microsites that enhanced its establishment and development (Pavanelli *et al.* 2011). *A. graveolens* is an emergent light-demanding and drought resistant high value hardwood timber species (Carvalho 2006). It is typical Neotropical SSF species which has been reported to be highly abundant in this forest type (Bianchini *et al.* 2010; Dias *et al.* 2002; Soares-Silva *et al.* 1992). Due to selective logging in the

natural distribution range, *A. graveolens* has been placed on the red list of endangered species in Paraná State, Brazil (Hatschbach & Ziller 1995).

Information on tree species population dynamics is critical in understanding how the differences in density among habitats are generated and maintained. The aim of this study was to investigate how population dynamics differed in topographically distinct areas. The following questions were addressed by this study; (i) Do vital rates (fecundity, mortality and growth) differ between slope (SA) and flat (FA) areas? (ii) Do population growth rates ( $\lambda$ ) differ between SA and FA?

## Materials and methods

### *Study site*

The field investigation was carried out in a SSF remnant in Ibiporã County, Paraná State, South Brazil (23°17'51''–23°18'34''S, 50°58'04''–50°59'33''W) at elevation of 464 m above sea level. The study site covers approximately 100 ha at the Tibagi river edge, on Doralice Farm (hereafter Doralice remnant). The area has been protected from human disturbance for at least the last 20 years. Large stems of hardwood timber species such as *Aspidosperma polyneuron* Müll. Arg and *A. graveolens* were recorded in accessible areas of this remnant (Soares-Silva *et al.* 1992), suggesting that the area was not severely logged in the past.

In the Doralice remnant, 105 tree species were sampled in a 1 ha area (Soares-Silva *et al.* 1992). The forest canopy height ranges from 8–12 m, discontinuous at some points due to the opening of gaps. The most common trees include *Gallesia integrifolia* (Spreng.) Harms (Phytolaccaceae), *A. polyneuron* (Apocynaceae), *Ficus* sp. (Moraceae) and *A. graveolens* (Anacardiaceae) and can reach up to 35 m of height. The understory is closed and dominated by species such as *Sorocea bonplandii* (Baill.) W.C. Burger, Lanj. & de Boer (Moraceae), *Trichilia casaretti* C. DC. (Meliaceae) and *Actinostemon concolor* (Spreng.) Müll. Arg. (Euphorbiaceae).

The Doralice remnant exhibits an area of high declivity close to the Tibagi River edge. The south-facing sloppy area (hereafter SA) extends for about 40–50 m and further ahead the topography gradually flattens until it becomes almost a plateau. The flat area (hereafter FA) shows weak to moderate steepness (< 10%), according to the steepness of conventional classes (Garcia &

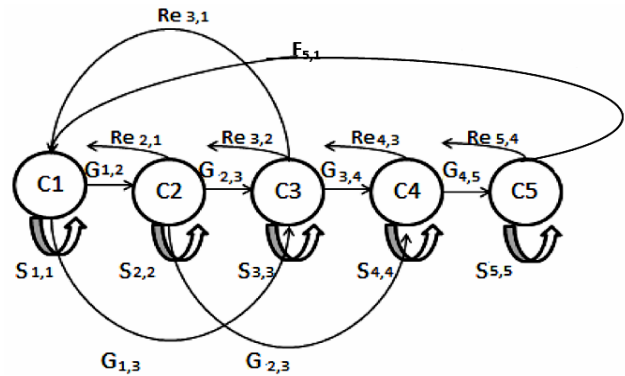
Piedade 1987), while SA, which is 300 m away from FA, shows very strong (20–40%) to extremely strong (> 40%) steepness. Soils in the SA are shallow and drier loam clay and loam soils that are poor in nutrients, with rocky outcroppings. The FA is dominated by deep clay and silty clay soils (Pavanelli *et al.* 2011; Soares-Silva *et al.* 1992).

The climate of the study site (Cfa in Köppen’s classification) is humid subtropical, with a hot and humid season (October–March) and a cool and dry season (April–September) (Bianchini *et al.* 2010). The average annual temperature is 21.8 °C, with February (24.6 °C) and July (17.8 °C) being the hottest and coldest months. The average annual precipitation is 1570 mm (Bianchini *et al.* 2010), with January being the wettest month (215.4 mm) and August the driest month (46.5 mm). The highest rainfall is received between November and February and the lowest from May to August (Costa *et al.* 2011).

*Data collection and analysis*

Data was collected in two 0.5 ha plots (SA and FA). The use of larger plots in the Doralice remnant was not possible due to small size of remnant and small dimension of sloppy area. Replications in other forest remnants were also not possible because we could not find another remnant with the same characteristics (slope, soil types, and proximity to the river, conservation status and historical use). Despite the limitation of the study due to plot size and lack of replication, the study is very important because *A. graveolens* is an endangered species distributed in a highly fragmented landscape, such as the one found in Southern Brazil.

All *A. graveolens* individuals were measured for height within each plot, using a Laser Distance Meter, and tagged with metal plates. As it was not possible to establish ontogenetic stages, the population was grouped into five height classes: C1: > 0–0.25 m; C2: > 0.25–0.5 m; C3: > 0.5–1 m; C4: > 1–8 m; C5: > 8 m. Height was chosen instead of stem base diameter to express the development of individuals because it represents the population structure more adequately in this light demanding species. The tallest class was considered to comprise the reproductive individuals (adults), because these individuals were at canopy or above it (emergent). Many big stems of trees such as *Bertholletia excelsa* Humb. & Bonpl., a light-demander (Zuidema & Boot 2002) only become



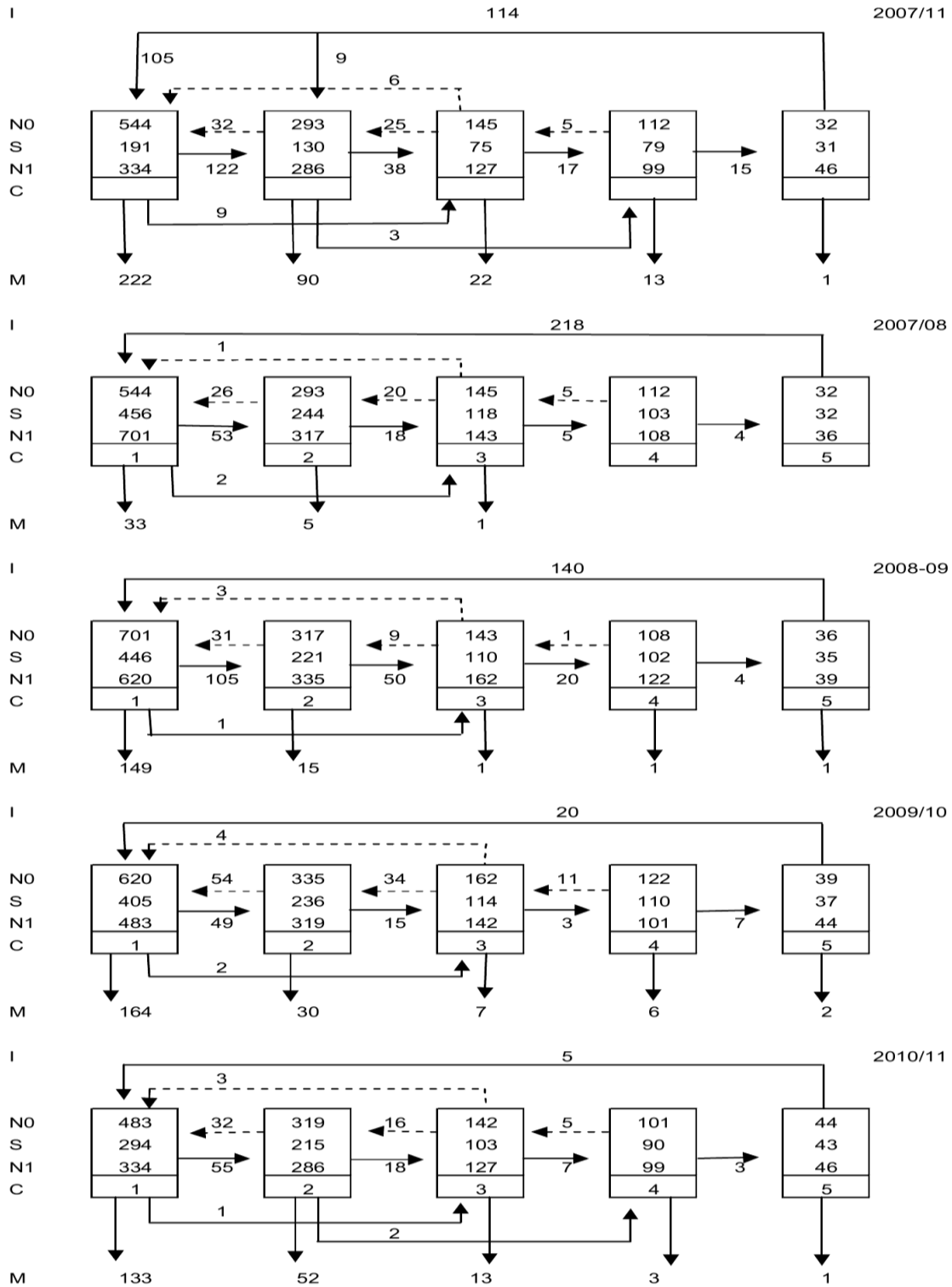
**Fig. 1.** Life-cycle diagram of *Astronium graveolens* showing the transitions used to construct the population model. Arrows represent transition probabilities between height classes (from one circle to another) or stasis probabilities (from a circle to the same one) and numbers represent the original (first number) and fate (second number) height classes. C1–C5 = height classes; F = fecundity; G = growth (progression); Re = retrogression; S = stasis.

reproductive after attaining a position in the canopy (Poorter *et al.* 2005).

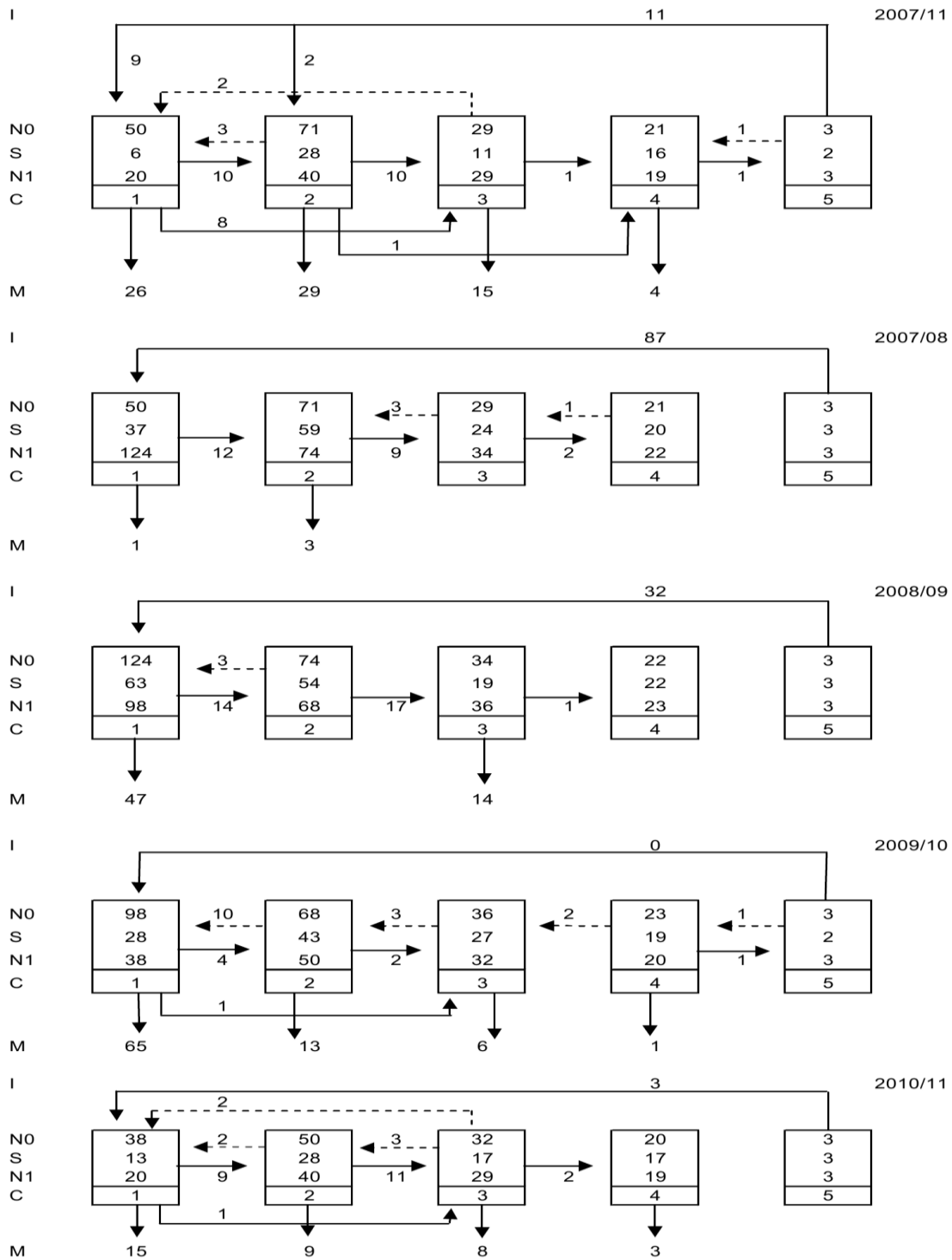
Five annual censuses were carried out between June and August from 2007 to 2011. The first two surveys were conducted by Pavanelli *et al.* (2011) and we calculated the transition probabilities among height classes (Fig. 1) for each annual interval, resulting in four annual intervals: 2007–2008, 2008–2009, 2009–2010 and 2010–2011.

A transition matrix model (Caswell 2001) was used to analyze the population dynamics of *A. graveolens*. The matrix formula is:  $n_{(t+1)} = A.n_{(t)}$ , where  $n$  is a column vector whose elements ( $n_i$ ) are the numbers of individuals in each height class at time  $t$  or  $t + 1$ .  $A$  is a square matrix containing transition probabilities among height classes during one time-step (transition matrix). Finite population growth rates ( $\lambda$ ) were calculated for both the SA and the FA using this model. A 95% confidence interval for  $\lambda$  was estimated using bootstrap with 1,000 permutations (Pulido *et al.* 2007) for each annual transition matrix.

Transition matrices for both the SA and FA were constructed for total interval (2007–2011) and for each annual interval (2007–2008, 2008–2009, 2009–2010 and 2010–2011). Transitions probabilities were calculated as the proportion of individuals in each class following different fates such as surviving and growing to the next height



**Fig. 2.** Diagram showing the different height classes (C) of a population of *Astronium graveolens* on a slope area of seasonal semideciduous forest fragment, Ibioporã County, Paraná State, Southern Brazil. I = recruitment of new seedlings; N0 = number of individuals at time  $t$ ; S = individuals that survived and remained (stasis) in the same height class at time  $t+1$ ; N1 = number of individuals at time  $t+1$ ; M = number of dead individuals; solid arrows (to the right) = progression for the next height class at time  $t+1$ ; dashed arrows = retrogression to the previous height class at time  $t+1$ .



**Fig. 3.** Diagram showing the different height classes (C) of a population of *Astronium graveolens* on a flat area of a seasonal semideciduous forest fragment, Ibiporã County, Paraná State, Southern Brazil. I = recruitment of new seedlings; NO = number of individuals at time  $t$ ; S = individuals that survived and remained (stasis) in the same height class at time  $t+1$ ; N1 = number of individuals at time  $t+1$ ; M = number of dead individuals; solid arrows (to the right) = progression for the next height class at time  $t+1$ ; dashed arrows = retrogression to the previous height class at time  $t+1$ .

class (sub-diagonal); surviving and remaining in the same height class (diagonal); surviving and retrogressing to the preceding height class (super-diagonal). To estimate fecundity of C5 (first row), the number of seedlings resulting from last reproduction was considered. Fecundity is calculated empirically by analyzing the relationship of seedlings censused in an area to total reproductive plant in the area (Menges 1990). In this study, we estimated C5 fecundity by dividing the number of new plants in C1 at time  $t+1$  by the number of plants in C5 at time  $t$ . A probability of 0.001 or 0.999 was assigned when entries of matrix were zero and one, respectively (Souza & Martins 2004).

The resulting annual transition matrices ( $n = 8$ ) were subjected to a log-linear analysis to test the effect of “years” and “locality” (SA and FA) on the fate of individuals (Caswell 2001; Pulido *et al.* 2007). This method evaluates the degree of interdependence between explanatory factors (years and areas) and the fate of individuals. This analysis was performed using the Statistica Program (StatSoft 2004). As the log-linear analysis indicated differences in annual transition matrices for years and localities, all transition matrices are presented.

We used prospective analyses (sensitivity and elasticity) to evaluate the relative contribution of matrix entries to  $\lambda$  by providing information on how much  $\lambda$  would change if matrix entries were modified (Caswell 2000, 2001). These analyses were performed for each time interval considered. Furthermore, we used a retrospective analysis (Life Table Response Experiment-LTRE), to identify which elements of the transition matrix contributed significantly to variations in  $\lambda$  in each locality. LTRE analyses are based on the construction of contribution matrices, which are derived from the observed variation in the matrix entries of the treatments combined with their sensitivities (Caswell 2000; Pulido *et al.* 2007). These contribution matrices indicate the extent to which each demographic rate increased or decreased the  $\lambda$  value of its corresponding transition matrix compared to the  $\lambda$  value of the average matrix (Pulido *et al.* 2007). As our questions involved the comparison of the SA and FA, we used a one-way fixed design, which analyzed the effect of locality. We used the total interval (2007–2011) transition matrix for each locality and these were used to construct contribution matrices for both SA and FA.

Matrix analyses and both prospective and retrospective analyses were performed using the R program, version 2.12 and popbio package (R Development Core Team 2010).

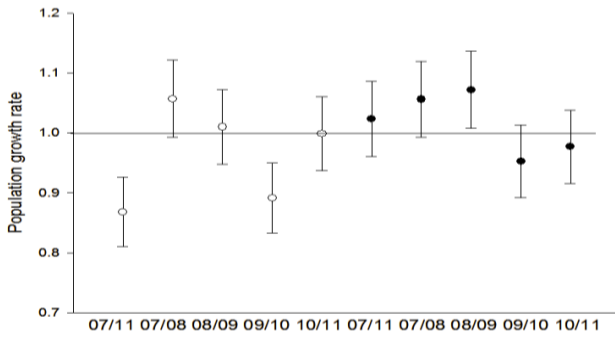
## Results

A higher density of *A. graveolens* was observed in the SA in all sampling years (2007 to 2011). In 2007, the density per 100 m<sup>2</sup> was  $22.5 \pm 25.4$  and  $3.48 \pm 2.98$  in the SA and FA, respectively. The size structure differed between the SA and FA, with a decrease in the number of plants from the first to the last height class in the SA (Fig. 2). The second class in FA revealed the highest number of plants (Fig. 3). The results show that the number of adults in C5 was 10 times higher in the SA compared to the FA (Figs. 2 and 3). During the study period, a decrease in the number of individuals was observed in both the SA (from 1,126 to 892) and the FA (from 174 to 111) (Figs. 2 and 3).

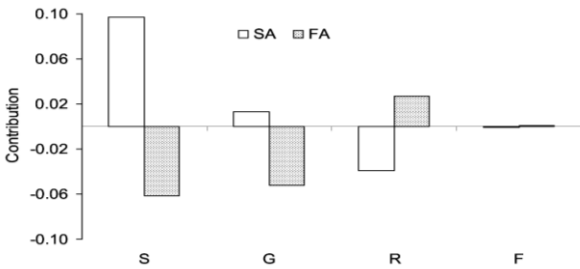
Considering the 2007–2011 interval, the fecundity was similar between the SA and FA, but the probability of individuals remaining in the same height class, especially in C1, C3 and C5 and the progression probability to C4 and C5 was higher in the SA compared to the FA (Appendices I and II). The proportion of deaths was lower in the SA than the FA, especially in C3 (Figs. 2 and 3). The  $\lambda$  values differed between the two areas, with the SA having a  $\lambda$  value greater than 1.0 and FA smaller than 1.0. However, 95% confidence interval of the  $\lambda$  value of SA included unity (Fig. 4).

In both the SA and FA, the population growth rate was more sensitive to changes in progression and persistence, especially for C4 and C5. In the SA, the persistence of C5 individuals showed the highest elasticity (Appendix III), while persistence of C4 and C5 individuals showed the highest elasticity in the FA (Appendix IV). Fecundity, progression and retrogression elements had relatively low contributions to the  $\lambda$  value. However, the relative importance of fecundity was higher in the SA than FA.

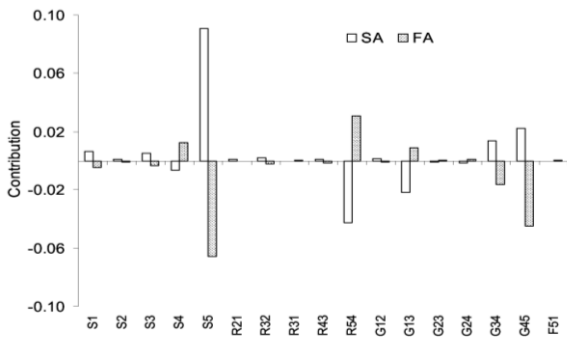
Considering the annual intervals in both areas, fecundity was higher from 2007–2009. However, fecundity of zero was observed from 2009 to 2010 in the FA (Fig. 3). Although the total number of new seedlings was higher in the SA (Fig. 2 and 3), overall, the fecundity was higher in the FA (Appendices I and II). In both areas, the



**Fig. 4.** Population growth rate ( $\lambda$ ) for each time interval considered (2007/2011, 2007/2008, 2008/2009, 2009/2010, 2010/2011) of *Astronium graveolens* in flat areas (open circles) and slope areas (solid circles) of a seasonal semideciduous forest remnant, Ibiporã County, Paraná State, Southern Brazil. Error bars indicate 95% confidence interval for  $\lambda$ .



**Fig. 5.** Contribution of the different demographic processes (F= fecundity; G = growth; R= retrogression; S= stasis), according to life–table–response–experiment (LTRE), to the observed variation in  $\lambda$  of two *Astronium graveolens* populations (FA = flat area; SA = slope area) of a seasonal semideciduous forest fragment, Ibiporã County, Paraná State, Southern Brazil.



**Fig. 6.** Detailed results of the life–table–response–experiment (LTRE), indicating the contribution of all matrix entries to the observed difference between the  $\lambda$  of each population (FA = flat area; SA = slope area) and that of the overall average matrix ( $\lambda_{PD}$ ). S = stasis; R = retrogressions; G = growth (progression); F = fecundity. The first numbers of the x-axis refers to the origin class and the second refers to the fate class.

number of dead individuals differed among years, with more death recorded from 2009 to 2010 (Fig. 2 and 3). Death in both areas occurred mainly in the first three height classes, with highest values observed in the C1 in all periods, except from 2007 to 2008 in FA (Fig. 2 and 3). Our results show that the proportion of dead individuals was higher in the FA. Progression was recorded in all height classes in the SA and only occurred in C2 and C3 in FA (Fig. 2 and 3). Therefore, in FA, numerical changes in the population involved individuals that had up to 1 m in height.

For the SA, the probability of remaining in the same height class was higher than 60% with little variation over the years. Lowest values were observed in C1 from 2010 to 2011. Progression occurred among all classes, with a maximum of 16% from 2008 to 2009 for C3 (Appendix D). In the FA, the probability of individuals remaining in the same height class varied greatly over the years, with lower values (29%) in C1 from 2009 to 2010. Progression to the next height class varied between the periods analyzed, with highest value (24%) recorded in C1 and C2 from 2007 to 2008 and 2010 to 2011 (Appendix II).

In both localities, population growth rates ( $\lambda$ ) were slightly under or above unity but all  $\lambda$  values included unity in 95% confidence interval, with the exception of 2008–2009 in the SA and 2009–2010 in the FA (Fig. 4). The population growth rate was more sensitive to changes in progression and persistence in both areas, especially for C4 and C5. Therefore, small changes in these rates will have major impacts on the  $\lambda$  value. The largest proportion of total elasticity is confined to stasis entries (Appendices III and IV). The highest elasticity was observed in the persistence of C5 individuals in the SA and in the persistence of C4 and C5 in the FA. Fecundity, progression and retrogression elements contributed relatively low to the  $\lambda$  value. However, the relative importance of fecundity was higher in SA than FA.

The LTRE analyses show that the  $\lambda$  value of the overall average matrix ( $\lambda_{PD}$ ) was 0.9529. The population in the SA exhibited a higher  $\lambda$  (1.0225) than the  $\lambda_{PD}$ , mainly due to the positive contribution of stasis (Fig. 5). In the FA population, the  $\lambda$  value was lower (0.8681) than the  $\lambda_{PD}$  due to the negative contribution of stasis and growth (Fig. 5). The differences in the  $\lambda$  values between the SA and the FA were mainly related to stasis in the C5 and progression of individuals from C3 to C4 and C4 to C5 (Fig. 6).

## Discussion

Although the probabilities in the 2007–2011 projection matrixes were calculated at an interval of four years, their projections indicate that the *A. graveolens* population would exhibit a decreasing trend in FA and increasing numbers in the SA. Light demanding tree species, such as *A. graveolens*, occur mainly in gaps and forest edges. Therefore, the maintenance of such species in the interior of mature forest depends on events that promote the rupture of the canopy, which are sporadic in time and space. The FA area has a more closed canopy (Pavanelli *et al.* 2011) when compared with SA, thus, having less favorable microsites for regeneration of light demanding tree species. The SA exhibited more favorable microsites for regeneration *A. graveolens* because not only was the canopy more open, but it also had the presence of shallow soil (less water retention capacity) that favors the occurrence of drought-resistant species.

The different values of the finite population growth rate among annual intervals might result from environmental stochasticity, with favorable and unfavorable years for population growth in both areas. Favorable environmental conditions (rainfall, temperature, etc) could increase the progression of individuals to subsequent height classes, decrease mortality and/or increase fecundity of the *A. graveolens* population (as observed in the two first survey of this study). As the  $\lambda$  values were very sensitive to changes in the first two vital rates, in favorable years its value would be higher and *A. graveolens* population size would increase. Years with very low temperatures (frost) or prolonged periods of low rainfall, as was the case in the winters of 2010 (153 mm) and 2011 (230 mm) in the region, can lead to increased mortality or decreased progression to next height class, which might be responsible for a decline in the  $\lambda$  value, as observed in the two last census in the SA and in 2009–2010 in the FA.

The higher density of *A. graveolens* in SA, probably resulted from higher survival and progression to next height class (growth height) in this area, suggests a greater number of favorable microsites for regeneration in the SA than in the FA. According to the hypothesis of “niche differentiation”, species density is higher in areas with favorable environmental conditions, and lower in marginal areas (Islam *et al.* 2016; Yamada *et al.* 2006, 2007). Changes in factors associated with slope, such as water availability,

soil composition and depth (Cielo Filho *et al.* 2007; Comita & Engelbrecht 2009; Daws *et al.* 2002; Gibbons & Newbery 2003), and especially solar radiation, might explain the greater number of favorable microsites for regeneration and density of *A. graveolens* in SA.

In more illuminated localities such as the SA, average air temperature and evapotranspiration are usually higher than in shaded localities such as the FA. All these factors may cause temporal and spatial heterogeneity and promote changes in vital rates and in  $\lambda$  values. Light-demanding and drought-tolerant species such as *A. graveolens* might be favored in sloppy areas as suggested by Pavanelli *et al.* (2011). The higher survival and growth height of *A. graveolens* in this area corroborates this information.

Competition can also promote changes in population size affecting birth and survival rates (Marques & Joly 2000). The highest proportion of deaths in C1 and C2 in the FA could also be associated with higher competition from herbaceous species compared to the SA, because several ground patches covered by dense herbaceous vegetation were observed in the FA. The more closed forest canopy in the FA (Pavanelli *et al.* 2011) associated with shading promoted by the canopy of herbaceous species might contribute to higher mortality and lower growth height observed in *A. graveolens*. Mory & Jardim (2001) also observed lower recruitment of *Goupia glabra* Aubl., a light-demanding species, in areas with lower solar radiation. Herbaceous species also exert competitive effect on seedling survival and growth on tropical forest (Islam *et al.* 2016; Saikia & Khan 2013)

Although other biotic factors could also be important in population dynamics, we did not record leaf herbivory or seed predation in *A. graveolens* in either area. In contrast, Klinger & Rejmánek (2010) observed that sites with high densities of seed predators had the highest rates of seed predation and lowest rates of seed germination, but a higher number of dispersed seeds and a higher density of seedlings, saplings, and adults of *Astrocaryum mexicanum* Liebm. ex Mart. in these sites.

The vital rates of *A. graveolens* differed between the FA and SA and stasis mostly contributed to the  $\lambda$  values. In the SA, progression occurred in all height classes, indicating that even with low fecundity and high mortality at the smallest height classes, this area offers favorable conditions for survival and growth of larger



individuals, which increases the probability of growth to the last height class (C5). In the FA, there was a deficit in progression to the last height class (C5) and stasis could be reduced to only 29%. The specific causes of mortality were not identified. However, competition in the FA provided by herbaceous plants could be an important factor, whereas in the SA the burial or uprooting of smaller individuals was probably the main cause of mortality.

High survival of larger individuals, especially adults (high values of elasticity), can ensure the maintenance of the population, given that the seeds produced by them could have an important role in the population dynamics (Nabe-Nielsen 2004).

### Conclusion

Our results indicate that vital rates of *A. graveolens* differed between areas; while the progression of individuals to subsequent height classes, mainly in C4 and C5 was higher in SA than in FA, the proportion of deaths and fecundity were lower in SA. For these reasons, population growth rates differed between the localities, although their values were always close to one. In general,  $\lambda$  values indicated that the *A. graveolens* population size would remain stable or decrease in FA, while population size would remain stable or increase in SA, if environmental conditions are maintained over time and the forest fragment is preserved.

The higher density of *A. graveolens* in SA might be caused by better adaptation of this species to the slope environment, indicating the importance of this species in the occupation of areas with steep slopes.

### References

- Becker, P., P. E. Rabenold, J. R. Idol & A. P. Smith. 1988. Water potential gradients for gaps and slopes in a Panamanian tropical moist forest's dry season. *Journal of Tropical Ecology* **4**: 173–184.
- Bianchini, E., C. C. Garcia, J. A. Pimenta & J. M. D. Torezan. 2010. Slope variation and population structure of tree species from different ecological groups in South Brazil. *Anais da Academia Brasileira de Ciências* **82**: 643–652.
- Botrel, R. T., A. T. Oliveira-Filho, L. A. Rodrigues & N. Curi. 2002. Influência do solo e topografia sobre as variações da composição florística e estrutura da comunidade arbóreo-arbustiva de uma floresta estacional semidecidual em Ingaí, MG [Soil and topography influence on the variations of the floristic composition and structure of tree and shrub community in a seasonal semideciduous forest in Ingaí, MG]. *Brazilian Journal of Botany* **25**: 195–213.
- Bruna, E. M. & M. K. Oli. 2005. Demographic effects of habitat fragmentation on a tropical herb: life-table response experiments. *Ecology* **86**: 1816–1824.
- Bunyavejchewin, S., J. V. La Frankie, P. J. Baker, M. Kanzaki, P. S. Ashton & T. Yamakura. 2003. Spatial distribution patterns of the dominant canopy dipterocarp species in a seasonal dry evergreen forest in western Thailand. *Forest Ecology and Management* **175**: 87–101.
- Carvalho, P. E. R. 2006. *Espécies Arbóreas Brasileiras* [Brazilian tree species]. Embrapa Florestas, Colombo.
- Caswell, H. 2000. Prospective and retrospective perturbation analyses: their roles in conservation biology. *Ecology* **81**: 619–627.
- Caswell, H. 2001. *Matrix Population Models: Construction, Analysis and Interpretation*. Sinauer Associates, Sunderland.
- Cielo-Filho, R., M. A. Gneri & F. R. Martins. 2007. Position on slope, disturbance, and tree species coexistence in a seasonal semideciduous forest in SE Brazil. *Plant Ecology* **190**: 189–203.
- Comita, L. S. & B. M. Engelbrecht. 2009. Seasonal and spatial variations in water availability drive habitat associations in a tropical forest. *Ecology* **90**: 2755–2765.
- Costa, J. T., D. A. Estevan, E. Bianchini & I. C. B. Fonseca. 2011. Composição florística das espécies vasculares e caráter sucessional da flora arbórea de um fragmento de Floresta Estacional Semidecidual no Sul do Brasil [Floristic composition of vascular species and successional character of the tree flora of a fragment of semideciduous forest in southern Brazil]. *Brazilian Journal of Botany* **34**: 411–422.
- Daws, M. I., C. E. Mullins, D. F. R. P. Burslem, S. R. Paton & J. W. Dalling. 2002. Topographic position affects the water regime in a semideciduous tropical forest in Panamá. *Plant and Soil* **238**: 79–90.
- Dias, M. C., A. O. S. Vieira & M. R. C. Paiva. 2002. Florística e fitossociologia das espécies arbóreas das florestas da bacia do rio Tibagi [Floristics and phytosociology of tree species of the Tibagi River Basin forests]. pp. 109-131. In: M. E. Medri, E. Bianchini, A. O. Shibatta & J. A. Pimenta (eds.) *A Bacia do Rio Tibagi*. Edição dos editores, Londrina.
- Durigan, G., R. R. Rodrigues & I. Schiavini. 2000. A heterogeneidade ambiental definindo a metodologia de amostragem da floresta ciliar [The environ-

- mental heterogeneity defining the sampling methodology of riparian fores]. pp. 159–167. In: R. R. Rodrigues & H. F. Leitão-Filho (eds.) *Matas ciliares: Conservação e Recuperação*. Edusp, São Paulo.
- Garcia, G. J. & G. C. R. Piedade. 1987. *Topografia Aplicada às Ciências Agrárias* [Topography Applied to Agricultural Science]. 5<sup>th</sup> edn. Nobel, São Paulo.
- Gibbons, A. J. & D. M. Newbery. 2003. Drought avoidance and the effect of local topography on trees in the understorey of bornean lowland rain forest. *Plant Ecology* **164**: 1–18.
- Hatschbach, G. G. & S. R. Ziller. 1995. *Lista Vermelha de Plantas Ameaçadas de Extinção no Estado do Paraná* [Red List of Threatened Plants of Extinction in the State of Paraná]. SEMA/GTZ, Curitiba.
- Harms, K. E., R. Condit, S. P. Hubbell & R. B. Foster. 2001. Habitat associations of trees and shrubs in a 50 ha neotropical forest plot. *Journal of Ecology* **89**: 947–959.
- Islam, M., S. H. Salim, M. H. Kawsar & M. Rahman. 2016. The effect of soil moisture content and forest canopy openness on the regeneration of *Dipterocarpus turbinatus* C.F. Gaertn. (Dipterocarpaceae) in a protected forest area of Bangladesh. *Tropical Ecology* **57**: 455–464.
- Klinger, R. & M. Rejmánek. 2010. A strong conditional mutualism limits and enhances seed dispersal and germination of a tropical palm. *Oecologia* **162**: 951–963.
- Lindner, A. 2011. Small scale structure of forest stands in the Atlantic Rainforest – notes on understorey light fluctuation. *Tropical Ecology* **52**: 139–150.
- Marques, M. C. M. & C. A. Joly. 2000. Estrutura e dinâmica de uma população de *Calophyllum brasiliense* Camb. em floresta higrófila do sudeste do Brasil [Structure and dynamics of a *Calophyllum brasiliense* Camb. population in swamp forest southeastern Brazil]. *Brazilian Journal of Botany* **23**: 107–112.
- Menges, E. S. 1990. Population viability analysis for an endangered plant. *Conservation Biology* **4**: 52–62.
- Mory, A. M. & F. C. S. Jardim. 2001. Comportamento de *Goupia glabra* Aubl. (cupiúba) em diferentes níveis de desbaste por anelamento em florestas naturais [*Goupia glabra* Aubl. (cupiúba) behavior at different levels of thinning by girdling in natural forests]. *Revista de Ciências Agrárias* **36**: 55–66.
- Nabe-Nielsen, J. 2004. Demography of *Machaerium cuspidatum*, a shade tolerant neotropical liana. *Journal of Tropical Ecology* **20**: 505–516.
- Pavanelli, A. P., J. A. Costa, E. Bianchini & J. A. Pimenta. 2011. Estrutura de tamanho, relações alométricas e distribuição espacial de *Astronium graveolens* Jacq. (Anacardiaceae) em áreas topograficamente distintas de fragmentos de floresta estacional semidecidual do sul do Brasil [Size structure, allometric relationships and spatial distribution of *Astronium graveolens* Jacq. (Anacardiaceae) in topographically distinct areas of seasonal semideciduous forest in southern Brazil]. *Pesquisa: Botânica* **62**: 345–363.
- Poorter, L., F. Bongers, F. J. Sterck & H. Wöll. 2005. Beyond the regeneration phase: differentiation of height-light trajectories among tropical tree species. *Journal of Ecology* **93**: 256–267.
- Poorter, L., L. Jans, F. Bongers & R. S. A. R. Vanrompaey. 1994. Spatial distribution of gaps along three catenas in the moist forest of Tai national park, Ivory Coast. *Journal of Tropical Ecology* **10**: 385–398.
- Pulido, M. T., T. Valverde & J. Caballero. 2007. Variation in the population dynamics of the palm *Sabal yapa* in a landscape shaped by shifting cultivation in the Yucatan Peninsula, Mexico. *Journal of Tropical Ecology* **23**: 139–149.
- R Development Core Team. 2010. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna. <http://www.R-project.org>.
- Saikia P. & M. L. Khan. 2013. Population structure and regeneration status of *Aquilaria malaccensis* Lam. in homegardens of Upper Assam, northeast India. *Tropical Ecology* **54**: 1–13.
- Soares-Silva, L. H., E. Bianchini, E. P. Fonseca, M. C. Dias, M. E. Medri & W. Zangaro-Filho. 1992. Composição florística e fitossociologia do componente arbóreo das florestas ciliares da bacia do rio Tibagi. 1. Fazenda Doralice – Ibiporã, PR [Floristic composition and phytosociology of the tree component of Tibagi River basin riparian forests: 1. Doralice Farm – Ibiporã County, PR]. *Revista do Instituto Florestal* **4**: 199–206.
- Souza, A. F. & F. R. Martins. 2004. Population structure and dynamics of a neotropical palm in fire-impacted fragments of the Brazilian Atlantic Forest. *Biodiversity Conservation* **13**: 1611–1632.
- Srinivasan, M. P., S. Bhatia & K. Shenoy. 2015. Vegetation-environment relationships in a South Asian tropical montane grassland ecosystem: restoration implications. *Tropical Ecology* **56**: 201–217.
- StatSoft. 2004. *Statistica for Windows*. StatSoft Inc, Tulsa.
- Takyu, M. A. S. & K. Kitayama. 2002. Effects of topography on tropical lower montane forests under different geological conditions on Mount Kinabalu, Borneo. *Plant Ecology* **159**: 35–49.

- Tateno, R. & H. Takeda. 2003. Forest structure and tree species distribution in relation to topography-mediated heterogeneity of soil nitrogen and light at the forest floor. *Ecological Research* **18**: 559–571.
- Tsujino, R. & T. Yumoto. 2007. Spatial distribution patterns of trees at different life stages in a warm temperate forest. *Journal of Plant Research* **120**: 687–695.
- Yamada, T., A. Tomita, A. Itoh, T. Yamakura, T. Ohkubo & M. Kanzaki. 2006. Habitat associations of Sterculiaceae trees in a Bornean rain forest plot. *Journal of Vegetation Science* **17**: 559–566.
- Yamada, T., P. A. Zuidema, A. Itoh, T. Yamakura, T. Ohkubo, M. Kanzaki, S. Tan & P. S. Ashton. 2007. Strong habitat preference of a tropical rain forest tree does not imply large differences in population dynamics across habitats. *Journal of Ecology* **95**: 332–342.
- Zuidema, P. A. & R. G. A. Boot. 2002. Demography of the Brazil nut tree (*Bertholletia excelsa*) in the Bolivian Amazon: impact of seed extraction on recruitment and population dynamics. *Journal of Tropical Ecology* **18**: 1–31.
- Zuidema, P. A., T. Yamada, H. J. During, A. Itoh, T. Yamakura, T. Ohkubo, M. Kanzaki, S. Tan & P. S. Ashton. 2010. Recruitment subsidies support tree subpopulations in non-preferred tropical forest habitats. *Journal of Ecology* **98**: 636–644.

(Received on 10.09.2014 and accepted after revisions, on 20.11.2015)

**Appendix I.** Transition matrices for the *Astronium graveolens* population on the slope area of a seasonal semideciduous forest fragment, Ibiporã County, Paraná State, Southern Brazil.  $\lambda$  = finite population growth rates  $\pm$  95% confidence interval. C = height class. The values with an asterisk (\*) have been adjusted as proposed by Souza and Martins (2004).

		C1	C2	C3	C4	C5
2007–2011 $\lambda = 1.023 \pm 0.063$ (n = 1,126)	C1	0.351	0.109	0.041		3.562
	C2	0.224	0.444	0.172		
	C3	0.017	0.130	0.517	0.045	
	C4		0.010	0.117	0.705	
	C5				0.134	0.969
2007–2008 $\lambda = 1.056 \pm 0.064$ (n = 1,126)	C1	0.838	0.089	0.007		6.813
	C2	0.097	0.833	0.138		
	C3	0.004	0.061	0.814	0.045	
	C4			0.034	0.920	
	C5				0.036	0.999*
2008–2009 $\lambda = 1.072 \pm 0.064$ (n = 1,305)	C1	0.636	0.098	0.021		3.889
	C2	0.150	0.700	0.063		
	C3	0.001	0.158	0.769	0.009	
	C4			0.140	0.944	
	C5				0.037	0.972
2009–2010 $\lambda = 0.953 \pm 0.061$ (n = 1,278)	C1	0.653	0.161	0.025		0.513
	C2	0.079	0.705	0.210		
	C3	0.003	0.045	0.704	0.090	
	C4			0.019	0.902	
	C5				0.057	0.949
2010–2011 $\lambda = 0.977 \pm 0.061$ (n = 1,089)	C1	0.609	0.100	0.021		0.114
	C2	0.114	0.674	0.113		
	C3	0.002	0.056	0.725	0.050	
	C4		0.006	0.049	0.891	
	C5				0.030	0.977

**Appendix II.** Transition matrices for the *Astronium graveolens* population on the flat area of a seasonal semideciduous forest fragment, Iporã County, Paraná State, Southern Brazil.  $\lambda$  = finite population growth rates  $\pm$  95% confidence interval. C = height class. The values with an asterisk (\*) have been adjusted as proposed by Souza and Martins (2004).

		C1	C2	C3	C4	C5
2007–2011 $\lambda = 0.868 \pm 0.058$ (n = 174)	C1	0.120	0.042	0.069		3.667
	C2	0.200	0.394			
	C3	0.160	0.145	0.379		
	C4		0.014	0.034	0.762	0.333
	C5				0.048	0.667
2007–2008 $\lambda = 1.057 \pm 0.064$ (n = 174)	C1	0.740				29
	C2	0.240	0.831	0.103		
	C3		0.127	0.828	0.048	
	C4			0.069	0.952	
	C5				0.001*	0.999*
2008–2009 $\lambda = 1.010 \pm 0.062$ (n = 257)	C1	0.508	0.041			10.667
	C2	0.113	0.730			
	C3		0.230	0.559		
	C4			0.029	0.999*	
	C5				0.001*	0.999*
2009–2010 $\lambda = 0.891 \pm 0.058$ (n = 228)	C1	0.286	0.147			0.001*
	C2	0.041	0.632	0.083		
	C3	0.010	0.029	0.750	0.087	
	C4			0.001*	0.826	0.333
	C5				0.043	0.667
2010–2011 $\lambda = 0.999 \pm 0.062$ (n = 143)	C1	0.342	0.040			1
	C2	0.237	0.560	0.094		
	C3	0.026	0.220	0.531		
	C4			0.063	0.850	
	C5				0.001*	0.999*

**Appendix III.** Elasticity matrices for the *Astronium graveolens* population on the slope area of a seasonal semideciduous forest fragment, Ibiporã County, Paraná State, Southern Brazil. Numbers in bold indicate the highest values and \*represents values below 0.001.

		C1	C2	C3	C4	C5
2007–2011	C1	0.021	0.003	0.0*		0.036
	C2	0.032	0.030	0.004		
	C3	0.008	0.025	0.035	0.001	
	C4		0.007	0.030	0.083	
	C5				0.036	<b>0.653</b>
2007–2008	C1	0.109	0.006	0.0*		0.022
	C2	0.025	0.116	0.006		
	C3	0.003	0.025	0.098	0.001	
	C4			0.023	0.158	
	C5				0.022	<b>0.385</b>
2008–2009	C1	0.055	0.004	0.0*		0.033
	C2	0.037	0.077	0.004		
	C3	0.0*	0.037	0.099	0.001	
	C4			0.035	<b>0.257</b>	
	C5				0.033	<b>0.326</b>
2009–2010	C1	0.011	0.001	0.0*		0.004
	C2	0.004	0.016	0.001		
	C3	0.0*	0.004	0.017	0.0*	
	C4			0.005	0.084	
	C5				0.004	<b>0.847</b>
2010–2011	C1	0.002	0.0*	0.0*		0.001
	C2	0.001	0.003	0.0*		
	C3	0.0*	0.0*	0.003	0.0*	
	C4		0.0*	0.0*	0.012	
	C5				0.001	<b>0.975</b>

**Appendix IV.** Elasticity matrices for the *Astronium graveolens* population on the flat area of a seasonal semideciduous forest fragment, Ibiporã County, Paraná State, Southern Brazil. Numbers in bold indicate the highest values and \*represents values below 0.001.

		C1	C2	C3	C4	C5
2007–2011	C1	0.003	0.0*			0.019
	C2	0.010	0.008			
	C3	0.010	0.004	0.011		
	C4		0.005	0.014	<b>0.536</b>	0.056
	C5				0.075	<b>0.248</b>
2007–2008	C1	0.049				0.021
	C2	0.021	0.108	0.009		
	C3		0.029	0.123	0.005	
	C4			0.026	<b>0.231</b>	
	C5				0.021	<b>0.358</b>
2008–2009	C1	0.006	0.0*			0.005
	C2	0.006	0.015			
	C3		0.005	0.007		
	C4			0.005	<b>0.473</b>	
	C5				0.005	<b>0.473</b>
2009–2010	C1	0.0*	0.0*			0.0*
	C2	0.0*	0.0*	0.0*		
	C3	0.0*	0.0*	0.003	0.0*	
	C4			0.0*	<b>0.718</b>	0.056
	C5				0.056	0.166
2010–2011	C1	0.0*	0.0*	0.0*		0.0*
	C2	0.0*	0.0*	0.0*		
	C3	0.0*	0.0*	0.0*	0.001	
	C4			0.0*	0.0*	
	C5					<b>0.997</b>