

A monocarpic tree species in a polycarpic world: how can *Tachigali vasquezii* maintain itself so successfully in a tropical rain forest community?

LOURENS POORTER*†‡, PIETER A. ZUIDEMA*†,
MARIELOS PEÑA-CLAROS*†§ and RENE G. A. BOOT*†¶

*Department of Plant Ecology, Utrecht University, PO Box 80084, 3508 TB Utrecht, the Netherlands, †Programa Manejo de Bosques de la Amazonía Boliviana (PROMAB), Casilla 107, Riberalta, Bolivia, ‡Forest Ecology and Forest Management Group, Wageningen University, PO Box 47, 6700 AA Wageningen, the Netherlands, §Instituto Boliviano de Investigación Forestal (IBIF), Casilla 6204, Santa Cruz, Bolivia, and ¶Tropenbos International, PO Box 232, 6700 AE Wageningen, the Netherlands

Summary

1 Although monocarpity is rare among long-lived plant species that grow in stable habitats, one monocarpic species, *Tachigali vasquezii*, is extremely abundant in the rain forests of the Bolivian Amazon. We analyse how *T. vasquezii* is able to maintain itself successfully by comparing its life-history traits with those of polycarpic tree species of the same community. We then evaluate the relative importance of such traits using population matrix models.

2 Monocarpic species are expected to have a high fecundity. Seed production per basal area for *T. vasquezii* is indeed nearly twice that of an average polycarpic species, but this is not sufficient to maintain stable populations.

3 Life-history theory predicts that a monocarpic strategy is advantageous if juvenile survival rates are high compared with adult survival. Although seedlings of *T. vasquezii* have a lower mortality rate than polycarpic species, its saplings have higher mortality.

4 We found that the success of *T. vasquezii* is due to its very high diameter growth rates in the larger size classes, which are four times higher than that of an average, co-occurring polycarpic species. Fast diameter growth is enabled by investment in large, leafy crowns and by a low wood density. Applying this high diameter growth in a population model yielded a population growth rate close to that of polycarpic species. Life table response experiment analysis of *Tachigali* and polycarp models showed that higher growth compensated for the negative demographic effect of 100% adult mortality following reproduction.

5 Rapid growth enables *T. vasquezii* to reach reproductive maturity in only 49 years, compared with 79 years for an average polycarpic species. It also reduces the risk of dying before reproducing, and 50% more seedlings survive to maturity for *T. vasquezii* compared with polycarpic species.

6 The dramatic negative demographic consequences of one-time flowering can therefore be completely balanced by taking a shorter time to reach maturity. Taking a time perspective, it appears that *Tachigali vasquezii* has an advanced, rather than a delayed, reproduction.

Key-words: demography, life history, matrix population model, monocarpity, reproduction, *Tachigali vasquezii*, tropical rain forest

Journal of Ecology (2005)

doi: 10.1111/j.1365-2745.2005.00958.x

Introduction

Monocarpic is a successful strategy for short-lived plant species growing in ephemeral habitats, but is rare among long-lived plants that grow in stable habitats. Surprisingly, where monocarpic is found in long-lived species, it is not restricted to those, such as the *Corypha* palm, that have a single vegetative axis ending in an inflorescence, and thus die after flowering, but is also found amongst trees with many shoot apices. There are only four genera, and about 30 species, of long-lived monocarpic trees (Whitmore 1990; Richards 1996), suggesting that monocarpic is an evolutionary dead end for long-lived species. One such species, *Tachigali vasquezii*, however, appears to be extremely successful and, in the rain forests of the northern Bolivian Amazon, it may be the 10th most common species, with densities of 13 trees ha⁻¹ (> 10 cm d.b.h.) (Poorter *et al.* 2001). Trees only become reproductive when they attain, on average, a diameter of 50–70 cm. Once the fruits are released, the bare, dead tree may stand for several years before it snaps off or topples over.

Over recent decades, four hypotheses have been proposed to explain how *Tachigali* can maintain itself so successfully in the tree community. The first is developed from the notion that species from the genus *Tachigali* are not only monocarpic, but that some of them also show masting behaviour (Foster 1977; Forget *et al.* 1999), possibly as a result of strong selective pressure by seed predators (Janzen 1976). By postponing reproduction, monocarpic masting species may avoid specialization by seed predators. An abundance of seeds during mast years may satiate seed predators and thus provide a window of opportunity for the successful establishment of the one and only seedling cohort. However, the majority of seeds of a masting Panamanian species (*T. versicolor*) were lost to insect and vertebrate predation (Kitajima & Augspurger 1989).

A second hypothesis is derived from life-history theory, which predicts that a monocarpic strategy is advantageous if juvenile survival rates are high and adult survival rates are low compared with polycarpic species (Stearns 1992). Kitajima & Augspurger (1989) found that survival of recently germinated seedlings of *T. versicolor* is indeed higher than that of other wind-dispersed species. Nevertheless, these initially higher survival rates are not maintained, and sapling survival is comparable with that of other forest species (Welden *et al.* 1991). It is therefore questionable whether a high seedling survival alone is sufficient to explain how monocarpic tree species are maintained in the forest community.

Foster (1977) suggested that the key to success is situated in the suicidal habit of the species. As dead standing trees slowly disintegrate, a gap is created in the forest canopy, creating a favourable environment for the growth and survival of its locally abundant offspring. Thus the mother tree may give way for her offspring, and *Tachigali* regeneration might be more successful and abundant right under the parent crown. This is in

sharp contrast with the Janzen-Connell hypothesis, which predicts that distance- and density-dependent mortality leads to more successful regeneration away from the parent tree. These hypotheses were tested by Kitajima & Augspurger (1989), who planted *T. versicolor* seedlings under dying parent trees, as well as under living conspecific and non-conspecific trees. Light levels were indeed higher under dying parent trees, leading to significantly higher survival and growth rates. *Tachigali* cannot take full advantage of the beneficial recruitment conditions below the parent crown, because it is wind dispersed, and only a small proportion of its regeneration occurs below the parent trees (Kitajima & Augspurger 1989).

A fourth hypothesis (Foster 1977) looks beyond the regeneration phase, suggesting that *Tachigali* may realize fast adult growth rates because the lack of annual investment of large amounts of carbon and nutrients into reproduction allow it rapidly to attain its reproductive size.

To unravel the paradox of a long-lived monocarpic species in a polycarpic world, we compare the life-history traits of *Tachigali vasquezii* with the traits of the other tree species in a Bolivian forest community. Traits for which *T. vasquezii* performs significantly better than the polycarpic species should provide the clue to why this species is so successful and matrix models are used to evaluate the role of such traits in maintenance of its populations. Finally, we use our results to evaluate the four hypotheses listed above.

Materials and methods

STUDY SPECIES AND STUDY SITE

Most of the research was carried out in and around forest reserve El Tigre in the northern Bolivian Amazon (10°59' S, 65°43' W). Annual rainfall in the region is about 1780 mm, with a distinct dry period (< 100 mm month⁻¹) from May to September. The forest is a lowland tropical moist forest, with some of the canopy trees being deciduous during the dry season. The forest canopy has a height between 25 and 35 m, with some emergent trees attaining heights up to 45 m.

Tachigali vasquezii Pipoly is a canopy tree known from the evergreen and semi-deciduous forests of Ecuador, Peru and Bolivia. The tree attains a maximal height of 30–35 m, and is locally abundant in the northern Bolivian Amazon (Alverson *et al.* 2000). *T. vasquezii* has been classified as a long-lived pioneer species, based on its pattern of abundance during secondary succession (Peña-Claros 2003).

COMPARISON OF THE MONOCARPIC *T. VASQUEZII* WITH POLYCARPIC SPECIES

For each of a number of life-history traits, we show boxplots, describing the performance of polycarpic tree species, and these are compared with the performance of *T. vasquezii*, using a two-sided one-sample *t*-test. Traits for which *T. vasquezii* performs significantly

better than the polycarpic species indicate the avenues by which the species may maintain itself successfully in the tree community. Mean values are reported for *T. vasquezii*, unless stated otherwise. We draw on a large body of published and unpublished studies to make the comparisons. The names of the polycarpic comparison species are given in Appendix S1 in Supplementary Material. The number of polycarpic reference species varies from 5 to 45, depending on study and trait under consideration. Sometimes the reference species represent a random selection from the tree community, but in other cases they deliberately included both pioneer and non-pioneer species. In the latter case, pioneer species are likely to be over-represented (it is estimated that 7% of the tree species in the region are pioneers, Poorter *et al.* 2001). In that case our test is extra conservative, as we expect that those features that lead to the success of a monocarpic species (a rapid completion of the life cycle) are the same as those characteristic of many pioneer species.

SEED PRODUCTION AND DISPERSAL

Seed production was evaluated for three reproductive *T. vasquezii* trees in May 1995. The trees had diameters at breast height (d.b.h.) of 66, 72 and 99 cm. Around each tree, 48 rectangular (4 × 1 m) seed plots were established; six plots in each of eight compass directions. The plots were situated at 3 (mean value, actually between 1 and 5 m), 13, 25.5, 40.5, 57.5 and 77.5 m from the stem base. Seeds and seedlings were counted. Surviving seedlings were tagged in February 1996 and their survival was evaluated, and their height and leaf number measured, in November 1997. Three different zones around the parent tree were distinguished: below the parent tree (plots at 3 m distance), near the parent tree (13 m), and away from the parent tree (> 25 m). To evaluate how distance to the parent tree affects seedling growth, we carried out a two-way ANOVA, with seedling height in 1997 as dependent variable, and parent tree and distance to the parent tree as dependent variables. To evaluate how distance to parent tree affects seedling survival, we calculated, for each combination of parent tree and distance, the percentage of seedlings established in 1995 that survived until 1997. Survival was analysed with a one-way ANOVA, with distance as the main effect.

Seed production and dispersal were estimated for each of the three trees. The total seed and seedling density in the plots was related to the distance to the parent tree using a logarithmic regression (coefficients of determination were 0.53, 0.74 and 0.78, respectively) and we calculated then total seed number and mean dispersal distance. Fecundity is proportional to plant size, and was therefore expressed as seed production cm⁻² basal area (Metcalf *et al.* 2003). As no comparative data are available for the seed production of other tree species at El Tigre, we compared the fecundity and dispersal distance of *T. vasquezii* with 80 species from Barro Colorado Island (BCI), Panama (Muller-Landau

2001). BCI has a comparable forest type, and has some species in common with El Tigre.

SEED MASS AND GERMINATION

Seed dry mass data (excluding wings and fruit pulp) were available for 45 tree species in the region (R. G. A. Boot, unpublished data). Germination was monitored for six species (Peña-Claros 2001). Seeds were germinated in mature forest at two sites, with two blocks per site and 18–200 seeds per species for each site × block combination. A larger number of seeds was used for the smaller-seeded species. Seeds were sown during the natural dispersal period of the species, between October 1997 and March 1998, and checked every 2 weeks for germination until no further germination occurred.

GROWTH ANALYSES WITH SEEDLINGS

A growth experiment was carried out in an experimental garden in Riberalta (11° S, 66° W) (Poorter 1999). Seedlings of 15 species were grown for 23 weeks in six shade houses, presenting light levels of 3, 6, 12, 25, 50 and 100% of full irradiance. For each species-treatment combination an initial harvest of eight seedlings and a final harvest of 10 seedlings was carried out following the methodology of Hunt (1978). Based on the harvest data, we calculated the relative growth rate (RGR; biomass growth per unit plant biomass, in mg g⁻¹ d⁻¹), net assimilation rate (NAR; biomass growth per unit leaf area, in g m⁻² d⁻¹), specific leaf area (SLA; leaf area/leaf mass, in m² kg⁻¹), and leaf area ratio (LAR; leaf area/total plant mass, in m² kg⁻¹). The whole-plant light compensation point (LCP) was estimated for each species from a linear regression of NAR against ln-transformed percentage daylight.

Seedling growth and survival were also monitored for seedlings grown in a natural forest environment. In March 1997, recently germinated seedlings of nine species were transplanted to a 20-year-old secondary forest (Peña-Claros 2001). The canopy openness of this secondary forest was similar to the canopy openness of mature forest, suggesting that light levels are typical of the levels found in the understorey of mature forest. The experimental design consisted of three replicated secondary forest sites, two plots per site, and nine transplanted seedlings per species per plot. Additional seedlings were harvested at the time of transplanting. Seedling survival was monitored 3, 6, 12, 18 and 24 months after transplanting and all surviving plants were harvested in March 1999, oven-dried, and weighed.

SAPLING GROWTH AND SURVIVAL IN THE FIELD

Sapling growth and survival were monitored for 10 species in the permanent sample plot (PSP) in El Tigre (Poorter & Arets 2003). Saplings between 0.7 and 1.9 m tall were tagged and their stem height was measured.

For each sapling the light environment was estimated using the crown illumination index (CII) (Clark & Clark 1992): 1 = no direct light, 1.5 = low amount of lateral light, 2 = medium amount of lateral light, 2.5 = high amount of lateral light, 3 = part of the crown receives direct overhead light, 4 = the whole crown receives direct overhead light, 5 = crown completely exposed. Sapling survival, stem height and CII were measured again after 2 years. Saplings that showed clear signs of stem breakage, or had a height decrease of more than 2 cm year⁻¹ (which is likely to be caused by damage or measurement error), were excluded from the height growth analysis. The correlation between growth and the CII was used to quantify the species' growth response to light. The light demand was defined as the percentage of saplings of a species that occur in high-light conditions (CII ≥ 2.5).

LEAF TRAITS AND ARCHITECTURE

We evaluated leaf characteristics for saplings of 15 species (Poorter *et al.* 2004). For each species, 10 saplings growing under intermediate light conditions were selected, and a random sample of three leaves per plant was taken. Leaf traits were measured that are related to the costs of leaf display (SLA) and photosynthesis (N content).

For each of six species the architecture and biomass allocation of 15 saplings was measured in detail (Poorter & Werger 1999). The saplings ranged from 0.5 to 3 m height and occurred along the whole light gradient from understorey to large gaps. Crown area, stem and branch volume and leaf area were measured non-destructively. Stem and branch volumes and leaf area were converted to mass, by multiplying them by specific stem mass or by the inverse of SLA. Using regression equations, we calculated the height and crown area at a standardized above-ground biomass of 65 g.

Adult architecture was determined for 15 species (van Ulf 1998; M. Peña-Claros and L. Poorter, unpublished data). An average of 30 trees per species, covering the full diameter range of the species, were searched in 25-year-old secondary forest and mature forest. For each individual, the height to the uppermost leaf, as well as stem and crown diameter, were measured. As species differ to a large extent in their maximal diameter, allometric comparisons were made over the shared size interval between 2 and 50 cm d.b.h. For each species $\log_{10}(\text{height})$ and $\log_{10}(\text{crown area})$ were regressed against $\log_{10}(\text{d.b.h.})$. Using the regression curves, we calculated the height and crown area for each species at a standardized diameter of 20 cm.

TREE GROWTH AND SURVIVAL

Tree growth and survival were monitored in a 4-ha PSP established in El Tigre in 1995 (Poorter *et al.* 2001). All trees > 10 cm d.b.h. were mapped, tagged and identified to species; d.b.h. and survival were measured annually between 1995 and 1999. In 1999 the amount

of light each tree received was estimated using the CII, but CII classes 1.5 and 2.5 were not used, because they are difficult to distinguish for large trees. Annual diameter growth was calculated by regressing five consecutive diameter measurements against time, for each tree. Trees that were difficult to measure (buttresses, termite nests, etc.) were excluded from the growth analysis. Growth was compared for those 32 species that had a sample size ≥ 10. The light demand of each species was defined as the percentage of individuals between 10 and 20 cm d.b.h. that occurred under high-light conditions (CII ≥ 3). The light demand was compared for those 28 species that had at least 10 individuals in the 10–20 cm d.b.h. interval.

Wood density of *T. vasquezii* was determined from 15 cm long wood samples collected with an increment borer from three mature trees at 1.3 m height, and compared with data from Gutiérrez-Rojas & Silva-Sandoval (2000) for polycarpic species.

MATRIX MODEL CONSTRUCTION AND ANALYSIS

Population dynamics of *T. vasquezii* and an imaginary polycarpic tree were analysed using stage-based matrix models (Caswell 2001). For the construction of transition matrices, 15 size categories were distinguished: two seedling categories (1–2) for seedlings of < 50 cm and 50–150 cm height; three juvenile tree categories (3–5) with trees of 1–10, 11–20 and 21–30 cm d.b.h.; five pre-reproductive categories (6–10) with non-reproductive trees of 31–40, 41–50, 51–60, 61–70 and > 70 cm d.b.h.; and five reproductive categories (11–15) with reproductive trees classified according to d.b.h. as in 6–10 (life cycle graph in Appendix S1 in Supplementary Material). Thus, trees of > 31 cm d.b.h. could be either in a non-reproductive category (6–10) or a reproductive category (11–15). This distinction allowed us to simulate monocarpy by setting survival and growth in reproductive categories to 0%, and polycarpy by letting a high proportion of reproductive trees survive. Inventory data show that, unlike its congener, *T. vasquezii* does not show masting behaviour, and that the probability of reproduction is similar each year (Appendix S2). The polycarpic transition matrix represented the demography of an imaginary polycarpic tree of the same stature as *T. vasquezii*, using adjusted values for those vital rates that differed substantially between *T. vasquezii* and the polycarpic trees within the community (see Results). The transition matrices were parameterized using values for four vital rates: survival (σ), growth to next size class (γ), probability of becoming reproductive (r) and seedling production (f). All values used for matrix parameterization were obtained from natural forest populations of *T. vasquezii* or polycarpic tree species, mostly in the El Tigre area (see Appendix S2 for detailed information on parameterization).

The transition matrix \mathbf{A} can be used to simulate population dynamics as $\mathbf{n}(t+1) = \mathbf{A} \times \mathbf{n}(t)$, in which \mathbf{n} is a

vector containing the population structure at time $t + 1$ and t (Caswell 2001). Asymptotically, the population in such a simulation will grow according to a fixed population growth rate equivalent to the dominant eigenvalue (λ), which is a mathematical property of matrix **A**. When this is the case, the population structure is stable and equal to the right eigenvector (**w**) of matrix **A**.

We calculated λ to compare population growth rates of *T. vasquezii* and the polycarpic tree, and performed elasticity analysis (De Kroon *et al.* 2000; Zuidema & Franco 2001) to analyse the importance of vital rates for population growth. We assessed the contributions of vital rates to differences in population growth between *T. vasquezii* and the polycarpic tree by applying a life table response experiment (LTRE; Caswell 2001). We did a fixed-effect LTRE analysis on lower-level parameters with the polycarpic matrix as reference, applying the sensitivities of a matrix 'midway' between those of *T. vasquezii* and the polycarpic tree. We compared observed population structures for *T. vasquezii* with the stable stage structure (**w**) obtained from the matrix analysis. We also constructed survivorship functions and calculated estimates for the age at which reproductive size was reached, for average generation time and for net reproductive rate (I_x , τ , μ and R_0 , respectively, in Cochran & Ellner 1992; see Appendix S2). Model output for *T. vasquezii* was compared with that of the imaginary polycarpic tree in order to understand differences in life-history strategy. All matrix analyses were done in MATLAB (The MathWorks Inc., Natick, MA, USA).

Results

SEED MASS, DISPERSAL AND GERMINATION

T. vasquezii had a mean dry seed mass of 0.314 g, which approaches the average seed mass of the species in the

community (Fig. 1a). The three reproductive *T. vasquezii* trees produced on average a total of 27 500 seeds (16 000, 23 000 and 44 000, respectively) to give a fecundity of 6.1 seeds cm^{-2} basal area (Fig. 1b), which was significantly higher (1.9 times) than the average of polycarpic species (log-transformed data). Both mean seed dispersal distance (29 m, Fig. 1c) and germination (50% in mature forests, Fig. 1d) were comparable with the other species.

SEEDLING GROWTH AND SURVIVAL

To compare the inherent growth potential of the species, we used the maximal value of RGR obtained from the measurements at six irradiance levels. *T. vasquezii* is a fast grower (Fig. 2a) compared with the other species. RGR can be factored into a physiological component, NAR, and a morphological component, LAR. NAR is an estimator of whole-plant carbon gain, and is closely correlated with the photosynthetic capacity of the plants (Poorter & van der Werf 1998). Neither NAR nor LAR of *T. vasquezii* were significantly different from the other species in the community (Fig. 2b,c). Light compensation point values (LCP, estimated as the irradiance level at which the NAR becomes zero) suggest that *T. vasquezii* is relatively light demanding at the seedling stage (its LCP of 1.2% is higher than for the other species, Fig. 2d).

In an additional experiment, we transplanted recently germinated seedlings to the shaded understorey of a 20-year-old secondary forest. The RGR in the field was substantially lower than the RGR under glasshouse conditions, because RGR tends to decline over time as plants increase in size. Realized RGR in the field was comparable for *T. vasquezii* and the other species (Fig. 2f). Annual mortality rate of *T. vasquezii* was 34% y^{-1} , which was significantly lower than that of other species (Fig. 2e).

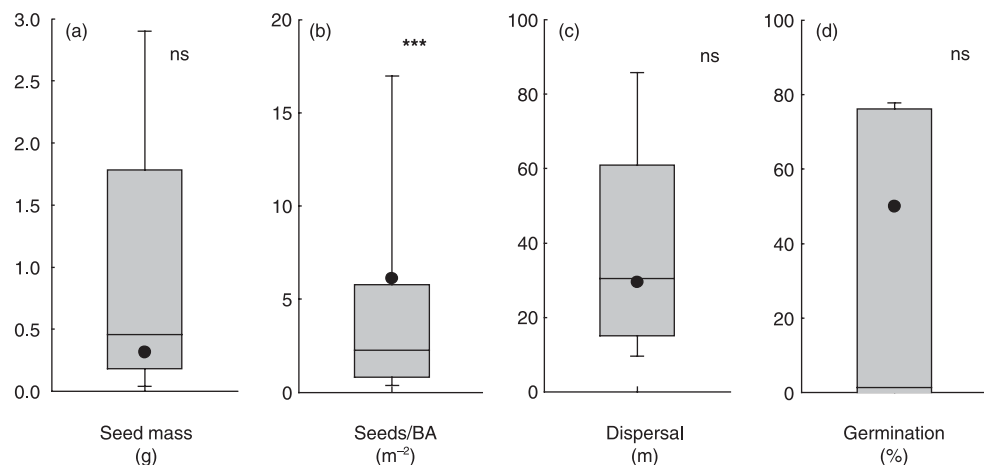


Fig. 1 (a) Seed mass ($n = 42$), (b) fecundity (seeds per basal area; $n = 81$), (c) mean dispersal ($n = 81$), and (d) germination ($n = 5$), of *Tachigali vasquezii* (large dot) and a reference group of polycarpic tree species (boxplot). The boxplots indicate the distribution values for co-occurring polycarpic tree species. The boxplots indicate 10th and 90th percentile (whiskers), 25th and 75th percentile (lower and upper end of boxes), and median (central line in box). Asterisks indicate the two-sided significance value of a one-sample t -test between *Tachigali vasquezii* and the polycarpic species. *** $P < 0.001$; ns, $P > 0.05$.

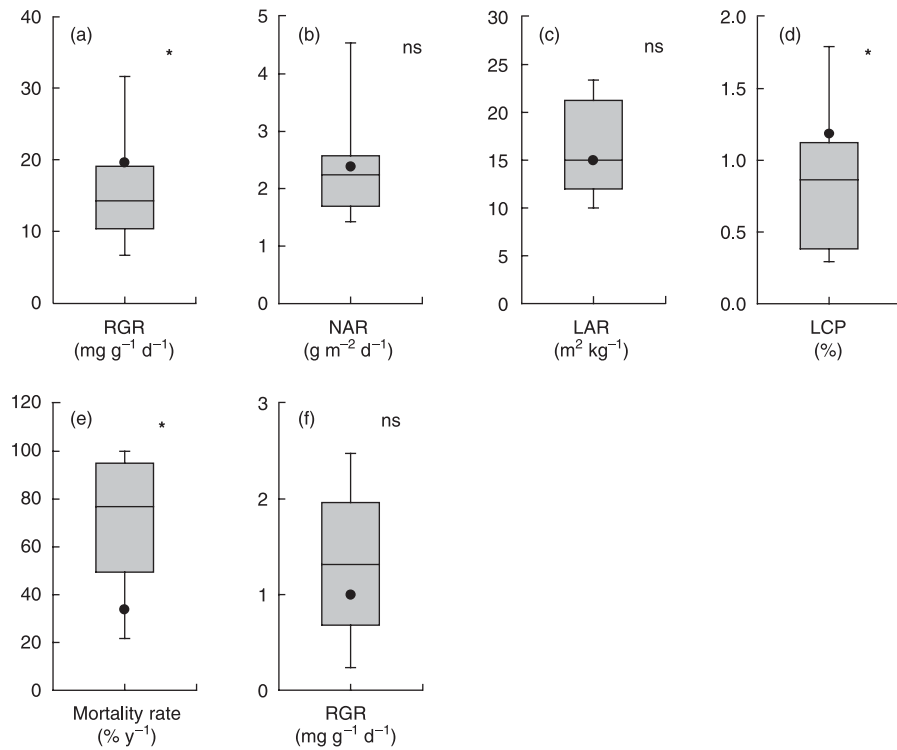


Fig. 2 Growth characteristics for tree seedlings grown in shade houses (a–d, $n = 14$) and in a late secondary forest (e, f, $n = 5$) for *Tachigali vasquezii* (large dot) and a reference group of polycarpic tree species (boxplot). See the legend for Fig. 1 for further explanation. RGR = relative growth rate; NAR = net assimilation rate; LAR = leaf area ratio; LCP = light compensation point. * $P < 0.05$; ns, $P > 0.05$.

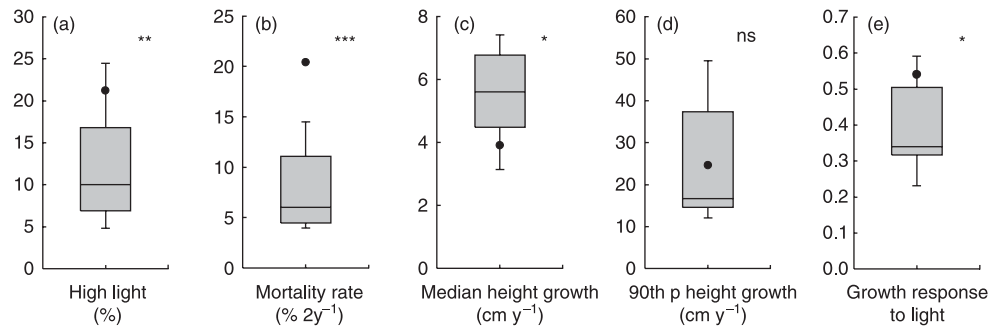


Fig. 3 Light preference and performance of saplings in the field: (a) the percentage of saplings occurring in high-light conditions that are typical of gaps, (b) mortality rate, (c) median height growth rate, (d) 90th percentile of height growth rate, and (e) the responsiveness of saplings to an increase in irradiance (expressed as the Spearman's correlation between height growth and CII). $n = 9$ species in all cases. *Tachigali vasquezii* is indicated by a large dot, and the boxplot indicates the distribution values for a reference group of polycarpic tree species. See the legend for Fig. 1 for further explanation. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; ns, $P > 0.05$.

SAPLING GROWTH AND SURVIVAL IN THE FIELD

Sapling growth and survival were monitored for a 2-year period under forest conditions (Fig. 3). The percentage of saplings that had a CII ≥ 2.5 , and therefore occurred in high-light conditions that are typical for gaps, was significantly larger for *T. vasquezii* (21%) than the other species (Fig. 3a). Sapling mortality rate (20% per 2 years, Fig. 3b) was, however, considerably higher than for other species and median height growth rate (4 cm year⁻¹, Fig. 3c) considerably lower. Nevertheless, the fastest growing individuals (i.e. the 90th

percentile of height growth) realized similar growth rates compared with the other species (Fig. 3d). *T. vasquezii* saplings were very responsive to an increase in irradiance, as indicated by a high correlation between height growth and CII (Fig. 3e).

SAPLING MORPHOLOGY AND LEAF TRAITS

The slow sapling height growth rates of *T. vasquezii* might be caused by differences in its architecture and its leaf traits. When compared with six other species at a standardized above-ground biomass of 65 g, *T. vasquezii* realized a very low height for a given biomass

(128 vs. 160 cm for the polycarpic species, $P < 0.05$). Much carbon is diverted from height growth to the formation of many long petioles and rachae so that, even as a sapling, *T. vasquezii* possesses a relatively large crown area (1.1 vs. 0.7 m² for the polycarpic species, $P < 0.01$).

T. vasquezii saplings have, compared with polycarpic species, a long leaf life span (3.2 vs. 1.5 years, $P < 0.01$), a similar SLA (both 20 m² kg⁻¹) and a high N concentration (2.47 vs. 2.27%, $P < 0.05$).

TREE ARCHITECTURE AND GROWTH

The architecture of the species was compared at a standardized diameter of 20 cm. At this diameter, *T. vasquezii* had a height of 16 m, which was 5 m lower than the average species in the community (Fig. 4e) and a crown area of 42 m² (15 m² larger than the average, Fig. 4f). *T. vasquezii* seems therefore to invest in growth of lateral stems and crown, rather than in height.

Juveniles of *T. vasquezii* occur in relatively bright light conditions (Fig. 4a). About 50% of the trees between 10 and 20 cm d.b.h. had a CII of 3 (partial overhead light) or more, whereas this was only 30% for an average species in the community. Juveniles and adults of *T. vasquezii* realized a median diameter growth rate of 0.9 cm year⁻¹, and a 'maximal' growth rate (the 90th percentile of diameter growth) of 2.1 cm year⁻¹ (Fig. 4b,c).

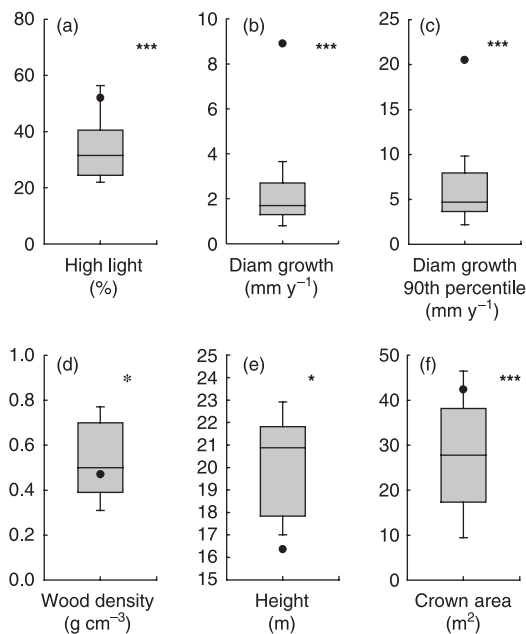


Fig. 4 Light, growth and architectural characteristics of juvenile and adult trees: (a) percentage individuals in high light ($n = 27$), (b) median diameter growth rate ($n = 31$), (c) 90th percentile diameter growth rate ($n = 31$), (d) wood density ($n = 41$), (e) height at a standardized diameter of 20 cm ($n = 12$), and (f) crown area at a standardized diameter of 20 cm ($n = 14$). *Tachigali vasquezii* is indicated by a large dot, and the boxplot indicates the distribution values for a reference group of polycarpic tree species. See the legend for Fig. 1 for further explanation. * $P < 0.05$; *** $P < 0.001$.

These growth rates were four times larger than the average growth rates of species in the community (or five times larger than the median for other species). *T. vasquezii* might realize high growth rates because of a high carbon gain, or because of cheap construction costs of its wood. Wood density, which is a good proxy for construction costs, was indeed significantly lower in *T. vasquezii* (0.47 g cm⁻³, Fig. 4d).

POPULATION GROWTH AND ELASTICITIES

The population growth rate (λ) for the *T. vasquezii* matrix model was slightly lower than 1 (0.998), suggesting that populations are stable in size. The population structure observed in the field (for categories 3–15) and that predicted by the model (**w**, stable stage structure) were not significantly different (Kolmogorov-Smirnov test, $Z = 0.19$, $P > 0.05$, $n = 197$), which indicates that our model realistically describes the dynamics of *T. vasquezii* populations, in spite of limited data on some of its parameters.

To compare population dynamics of *T. vasquezii* with an imaginary polycarpic tree, we identified those vital rates that differed significantly between *T. vasquezii* and the rest of the community: seed production (Fig. 1b) and diameter growth (Fig. 4b) were higher and sapling survival and growth (Fig. 3b,c) were lower than the average. These four vital rates, as well as the survival of reproductive trees, were used to convert the transition matrices to simulate the dynamics of a polycarpic tree (see Appendix S2).

This polycarpic model yielded a population growth rate very close to that of *T. vasquezii* ($\lambda = 1.007$), indicating that the negative demographic effect of 100% adult mortality was balanced by increased rates of seed production and diameter growth. To analyse which of the two contributed most to this compensation, we changed these rates from the lower value obtained for polycarps to the higher observed for *T. vasquezii* and calculated λ . The results (Fig. 5) showed that the negative influence of monocarpy on λ (a decrease from 1.007 to 0.969) was largely compensated for by an increase in tree growth but an increase in seed production had little effect.

Although the population growth rates for *T. vasquezii* and the polycarpic tree are very similar, the underlying dynamics are fundamentally different. This can be seen in the results of elasticity analysis, in which the importance of vital rates and categories for the population growth rate were compared (Fig. 6a,b). For *T. vasquezii*, 91% of the total elasticity value is accounted for by the survival of seedlings and juveniles (categories 1–5) and non-reproductive trees (6–10). This is much higher than in the polycarpic model (55%) and shows that survival until maturity is much more important for *T. vasquezii* than for the polycarpic tree. The latter species may compensate for a lower survival to reproductive size by a much longer reproductive life. A long reproductive life is actually rather important for

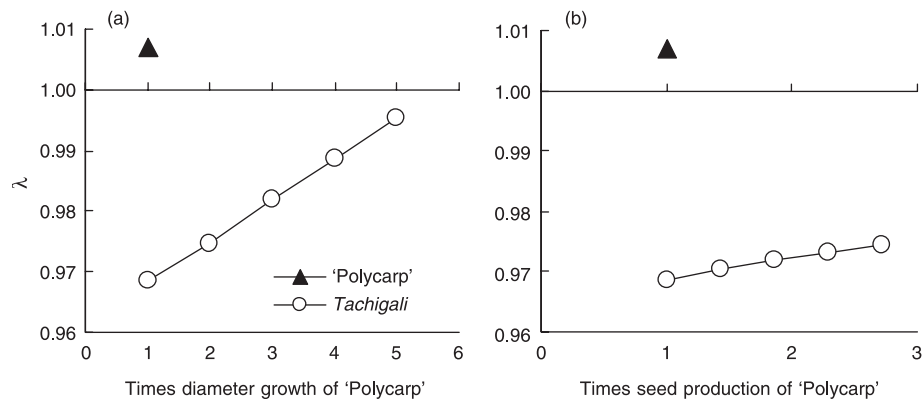


Fig. 5 Compensation for the negative effect of 100% adult mortality on population growth rates (λ) by increased diameter growth (a) and increased seed production (b). Increases in diameter growth and seed production are expressed relative to the value for the polycarpic tree. The filled triangle is the population growth of an imaginary polycarpic tree. In this comparison, transition matrices for *Tachigali vasquezii* only differed from the polycarpic tree with respect to adult mortality (= 100%) and in either diameter growth (a) or seed production (b). The observed values for *T. vasquezii* are the right-most symbols in the graph.

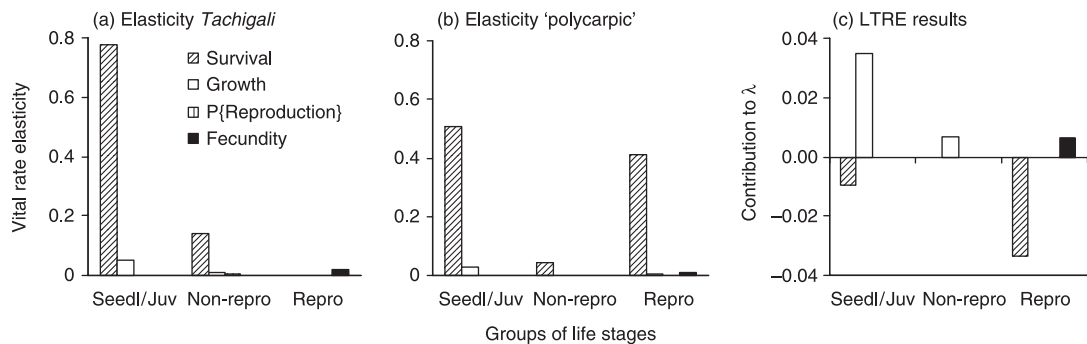


Fig. 6 Results of elasticity and life table response experiment (LTRE) analyses for *Tachigali vasquezii* and an imaginary polycarpic tree. Elasticity values show the importance of four vital rates for population growth rate (λ) for both *Tachigali vasquezii* (a) and the imaginary polycarpic tree (b). LTRE results are shown as contributions of four vital rates to the impact of monocarpic on λ (that is, the differences in λ between the two matrix models). Elasticities and contributions are summed for groups of categories: seedlings and juveniles (categories 1–5; < 30 cm d.b.h.), non-reproductive trees (6–10; 30–> 70 cm d.b.h.) and reproductive trees (11–15; 30–> 70 cm d.b.h.). Note that elasticities and contributions are not calculated for elements in the transition matrix, but for the underlying vital rates (see Appendix S2). Survival = annual survival probability; Growth = annual probability of moving to the next category for a surviving individual; P{Reproduction} = annual probability of becoming reproductive; Fecundity = number of seedlings produced annually by a reproductive tree.

polycarps, as shown by the high elasticity for survival of reproductive individuals (41% of total elasticity). Smaller differences in elasticities between the two models were found in seedling and juvenile growth, the probability of becoming reproductive and fecundity, all of which were larger for *T. vasquezii*. These differences point to the greater importance of rapid growth to maturity and reproduction for *T. vasquezii* compared with the polycarpic tree.

The small difference in lambda between the models for *T. vasquezii* and the polycarpic tree was mirrored by a low total contribution of vital rates (0.0049) in the LTRE analysis. The low total contribution was the net result of counteracting contributions on λ , which were large and negative for survival, and large and positive for growth and fecundity (Fig. 6c). Thus, the strongly negative effect of zero adult survival on population growth was almost entirely compensated for by the positive effect of increased growth and, to a lesser extent, fecundity. The LTRE analysis therefore confirmed the

finding that increasing tree growth has more impact on population growth than increasing seed production (Fig. 5).

AGE CALCULATIONS

How can high diameter growth outweigh the negative consequences of 100% adult mortality? To evaluate this, we constructed survivorship functions and calculated mean generation time for *T. vasquezii* and the imaginary polycarpic tree (Fig. 7). When following the survival of a cohort of newborns, the average proportion of individuals surviving at a given age, is slightly higher for the polycarpic tree than *T. vasquezii*. Lower survival of *T. vasquezii* individuals is caused by higher sapling mortality and by the 100% adult mortality. However, due to the high rates of diameter growth, *T. vasquezii* is able to reach reproductive size at a much lower age (49 vs. 79 years; Fig. 7). As a result, the proportion of newborns that reaches reproductive size is

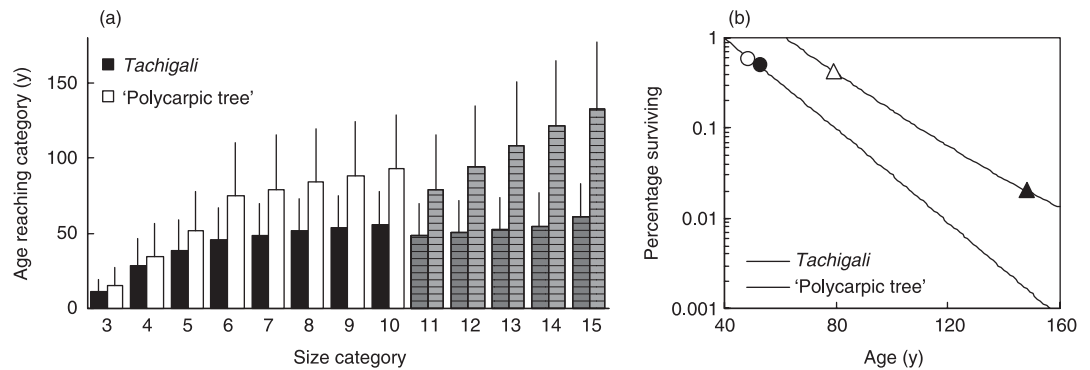


Fig. 7 Age at reaching size categories (a) and survivorship curves (b) for *Tachigali vasquezii* and an imaginary polycarpic tree. Size categories (a) are based on diameter at breast height and are 10 cm wide, starting at 1 cm; size categories 11–15 contain reproductive trees of the same size as those in 6–10. In the survivorship curves (b) the age at reaching the first reproductive category (category 11; open symbols) and mean generation time (closed symbols) for *Tachigali vasquezii* (circles) and the polycarpic tree (triangles) are shown.

higher for *T. vasquezii* (0.6%) than for the polycarpic tree (0.4%). Furthermore, the mean generation time (mean age at which a cohort produces offspring) is also considerably lower (mean 51 years, SD 22 years vs. mean 142 years, SD 65 years). At its mean reproductive age, 0.5% of a cohort of *T. vasquezii* is still alive, compared with only 0.02% for the polycarpic tree, although one should bear in mind that at this age (142 years), the polycarpic tree has already been reproducing for 63 years. In short, *T. vasquezii* is able to reach reproductive size at a much lower age than comparable polycarpic trees, and therefore has a higher probability of reaching maturity.

Given the differences in survival to maturity and in reproductive life span between *T. vasquezii* and the polycarpic tree, it is interesting to compare the total number of new reproductive individuals produced by one tree during its entire life span. This value (R_0 , the net reproductive rate) can be calculated by combining the survivorship function with the mean number of newborns produced by an individual at a certain age (Cochran & Ellner 1992). It appears that, in spite of the much shorter reproductive life of *T. vasquezii*, its net reproductive rate (0.91) is only lower by a factor of 3 than that of the polycarpic tree (2.9). Thus, high survival to maturity in *T. vasquezii* secures a reasonably high level of reproductive output at the population level, in spite of having only one reproductive event.

Discussion

AUTOECOLOGY OF *TACHIGALI VASQUEZII*

T. vasquezii is a non-pioneer species, as it can germinate and establish in the shade (Figs 1d and 2e). At the same time it is relatively light demanding because it has a high light compensation point as a seedling (Fig. 2d), and a large proportion of the saplings and juveniles are found in high-light conditions (Figs 3a and 4a). It starts out with many seedlings in the shaded understorey, but a high mortality of low-light individuals in the sapling stage (Fig. 3b) leads to an increasingly larger

amount of high-light individuals over time. *T. vasquezii* has many characteristics that are typical of light-demanding species (reviewed in Strauss-Debenedetti & Bazzaz 1996; Veneklaas & Poorter 1998; Walters & Reich 1999): it has a fast potential biomass growth rate, a high photosynthetic capacity, a high leaf nitrogen content and a strong growth response to an increase in irradiance (Fig. 3e). Despite its high potential biomass growth rate, *T. vasquezii* realizes very slow height growth rates as a sapling (Fig. 3c). This is probably due to its very particular morphology. As a sapling it makes large compound leaves but, because of a heavy investment in leaves and rachae, it only realizes a small height (growth rate) at a given biomass. At the same time it makes a large and leafy crown, because of the long rachae, and persistent leaves (cf. Poorter & Werger 1999). *T. vasquezii* follows the same allocation strategy in the pre-adult stage, investing in lateral branches (Fig. 4f) at the expense of height growth (Fig. 4e). A large crown with a large leaf area and little self-shading allows for a high whole-plant carbon gain, most of which can be invested in lateral stem and crown expansion, because leaf turnover is very slow. The high investment in stem material, in combination with cheap construction costs of the wood (Fig. 4d), allow for exceptionally high stem diameter growth rates (Fig. 4b,c).

These results are in sharp contrast to those for *Tachigali versicolor*, a monocarpic congener from Panama. *T. versicolor* appears to be a relatively shade-tolerant species, with a large number of seedlings waiting in the understorey for the formation of a canopy gap, to which they respond opportunistically (Kitajima & Augspurger 1989). *T. vasquezii*, on the other hand, is a relatively light-demanding species whose success is rooted in its performance in the juvenile, rather than the seedling stage.

A MONOCARPIC SPECIES IN A POLYCARPIC WORLD

Of the original four hypotheses, the first states that the success of *T. vasquezii* is rooted in the reproductive and

seed stage of the life cycle. Although other species from the genus show masting behaviour, and this may potentially lead to predator satiation (Forget *et al.* 1999), the probability of reproduction in *T. vasquezii* is similar each year. Monocarpic species are thought to have a high reproductive effort and copious seed production (cf. Gadgil & Bossert 1970), an efficient dispersal, low seed predation (Janzen 1976) and high germination rate. *T. vasquezii* does indeed have high fecundity (seed production per unit basal area is nearly two times as high as for an average species) but increased seed output alone appears insufficient to maintain *T. vasquezii* populations (Fig. 5). With respect to other reproductive traits, *T. vasquezii* performed surprisingly similarly. A low seed mass would allow a plant to realize a larger seed production with the same reproductive effort (Smith & Fretwell 1974) but the seed mass of *T. vasquezii* is very similar to both *T. versicolor* (Kitajima & Augspurger 1989) and our polycarpic species. The same applies for its dispersal distance and germination rates.

The second hypothesis is derived from life-history theory, which predicts that a monocarpic strategy is advantageous if juvenile survival rates are high (Stearns 1992). As a seedling, *T. vasquezii* indeed has one of the lowest mortality rates (Fig. 2e), a phenomenon that has also been observed for *T. versicolor* (Kitajima & Augspurger 1989) but as a sapling it experiences one of the highest mortality rates (Fig. 3b). The juvenile survival hypothesis is elegant because of its simplicity, but its predictions do not hold for our case.

The third hypothesis (Foster 1977) stated that the favourable environment for seedling growth and survival below the crown of the dying adult is beneficial for regeneration. For our three study trees, survival for the first 2.5 years is higher near the parent tree (39.2%) than below (17.0%) or away from it (20.8%) (ANOVA, $F_{2,6} = 13.9$, $P < 0.01$). Seedlings are tallest (18.2 cm) below, intermediate (16.1 cm) nearby and smallest (15.5 cm) away from the parent tree (ANOVA, $F_{2,686} = 6.3$, $P < 0.01$). It seems therefore that seedlings near the parent tree profit most from the increased light levels, and suffer least from falling debris or density-dependent mortality. The suicidal habit of *T. vasquezii* may enhance the chances for regeneration to some extent, but the effect is too small to explain its successful maintenance in a polycarpic tree community.

As an alternative, Foster (1977) hypothesized correctly that *T. vasquezii* realizes faster growth rates compared with similar-sized polycarpic species. Faster growth can be realized through the formation of a wide, leafy crown (Fig. 4f) that contributes to an increased carbon gain, and through the formation of cheap, low density wood (Fig. 4d). The monocarpic species needs less persistent wood, because it needs to live through only one reproductive event. The fast growth implies that the species can rapidly attain its reproductive size. From the initial seedling stage, it takes *T. vasquezii*

individuals only 49 years to reach the first reproductive category, compared with 79 years for an imaginary polycarpic tree with a median diameter growth rate that is five times lower (Fig. 7). A fast growth also reduces the risk of dying before reproducing. This risk is especially relevant in long-lived monocarpic species, which need to weigh the advantage of increased reproduction at larger size (and higher age) with the risk of dying before reproducing (Metcalf *et al.* 2003). Fifty per cent more seedlings survive to maturity for *T. vasquezii* compared with slower-growing polycarpic tree species (Fig. 7). As we showed in perturbation and LTRE analyses, the positive effect of fast growth to maturity on the growth of *T. vasquezii* populations may completely compensate for the negative consequences of having only one reproductive event (Figs 5 and 6c).

Conclusions

Tachigali vasquezii is a relatively light-demanding species that can establish in the forest understorey. In contrast to earlier hypotheses about monocarpy (Janzen 1976; Stearns 1992) it seems that its success is due to the post-regeneration phase. The species attains rapidly its reproductive size because of investment in large, leafy crowns and because of the cheap construction costs of its wood. In concert, these traits allow *T. vasquezii* to attain a higher survival to maturity, compared with slower-growing polycarpic species. The potentially dramatic negative demographic consequences of a one-time flowering event are largely compensated for by a higher growth rate and to a smaller extent by a higher seed output. *T. vasquezii* becomes reproductive at a larger d.b.h. than most other (polycarpic) species, and this seemingly delayed reproduction has contributed to a monocarpic species in a long-lived tree community appearing paradoxical. However, taking a time perspective, it seems that *T. vasquezii* has advanced rather than delayed reproduction. Other perennial monocarpic species may follow the same, unexpected, strategy.

Acknowledgements

We thank Yaskara Hayashida, Nico Divico, Miguel Cuadiay, Rene Aramayo, Luis Apaza, Jhon Leigue, Marjoke van de Plassche, Sonja Willems, Roel Brienen and staff of Programa Manejo de Bosques de la Amazonía Boliviana (PROMAB) for their support during different phases of the research. Bert van Uft, Helene Muller-Landau and Joe Wright kindly allowed us to use their unpublished data, and comments by Karen Rose and an anonymous reviewer improved the manuscript. PROMAB is partly funded by grants BO 009701 and BO 009703 from the Netherlands Development Assistance. LP is supported by Veni grant 863.02.007 from the Netherlands Organization of Scientific Research.

Supplementary material

The following material is available from <http://www.blackwellpublishing.com/products/journals/suppmat/JEC/JEC958/JEC958sm.htm>

Appendix S1 Polycarpic tree species used in species comparisons and matrix model parameterization.

Appendix S2 Construction and parameterization of the transition matrices.

References

- Alverson, W.S., Moskovits, D.K. & Schopland, J.M. (2000) *Bolivia: Pando, Rio Tahuamani*. Rapid Biological Inventories Report 1. The Field Museum, Chicago.
- Caswell, H. (2001) *Matrix Population Models*, 2nd edn. Sinauer Associates, Sunderland, Massachusetts.
- Clark, D.A. & Clark, D.B. (1992) Life history diversity of canopy and emergent trees in a neotropical rain forest. *Ecological Monographs*, **62**, 315–344.
- Cochran, M.E. & Ellner, S. (1992) Simple methods for calculating age-based life history parameters for stage-structured populations. *Ecological Monographs*, **62**, 345–364.
- De Kroon, H., van Groenendael, J. & Ehrlén, J. (2000) Elasticities: a review of methods and model limitations. *Ecology*, **81**, 607–618.
- Forget, P.M., Kitajima, K. & Foster, R.B. (1999) Pre- and post-dispersal seed predation in *Tachigali versicolor* (Caesalpiniaceae): effects of timing of fruiting and variation among trees. *Journal of Tropical Ecology*, **15**, 61–81.
- Foster, R.B. (1977) *Tachigali versicolor* is a suicidal neotropical tree. *Nature*, **268**, 624–626.
- Gadgil, M. & Bossert, W.H. (1970) Life history consequences of natural selection. *American Naturalist*, **104**, 1–24.
- Gutiérrez-Rojas, V.H. & Silva-Sandoval, J. (2000) *Información Técnica Para El Procesamiento Industrial de 134 Especies Maderables de Bolivia*. Serie Técnica 11. FAO-PAFBOL, La Paz, Bolivia.
- Hunt, R. (1978) *Plant Growth Analysis*. Edward Arnold, London.
- Janzen, D.H. (1976) Why bamboos wait so long to flower? *Annual Review of Ecology and Systematics*, **7**, 347–391.
- Kitajima, K. & Augspurger, C.K. (1989) Seed and seedling ecology of a monocarpic tropical tree, *Tachigali versicolor*. *Ecology*, **70**, 1102–1114.
- Metcalf, J.C., Rose, K.E. & Rees, M. (2003) Evolutionary demography of monocarpic perennials. *Trends in Ecology and Evolution*, **18**, 471–480.
- Muller-Landau, H.C. (2001) *Seed dispersal in a tropical forest – empirical patterns, their origins, and their consequences for forest dynamics*. PhD thesis. Princeton University, Princeton.
- Peña-Claros, M. (2001) *Secondary Forest Succession. Processes Affecting the Regeneration of Bolivian Tree Species*. PROMAB Scientific Series 3. PROMAB, Riberalta, Bolivia.
- Peña-Claros, M. (2003) Changes in forest structure and species composition during secondary succession in the Bolivian Amazon. *Biotropica*, **35**, 450–461.
- Poorter, H. & van der Werf, A. (1998) Is inherent variation in RGR determined by LAR at low light and by NAR at high light? *Inherent Variation in Plant Growth. Physiological Mechanisms and Ecological Consequences* (eds H. Lambers, H. Poorter & M.M.I. van Vuuren), pp. 309–336. Backhuys, Leiden.
- Poorter, L. (1999) Growth responses of fifteen rain forest tree species to a light gradient; the relative importance of morphological and physiological traits. *Functional Ecology*, **13**, 396–410.
- Poorter, L. & Arets, E.J.M.M. (2003) Light environment and tree strategies in a Bolivian tropical moist forest; a test of the light-partitioning hypothesis. *Plant Ecology*, **166**, 295–306.
- Poorter, L., Boot, R.G.A., Hayashida, Y., Leigue, J., Peña, M. & Zuidema, P. (2001) *Estructura Y Dinámica de un Bosque Húmedo Tropical En El Norte de la Amazonía Boliviana*. PROMAB Informe Técnico 2. PROMAB, Riberalta, Bolivia.
- Poorter, L., van de Plassche, M., Willems, S. & Boot, R.G.A. (2004) Leaf traits and herbivory rates of tropical tree species differing in successional status. *Plant Biology*, **6**, 746–754.
- Poorter, L. & Werger, M.J.A. (1999) Light environment, sapling architecture and leaf display in six rain forest tree species. *American Journal of Botany*, **86**, 1464–1473.
- Richards, P.W. (1996) *The Tropical Rain Forest*. Cambridge University Press, Cambridge.
- Smith, C.C. & Fretwell, S.D. (1974) The optimal balance between size and number offspring. *American Naturalist*, **108**, 499–506.
- Stearns, S.C. (1992) *The Evolution of Life Histories*. Oxford University Press, Oxford.
- Strauss-Debenedetti, S. & Bazzaz, F. (1996) Photosynthetic characteristics of tropical trees along successional gradients. *Tropical Forest Plant Ecophysiology* (eds S.S. Mulkey, R.L. Chazdon & A.P. Smith), pp. 162–186. Chapman & Hall, New York.
- van Ulf, B. (1998) *Morphology in ten neotropical tree species: differences among species, and among ontogenetic and successional stages in eight morphological traits*. MSc thesis. Department of Plant Ecology and Evolutionary Biology, Utrecht University, Utrecht.
- Veneklaas, E.J. & Poorter, L. (1998) Growth and carbon partitioning of tropical tree seedlings in contrasting light environments. *Inherent Variation in Plant Growth. Physiological Mechanisms and Ecological Consequences* (eds H. Lambers, H. Poorter & M.M.I. van Vuuren), pp. 337–361. Backhuys, Leiden.
- Walters, M.B. & Reich, P.B. (1999) Low-light carbon balance and shade tolerance in the seedlings of woody plants: do winter deciduous and broad-leaved evergreen tree species differ? *New Phytologist*, **143**, 143–154.
- Welden, C.W., Hewett, S.W., Hubbell, S.P. & Foster, R.B. (1991) Sapling survival, growth and recruitment: relationship to canopy height in a neotropical forest. *Ecology*, **72**, 5–50.
- Whitmore, T.C. (1990) *An Introduction to Tropical Rain Forests*. Clarendon Press, Oxford.
- Zuidema, P.A. & Franco, M. (2001) Integrating vital rate variability into perturbation analysis: an evaluation for matrix population models of six plant species. *Journal of Ecology*, **89**, 995–1005.

Received 17 March 2004

revision accepted 22 September 2004

Handling Editor: Hans de Kroon