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Demography of the seedling bank of *Manilkara zapota* (L.) Royen, in a subtropical rain forest of Mexico

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Abstract

Selection of individuals in tropical trees, occurs mainly in the seedling phase, which in part explains the low densities of most species. The main objective of this work was to gain an insight into those factors that influence growth and survival of *Manilkara zapota* seedlings, one of the most abundant species in the lowland forests of Mexico and Central America. Eight 10-m^2 rectangular plots (5m×2m) were established, in which all $<$ 35-cm-high *M. zapota* seedlings were marked, measured and enumerated at bimonthly intervals. In each census seedling height, number of leaves, length of largest leaf, type of damage and seedling death were registered. Seedling survival during 2 yr was high, reaching 82% including newly emerged seedlings. A maximum likelihood regression analysis showed that both number of leaves and length of largest leaf had a direct influence on seedling survival; however, neither type of damage nor seedling density and height had significant effect. Seedling height growth averaged 2.8 cm in the 2 yr of study. The combined effect of high seedling survival, reduced growth, and impact of physical damage mainly due to falling branches and leaves reveals the occurrence of a persistent seedling bank. Such a bank would contribute to recruitment of individuals in the juvenile and eventually in the adult stages. This seedling bank could explain the high density of individuals of *M. zapota* in the tropical forests of Mexico.

Introduction

Regeneration patterns and species composition of mature forests are closely related to processes of seedling establishment, growth, and persistence on the forest floor. On the seedling stage, however, occurs one of the greatest selection pressures in any particular tropical tree species. In this stage, a high rate of mortality occurs (Fenner 1987; Whitmore 1996), mainly caused by density-dependent and density-independent factors. Among the former are natural enemies, *i.e.,* pathogenic fungi (Augspurger 1988), and herbivores (Janzen 1970; Clark and Clark 1984; Clark and Clark 1985). Among the later are water stress (Poorter and Hayashida-Oliver 2000), nutrient (Whitmore 1996), and light limitation (Malcolm et al. 1996), and mechanical damage due to falling branches and leaves (Clark and Clark 1989; Clark and Clark 1991; Scariot 2000).

Seedlings beneath closed canopies are limited mainly by their ability to fix C with very little light (Pearcy 1983; Peters 1989; Kobe et al. 1995; Walters and Reich 1996). Shade-tolerant tree seedlings typically have slow growth rates (Hubbell and Foster 1992; Walters et al. 1993; Reich et al. 1998), a trait that is characteristic of plants growing in resource-poor habitats (Grime 1977; Chapin 1980; Lambers and Poorter 1992).

Rates of mortality are much higher for light-demanding than for shade-tolerant seedlings (Still 1996). In the first case, most of the seedlings die a few weeks after germination, while the latter ones are able to survive for longer times, with reduced rates of both mortality and growth (Clark 1994; Mack et al. 1999). Such suppressed seedlings frequently persist for long periods of time with constant numbers of leaves, long leaf life spans, and heights below 50 cm, resulting in the development of a seedling bank (Meijer and Wood 1964; Harper, 1977; Still 1996).

Several authors have pointed out that seedling banks are limited in growth until a gap is created in the forest canopy to allow light to reach the forest floor (Sasaki and Mory 1981; Canham 1988; Uhl et al. 1988; De Steven 1994, but see Turner 1990). It is assumed that seedlings have evolved physiological, morphological and anatomical plasticity to successfully cope with changes in quantity and quality of light and variations in soil moisture and temperature, litter mineralization, and release of nutrients in ever-changing environments (Bongers et al. 1988).

Sarukhán (1976) pointed out that dominant species of tropical trees, especially those in mature forests, frequently tend to develop a conspicuous seedling bank on the forest floor. Seedling banks may be crucial for old-growth forests because they provide individuals that will eventually reach the canopy and may have a significant influence on the composition of forest communities (Swaine 1996, but see Lieberman 1996). For the understanding of demographic processes and growth of seedling banks, it is important to recognize the survival rates and risk probabilities for individuals in the transition from this stage to the next in the life-history of a species (De Steven 1994).

Manilkara zapota (L.) Royen (Sapotaceae), along with *Terminalia amazonia* (J.F. Gmel.) Exell (Combretaceae), *Brosimun alicastrum* Sw. (Moraceae), and *Aphananthe monoica* (Hemsl.) Leroy (Ulmaceae), are important components of the tropical and subtropical vegetation of Mexico (Pennington and Sarukhán 1998). *Manilkara zapota* frequently has high densities and it becomes the dominant species in the north-central region of Veracruz and the Yucatan Peninsula (Gómez-Pompa 1977). The shade-tolerant seedlings of *M. zapota* belonging to different cohorts exhibit high densities beneath closed forest canopies. Seed size ranges from 16-23 mm long, 8-16 mm wide, and 0.3 g wet mass. After germination, the cotyledons of the phanerocotylar-epigeal-foliaceous type (*sensu* Miquel 1987) are persistent, exposed, leaf-like, green structures that may have a photosynthetic function. A seedling of *M. zapota* is able to survive 8 mo without developing true leaves. In addition, as individual growth progresses, seedlings show significant variation in leaf size and shape. The first true leaves of established seedling are elliptical reaching 4-5 cm length and 1.5 cm width. Later, just before reaching 20-25 cm height, seedlings of *M. zapota* develop oblong leaves from 5 to 20 cm length and 2 to 7 cm width. Finally, the tallest seedlings produce also oblong leaves up to 32 cm length and 7 cm width. However, leaves of mature trees typically average 15 cm length (Pennington 1992). Based on these field observations, we postulate that mixed age seedlings of *M. zapota* are able to survive beneath the closed forest canopy by modifying leaf size and morphology and eventually are able to respond to small canopy openings. To test this hypothesis, we conducted a 2-yr long demographic evaluation of growth dynamics in a *M. zapota* seedling bank in a mature forest of central Veracruz, Mexico.

In this paper we report on the effects that the variation in leaf size, type of damage, seedling density, and growth on seedling survival time. The latter may be an important component of the population dynamics of the *M. zapota*.

Study site

This research was carried out in Santa Gertrudis, an area of protected flora and fauna of about 925 ha, in the municipality of Vega de Alatorre, State of Veracruz, Mexico (Diario Oficial de la Federación 1982). The dominant vegetation of the area is a Selva Mediana Subperennifolia (*sensu* Miranda and Hernández X. 1963). This area is located in central Veracruz on the coastal plain of the Gulf of Mexico between 19°49'37″ − 19°51'50″N and 96°32'37″−96°37'39″W, and from 400 to 850 m elevation on the northeastern slope of the Sierra de Chiconquiaco. This protected area is private property and has not been intensively exploited for nearly 100 yr. The vegetation of Santa Gertrudis is a mosaic of patches of subtropical rain forest or Selva Mediana Subperennifolia, affected mostly by natural disturbances, and to a lower extent by human management. In the area, there are 40 ha dedicated to cattle ranching and grazing, and c. 25 ha to coffee plantations. In wind-protected sites, however, some small patches less than 2 ha contain relictual remnants of *Quercus oleoides* Cham. and Schltdl. (Fagaceae) forest. Most of the soils in the site are derived from calcareous rock and some small portions from volcanic rock.

The climate of the area, inferred from the nearest meteorological station (Misantla) c. 25 km away, is subtropical and seasonal, with 2217 mm of annual rainfall and a mean annual temperature of 20.2 °C. The rainy season from June to November contributes 30% of total rainfall. In the dry season, December to April, c. 40% of the tree species lose their leaves (Gomez-Pompa 1977; Godínez-Ibarra and López-Mata 2002).

Methods

Seedling plots

We randomly selected eight 10-m^2 (5-m × 2-m) plots beneath the closed canopy of a mature forest stand co-dominated by *Brosimum alicastrum* and *Manilkara zapota*. Canopy density was estimated using a spherical crown densiometer (Lemmon 1956) which measures the relative amount of cover of the canopy. Canopy trees reach up to 35 m in height and more than 100 cm in stem diameter at breast height (DBH). Within each plot, all seedlings of *M. zapota* less than 35 cm tall were located, tagged, measured and their stage (healthy/damaged) determined. The seedling attributes measured were height (mm), type and number of leaves, length of largest leaf (LLL, mm), and type of damage due to herbivores, fungal pathogens, pupae, or physical damage from falling branches. Length of largest leaf was selected because the seedlings have leaves of different sizes along the stem. Smaller leaves are located in the stem base and largest in the apex, which indicates the progress in seedling development. Seedling attributes and damage, as well as the timing and likely causes of mortality, were evaluated 12 times over the 2-yr period and at 1.6-2.5-mo intervals. During the 6th census, newly-emerged seedlings were marked and monitored until the end of the study. Therefore, the exact ages of these seedlings were known.

Seedling survival

Because the exact times of seedling death (T) were unknown, seedling evaluations were conducted under a census interval schedule (Allison 1995). The survival function is defined as $S(t)=Pr\{T > 1\}$ = 1-F(t), where F(t) is a cumulative distribution function. This survival function gives the probability of survival of a seedling after time t. In addition, the risk function estimates the probability of a death occurring within a given interval of time (Allison 1995).

The seedling survival function was obtained with the method of life tables from grouped data in the LIFETEST procedure of SAS (SAS 1989). This procedure estimates survival and risk probabilities for data that provide only (a) the boundaries of the intervals; (b) the number of deaths within each interval, and (c) the number of censused cases in each interval. This procedure calculates survival and the corresponding risk curves. The individual seedlings showed important variations in height, leaf number, and length of largest leaf (LLL). Some seedlings displayed leaf-like cotyledons, others possessed both cotyledons and true leaves, and most had only true leaves. This means that the analysis evaluated seedlings belonging to different cohorts and phases of development. The effects of these attributes as well as the type of damage and density (individuals per 10-m^2) on seedling survival times were evaluated with the maximum likelihood parametric regression model in the LIFEREG procedure (SAS 1989). Damage by pupae was set as a dummy variable due to its null effect on seedling survival. The LIFEREG procedure fits parametric models to interval-census failure-time data. It also tests the form of the hazard function and allows an analysis of categorical variables with multiple values (Allison 1995).

To improve estimates of the regression coefficients which had smaller standard errors, a goodness of fit test was conducted to determine the distribution type of time of death. The observed distribution was compared with the Weibull, exponential, gamma, log-logistic and log-normal theoretical distributions. The coefficients of the quantitative variables (β_i), were transformed to $100(e^{\beta i} - 1)$, which, according to Allison (1995), provides the percent increment in the survival time for one unit increment in the variable. Values of the covariables incorporated in the analysis were those recorded at the beginning of the observations. The association of type of damage and seedling mortality was tested.

Seedling growth

Seedling growth rates were determined from the height measurements at each census by calculating the absolute (AGR) and relative growth rates (RGR):

$$AGR = (H_t - H_o)/t; \quad RGR = 100(\ln H_t - \ln H_o)/t,$$

where H_o is the initial height and H_t is the height after time t (Hunt 1990). The units of RGR (cm cm^{-1} yr^{-1}) × 10^2 are expressed as percent yr^{-1} or more economically as % yr^{-1}.

Correlation analysis was performed to evaluate the relationship between LLL and seedling AGR or RGR. Seedlings were classified in four classes, I: ≤ 10 cm; II: 10.1-15 cm; III: 15.1-20 cm, and IV: $>$ 20 cm. Following Still (1996) growth rates were classified as: (i) negative growth if RGR was < 0 % yr^{-1}; (ii) a latent stage occurred when RGR was 0 − 4 % yr^{-1}; (iii) slow growth occurred when RGR was 4.1 − 20 % yr^{-1}; and (iv) fast growth occurred with RGR $>$ 20 % yr^{-1}. These criteria were obtained from frequency distribution of RGR. To estimate the magnitude of variation in leaf size, the LLL of each seedling at the beginning was compared with its LLL at the end of the study. Number of leaves per seedling were recorded in a similar way.

Results

The seedling bank demography of *M. zapota* was based on 631 individuals < 35 cm tall (regardless of age) distributed among the eight plots. Relative canopy coverage over these plots were relatively homogeneous ranging from 89.4 to 91.8% and most irradiation entering the understorey was in form of lightflecks. There were no significant differences in canopy cover between plots (Kruskal-Wallis test, $\chi^2 = 10.36$; df = 7; $P = 0.07$). Mean seedling density (± SD) was 78 ± 40.6 seedlings per plot, ranging from 0.9 to 12 seedlings m^{-2} among plots. Differences in seedling height, leaf number and leaf size were important since this indicated that seedlings belonged to different cohorts. The number of leaves per seedling was the variable with the greatest coefficient of variation (CV=43%, mean = 5.3 ± 2.11), some individual seedlings displaying from between 0 to 12 leaves. Length of largest leaf varied over time from 3 to 26 cm (mean = 6.8 ± 2.94, CV = 41%) in the first census, and 3 to 30 cm in the twelfth census (mean = 8.1 ± 3.7, CV = 45%). Differences in seedling height, although smaller, were also important (mean = 13.6 ± 2.83; CV = 27%).

Out of the 631 seedlings, only 85 (13.5%) had cotyledons at the beginning of the study. The cotyledons of *M. zapota*, however, are very persistent; on average, a seedling is able to hold them for up to 8 mo before developing true leaves. In November 1999, 40 new seedlings belonging to a new cohort were recorded in the plots; they had small cotyledons and an average height of 7.6 ± 1.2 cm.

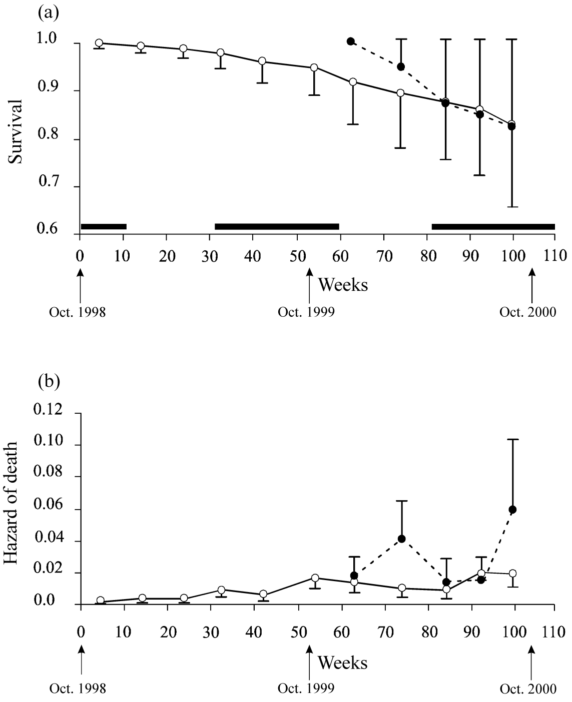

Figure 1. Changes in (a) survivorship and (b) mortality hazard for seedlings (+ or − SE) of *Manilkara zapota* at Santa Gertrudis, Mexico. Uneven-age seedlings (open circles, solid line) and 1999-single cohort (closed circles, dashed line). Uneven-age seedlings were monitored during two consecutive years (104 weeks) at 2 mo intervals, and the 1999 cohort was monitored for 11 mo at same periodicity. Solid bars indicate rainy seasons.

Seedling survival

After 2 yr of monitoring, *M. zapota* seedlings exhibited a very high rate of survivorship (0.82 ± 0.17; mean ± SE), one of the highest for a tropical tree species (Figure 1a). In each of the 12 censuses, the hazard mortality rate was less than 0.025. Seedling hazard mortality was irregular and it did not show any relationship with the seasonality of this site (Figure 1b). Seedling survival after 12 mo of monitoring for the November 1999 cohort was also very high (0.82 ± 0.06; Figure 1a). In this case, although hazard mortality increased as time progressed, the maximum was always less than 0.06. Hazard mortality was

Table 1. Maximum likelihood regression coefficients (β_i ± SE (standard error)) for seedling survivorship times of *Manilkara zapota*. Quantitative and qualitative covariates are included. The log-logistic model selected is based on the lower magnitude of the log-likelihood value (−191.6).

Variables	d.f.	Regression coefficients (β ± SE)	Chi- squared	P
Intercept		2.00 ± 0.27	54.11	0.0001
Seedling height	1	-6.0×10^{-3} ± 0.017	0.12	0.7282
Leaves number	1	9.9×10^{-2} ± 0.023	18.06	0.0001
Cotyledonary leaves	1	− 0.11 ± 0.099	1.37	0.2415
Length of largest leaf	1	3.4×10^{-2} ± 0.018	3.40	0.0500
Seedlings density	1	8.4×10^{-3} ± 0.013	0.41	0.5208
Type of damage	4		4.94	0.2935
Healthy	1	−0.205 ± 0.18	1.26	0.2604
Fungal pathogens	1	−0.09 ± 0.14	0.41	0.5208
Herbivores	1	−0.08 ± 0.19	0.17	0.6742
Physical	1	−0.55 ± 0.27	4.03	0.0546
Pupae	0	0	–	–

higher during both the dry and the rainy seasons of the year, from February to April, and from August to October, respectively (Figure 1b).

The regression analysis indicated that variables with significant effects over all seedling survival times were leaf number and LLL (Table 1). By contrast, non-significant regression coefficients were detected for seedling density, height, and cotyledon number (Table 1). The transformation $100(e^{\beta i} - 1)$ predicted that a 1-cm increment in LLL would increase the expected survival time by 3.5%; and in the case of leaf number (LN) the increment would be 10.4%.

Seedling growth

The high survival rates of seedlings contrasted with their low growth rates. The average AGR (± SD) was only 1.5 ± 0.95 cm yr^{-1}, while the RGR was 12.58 ± 7.64 % yr^{-1}. Although some seedlings had reduced sizes, mainly because of herbivore effects (RGR from −15.3 to −5 % yr^{-1}, n = 5), most of them displayed a positive RGR between 5 and 15 % yr^{-1}. In addition, a positive correlation existed between seedling height and LLL (r = 0.80, n = 555, $P \leq 0.01$); that is, seedlings with larger leaves were also taller. However, although there was a significant correlation between AGR and LLL (r = 0.31, n = 317, $P < 0.0001$), there was no correlation between RGR and LLL (r = − 0.04, n = 317, $P = 0.485$).

The RGR variability displayed in each of the seedling classes indicated that individuals grew at different rates. The analysis of growth rate, showed that nearly 20% of individuals in classes I, II and III were in a stage of latent growth (RGR between 0 and 4 % yr^{-1}), and they even exhibited negative growth (RGR < 0 % yr^{-1}). Nearly 60% of seedlings in classes I, II, and III had slow growth rates with a RGR between 4 and 20 % yr^{-1}, and the remaining 20% a fast growth rate with a RGR > 20 % yr^{-1}. Finally, in class IV, 75% of the seedlings had slow growth rates and the remaining 25% fast rates (Figure 2).

By contrast, the November 1999 seedling cohort showed an average RGR of 18.9 ± 2.06 % yr^{-1} and an average AIH of 1.9 ± 2 cm yr^{-1}, both of which were higher than those for the mixed-age seedlings already established. The analysis of their growth showed that nearly 55% of them grew fast, 30% grew slowly, and the remaining 15% exhibited latent or negative growth (Figure 2).

Growth and leaf turnover

After 2 yr most of the uneven aged seedlings did not change their leaves sizes. In that time, the mean (± SD) increment of LLL was 0.84 ± 2.24 cm. However, there were exceptional increments and decrements of up to 8.8 and 9.8 cm, respectively. The maximum increments were recorded for seedlings with leaves between 15-20 cm in length at the beginning of the observations. Average leaf increments in seedlings, whose leaves were shorter or longer than 15-20 cm, were nearly zero.

In June 1999, 70% of the seedlings displayed new leaves, while 12 mo later newly displayed leaves occurred in only 16% of them. Comparing the number of leaves per seedling at the beginning and at the end of monitoring revealed that the mean (± SD) change

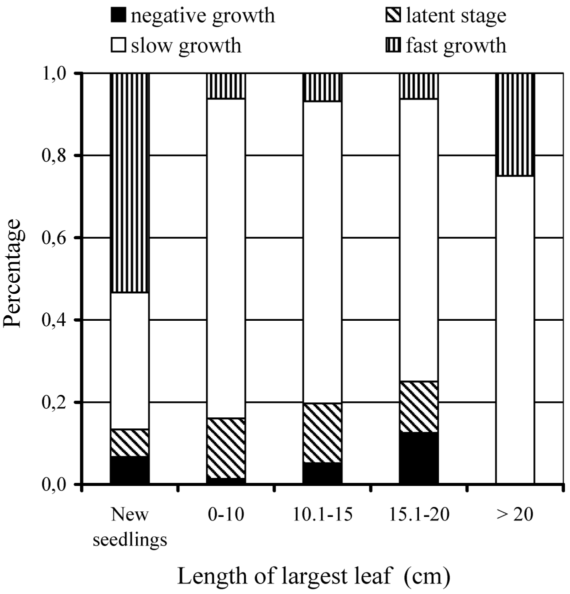

Figure 2. Frequency distribution of seedlings of *Manilkara zapota* at Santa Gertrudis, Mexico, in different relative growth rates (RGR) classes as a function of the length of largest leaf. Negative growth for seedlings with RGR < 0 % yr^{-1}; latent growth for seedlings with RGR between 0 and 4 % yr^{-1}; slow growth for seedlings with RGR between 4 and 20 % yr^{-1}; and fast growth seedlings with RGR > 20 % yr^{-1}.

was only 0.2 ± 2.43 leaves per seedling. In spite of this overall small positive balance of leaf set and fall, a large proportion of seedlings (66%) showed gains and losses of up to six leaves. On the other hand, the November 1999 cohort developed 1.06 ± 0.64 true leaves, and most of these seedlings held at least one cotyledon after 1 yr (mean ± SD; 1.6 ± 0.3 cotyledons).

Discussion

The high probability of seedling survival and low hazard mortality rates shown by both the mixed-age and the 1999 cohorts contrasts with the numerous reports that mortality in the seedling stage of tropical trees is excessively high (Sarukhán 1980; Clark 1994; De Steven 1994; Alvarez-Buylla et al. 1996; Lieberman 1996). The $> 80\%$ probability of survival for the single age cohort and mixed-age *M. zapota* seedlings contrasts strongly, for example, with the average life expectancy of 2.5 mo found by Li et al. (1996) for several species in Costa Rica.

The highly persistent phanerocotylar epigeal foliaceous cotyledons constitute an important characteristic for seedlings of *M. zapota*. An average seedling holds its cotyledons for up to 8 mo, without developing true leaves; during this time no other manifestation of growth occurs except for stem lengthening. The remarkable changes in seedling morphology that occur up to the development of true leaves suggest that cotyledons may function as photosynthetic structures providing the necessary organic compounds for seedling maintenance and further growth, including production of true leaves. Nevertheless, it would be necessary to clarify the role of seed energy reserves, as well as the potential for mycorrhiza associations in providing part of the seedling's requirements. Seed energy primarily stored in the form of proteins, lipids, or carbohydrates (either starches or sugars) may be crucial very early in the life history of *M. zapota*. For instance, seed energy may be critical immediately after germination, in determining both root and stem growth just before it becomes a self-sustaining seedling. Average weight of *M. zapota* seeds is 0.3 g and, according to Foster and Janson (1985) they are able to germinate beneath closed canopies and or in small gaps (< 50 m^2).

On the other hand, it is apparent that the seedling survival rate improves with age and size. Turner (1990) found that increments in height diminish the probabilities of seedling mortality up to 10-fold in *Shorea* species of Malaysia. However, the established *M. zapota* seedlings with true leaves showed a probability of survival that correlated positively with the length of largest leaf (LLL). The impact of LLL on seedling survival is so important that during 2 yr of observations, only individuals with LLL less than 10 cm died. The process of increasing leaf length could be more important than seedling height growth, although non-significant changes were detected in both cases during the 2 yr of monitoring.

Both AGR and RGR indicate that even seedlings with large leaves had limited growth. These individuals displayed short internodes, suggesting reduced vertical and horizontal lengthening. Seedlings are able to produce large leaves in spite of their limited growth beneath closed canopies. However, observations outside of the monitored plots, indicated that seedlings with similar LLL, but growing in more open canopies, could display larger internodes and taller stems. This idea was explored by King (1994) who found that height growth rate was positively correlated with internode length in 10 tropical sapling species from Panama.

The development of large leaves in seedlings beneath closed canopies is a slow but critical process for individual survival, often requiring several years to complete. Similar processes of large leaf formation have been described for juvenile stages of pioneer species from Malaysia (Whitmore 1984), as well as for shade-tolerant species in semi-warm rain forests of southern Japan (Kohyama 1987), and in tropical rain forests of Indonesia (Kohyama 1991). In all these cases, authors postulate the advantages of large increments in the photosynthetic leaf surface for individual growth.

Seedlings of *M. zapota* have been found to display low values of specific leaf area, regardless of leaf size (authors' unpublished data). Seedlings with largest leaves showed the lowest SLA values (11.6 m^2kg^{-1}), whilst those with smallest leaves showed the highest SLA values (18.2 m^2kg^{-1}). According to Wilson et al. (1999), specific leaf area indicates the degree to which individuals can exploit environments with variant levels of resources. High values of specific leaf area are associated with highly productive leaves, highly vulnerable to herbivores, and short life-span (e.g., pioneer species), reasons for which their performance is better in resource-rich environments. By contrast, leaves with low specific leaf area grow better in resource-poor environments where retention of previously captured resources is a priority (e.g., shade-tolerant species). This idea is confirmed by comparing the values of specific leaf area for *M. zapota*, with those given by Poorter and de Jong (1999) for 15 environments with different productivities. Typically, in environments with low productivity, SLA tends to vary between 6.5 and 15 m^2kg^{-1} whilst in those with high productivity range from 20 to 30 m^2kg^{-1} (Poorter and de Jong 1999).

From this standpoint, the efficiency of assimilation is closely related with leaf shape and size, as well as with the energy allocation to the support tissues (Givnish 1986). It is possible that combined effects of increments in photosynthetic leaf surface and low growth rates allow the storage of resources in stem and root. In that way seedlings would be able to tolerate limited light conditions and produce new leaves as needed, especially if they were damaged by natural enemies or physical agents. In addition, it can be expected that production of progressively longer leaves also requires allocating previously accumulated resources. A seedling spends a great part of its life accumulating energy for further allocation to larger leaves and later to increasing height. High costs of construction of largest leaves would explain their absence in the very first years of seedling life. Although number of leaves had a significant effect on seedling survival time, seedlings that had completely lost their leaves were able to survive for 4 − 6 mo before starting to decline or to produce new leaves. Starch stored in the stem tissues and roots probably plays a role in such circumstances. Preliminary observations of seedling stem anatomy showed a large quantity of starch granules stored in the cortical tissue and xylem parenchyma.

The analysis of damage effects on the survival probabilities showed that herbivores and mechanical damage did not increase mortality rates. In fact, there was a higher proportion of herbivore-damaged leaves on the surviving seedlings than on dead individuals. Leaf damage was rarely severe, and in most cases, leaf tissue was not entirely consumed. Seedling latex is present from early stages, and it is probable that this limits consumption of whole leaves (Angulo-Sandoval and Aide 2000). It was therefore difficult to establish the real causes of seedling mortality because of the non-significant effects of the evaluated types of damage and the high rates of seedling survivorship.

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