

The effect of light on the survival and growth of *Dipteryx micrantha* seedlings and saplings in an Amazonian rain forest

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Abstract

The effect of light on the survival and growth of seedlings and sapling of *Dipteryx micrantha* (Leguminosae) growing in mature, late successional and young successional floodplain forests was studied at Cocha Cashu, Madre de Dios, Peru during two years. Light was represented by % openness, a measure obtained through the analysis of hemispherical photographs. The median light levels received by individuals in mature and young successional forest were 1.9-2.3% and 1.9-3.5%, respectively. In general, the mature and late successional forests had a higher proportion of seedlings (<10 mm stem diameter) and a smaller proportion of saplings (10 mm-30 mm diameter) than the young successional forest. Initial plant size (diameter, height or number of leaves) was a better predictor of survival than the light levels experienced by the plant, but variation occurred between observation years. Growth in both diameter and height was significantly related to light levels especially in mature forest, but change in the number of leaves was mainly not related with light. Initial number of leaves was a good predictor of growth in diameter and height in both mature and young successional forest. Multiple regression analyses showed that the relative influence of light, initial diameter and initial number of leaves on seedling growth varied with forest type and observation year. In most of the cases where two independent variables remained significant in the regression model, one of them was light and the other was number of leaves.

Introduction

The large species pool of tropical trees makes it difficult to predict which tree species will regenerate and reach the canopy at a given site. Indeed, it has been argued that the species composition of tropical forests is fundamentally unpredictable, as the species come and go in a random walk (Hubbell 2001). However, there is also evidence that different plant species tend to occur in different microhabitats that are related to topography, soil moisture or light conditions (Clark et al. 1998, Harms et al. 2001, Svenning 2001, Valencia et al. 2004). These requirements might change along the life of a plant affecting the survival and growth accordingly.

Information on factors that can affect survival and growth of saplings and seedlings helps to understand the spatial distribution of adult trees. Biotic factors such as herbivory (Sork 1987, Shupp 1988, Molofsky and Fisher 1993) and pathogens (Augsburger 1984) have been found to account for 10-75% of seedling mortality in the species studied, but not to be important for saplings. Mechanical damage from falling trees or branches can produce up to 11-20% annual mortality in seedlings and 2% in saplings, and in addition slow down growth of survivors by damaging their apical meristem (Clark and Clark 1991). Intrinsic factors, such as seed mass, are also important because seed size is related to seedling size, and larger seedlings have higher initial survival (Boot 1995, Mack 1998, Harms and Dalling 1997, Dalling and Harms 1999, Dalling and Hubbell 2002) and growth rates (Osunkoya et al. 1993, Kobe 1999). Number of leaves or leaf area have also been found to be related to survival, especially in the youngest stages, both for *Dipteryx panamensis* (Clark and Clark 1987) and other species (Sterk et al. 1999, Poorter and Hayashida-Oliver 2000).

The importance of soil moisture for survival is indicated by a positive relationship between soil moisture and increase in leaf area ratio (leaf area/plant mass) (Hall et al. 2003). Tree seedlings experience increased mortality in years with unusually severe drought, which accentuates the importance of variation in soil moisture for survival (Leigh et al. 1990, Brown and Whitmore 1992, Veenendaal et al. 1995, Cao 2000, Delissio and Primack 2003). Seedlings of shade-tolerant species that are likely to survive the dry season have greater root:shoot mass when entering the dry season

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than those of less tolerant species, suggesting that seedlings entering the dry season with well developed roots tolerate drought stress better (Kitajima 1996). Soil moisture availability is also important for growth (Bonel and Guehl 2001, Hall et al. 2003).

Nutrient availability and the importance of different nutrients may vary. For shade-tolerant species, cation (K, Mg, Ca) limitation may be more significant than P limitation (Burslem et al. 1995, Fetcher et al 1996, Hall et al. 2003). Apparently, as long as seedlings stay in the shade, soil minerals do not limit growth for a very long time because nutrient reserves in seeds suffice to support early seedling growth (Kitajima 1996). In general, it seems that nitrogen availability in tropical soils limits seedling growth less often than phosphorus availability (Burslem et al. 1995)

Together with the above mentioned factors, light may be one of the most decisive in controlling growth and survival of young trees (Welden 1991, Clark et al. 1993, Molofsky and Fisher 1993, Osunkoya et al 1994, Poorter 1999, Kobe 1999, Dalling et al 1999). Characterization of these generally recognized regeneration niches for tropical trees is not so clear-cut. A major distinction is generally made between light-demanding pioneer species that reproduce in forest clearings or other open areas, and shade-tolerant species that are able to germinate and survive in the shade (Hartshorn 1978, Garwood 1983, Augspurger 1984, Brokaw 1985, Hubbell and Foster 1987, Denslow 1987, Swaine and Whitmore 1988). However, the distinction is not clear-cut: saplings of gap species can survive and grow in the forest understory (Clark and Clark 1984, Clark and Clark 1987), and shade-tolerant species can utilize the increased light levels provided by gaps to grow into the canopy (Denslow 1987). Patterns for both pioneer and shade-tolerant species suggest a trade-off between low-light survival and high-light growth rate (Welden et al 1991, Kitajima 1994, Pacala et al 1996, Kobe 1999, Dalling and Hubbell 2002). Demographically, this might explain why shade-tolerant species are relative more abundant as seedlings and saplings compared to light-demanding species (Wright et al 2003).

The their light requirement *Dipteryx panamensis*, a congener species of *D. micrantha*, which has been well studied in Central America, has been found to germinate and establish in the understory in the absence of gaps, but to require gaps to reach the canopy (Clark and Clark 1992). Shade-tolerant species often grow slowly, so recruitment into the canopy can take a very long time (Canham 1989, Hubbell 1998, Connell and Green 2000, Delissio et al. 2002). Indeed, the median age of *Dipteryx panamensis* saplings at 4 cm dbh (diameter at breast height) was estimated to be 72 years (Clark and Clark 1992, 2001). The effects of light on the survival and growth of seedlings and saplings of *Dipteryx panamensis* are relatively well understood (De Steven and Putz 1984, Clark and Clark 1987, Fetcher et al. 1987, Oberbauer et al. 1988, De Steven 1988, Clark and Clark 1992, Castro et al. 1995, Sterck et al. 1999, Clark and Clark 2001, Montgomery and Chazdon 2002). Survival and growth have been found to be higher in gaps and forest clearing than under an intact canopy (De Steven 1988). When seedlings were experimentally transplanted to secondary forest, highest growth rates were found at intermediate light levels (3-7% diffuse transmittance, Montgomery and Chazdon 2002).

Much less is known about the factors that affect the survival and growth of *Dipteryx micrantha*, which is a common emergent tree at Cocha Cashu biological station in the Manu National Park in southern Peruvian Amazonia (Janson and Emmons 1990). Cintra and Horna (1997) found that 35% of seedlings transplanted to gaps survived for one year, and that survival was higher in small gaps than large gaps. Later, Cintra and Terborgh (2000) found that *Dipteryx* seedling survival was significantly affected by the number of other woody plants within a 20-cm radius. Incident light and growth rate also had a significant positive effect on *Dipteryx* seedling survival. However, the faster-growing seedlings in more illuminated microsites were more vulnerable to browsing by vertebrate herbivores.

Due to river dynamics, the floodplain forests along the Manu river are intermittently disturbed, after which forest succession proceeds in a predictable manner through different successional stages to mature forest (Salo et al. 1986, Terborgh and Petren 1991, Terborgh 1993). In general, light levels in successional forests are higher than those in mature forest, where they are often only 2% of full sunlight (Chazdon and Fetcher 1984, Chazdon 1988, Canham 1989, Smith et al 1992, Clark et al 1993, Osunkoya et al. 1993, Osunkoya et al. 1994, Zagt 1997, Nicontra et al. 1999, Emmons and Dubois 2003). Such differences in light characteristics among forest types may affect the probabilities of survival and growth of tree seedlings and saplings in them.

The purpose of the present study is to clarify the importance of light availability on the survival and growth of *Dipteryx micrantha* seedlings and saplings in natural populations in floodplain forests of different ages (young successional, late successional and mature) during two years. The focus was to assess the range of spatial variation in light (different forest types) and also the possible interannual variation in light.

Material and Methods

Study site

Cocha Cashu Biological Station in Madre de Dios, Peru, is located near the climatic limit between Tropical and Subtropical Moist Forest. The site has a mean annual temperature of 23-24 °C and mean annual precipitation of 2300 mm (1991-2001). Normally, rainfall is concentrated in the rainy season (November-May), with around 300-600 mm falling in the dry season, but considerable variation in rainfall can occur among years. Years with an ENSO (El Niño) event are characterized by heavy rains and strong flooding in the rainy season, whereas years with “La Niña” event are associated with a pronounced dry season. The present study was carried out between September 1998 and November 2000, with “La Niña” dominating in 1998-1999. The dry seasons (June-October) of years 1998 and 1999 had two months of drought (as interpreted from Walter-type climate diagrams) while the year 2000 had only one month of drought. Climatic data from Cocha Cashu (accessible at www.duke.edu/~manu) show that annual precipitation for the period October-September was 2570 mm in 1998-1999 and 2230 mm in 1999-2000.

Survival and growth of *Dipteryx micrantha* seedlings and saplings were studied in three kinds of forest in the vicinity of Cocha Cashu: young successional, late successional and mature forest. All forest types are located in the floodplain of the Manu river, and may be inundated during the rainy season. The depth of inundation varies locally with elevation, and temporally with the intensity of rains in the catchment area of the river. For an extensive description of the site, see Gentry and Terborgh (1990) and Foster (1990).

The young successional forest studied was located one meander curve upriver from Cocha Cashu across the river. Trees of the genus *Cecropia* were very common, but other tree species were present as well. The late successional forest was located in the inside curve of Cocha Cashu lake. The terrain had a levee-depression topography where water accumulated in the depressions. The forest was characterized by a high abundance of small palms and patches of dense *Heliconia* growth. The mature forest was situated in the immediate surroundings of the Cocha Cashu station, and was among the largest patches of mature floodplain forest along the Manu River. *Dipteryx micrantha* was so abundant that the forest has been called *Dipteryx-Quararibea* forest (Janson and Emmons 1990). The mature forest was taller than the successional forests, and its canopy was more closed.

Light levels on the forest floor depend on the structure and density of the forest canopy. Both the stature of the forest and the density of the canopy increase as succession proceeds. Terborgh and Petren (1991) provide a detailed description of the development of the forest structure during succession. Leaf area index (LAI) seems to increase rapidly in young successional forest, but to stabilize in later successional stages (Emmons and Dubois 2003), which suggests that light intensity in young successional forests is higher than in the later stages, but that there may not be much difference between late successional and mature forest. In mature forest, the highest light levels occur in tree fall gaps and in areas close to other open areas such as water bodies or swamps.

Data collection

To analyze the survival and growth of *Dipteryx micrantha*, the study area was searched for naturally occurring seedlings and saplings. In late successional and mature forest, the Cocha Cashu trail system provided invaluable help in accessing the forest. Because the trail system did not extend to young successional forest, temporary trails had to be established there for the purposes of

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the present study, and not as much area could be covered. An area of young successional forest that had enough seedlings and saplings to make a sufficient sample was selected for the study. In all cases, the search was extended to 3 m on each side of the trail.

In mature forest, an area of about 16.3 ha was surveyed and a total of 668 seedlings and saplings were found. In the 10.1 ha of late successional forest, 129 seedlings and saplings were found, and in the 0.5 ha of young successional forest, 167 seedlings and saplings were found. The seedlings monitored in the years 1998, 1999 and 2000 will hereafter be called the extended sample. New seedlings were added to the data in the second year to compensate for reduced sample size due to mortality. For a sub-sample of seedlings, selected to cover all size classes, light availability was quantified with hemispherical photographs (method explained below).

The first census was made in September–November 1998. All encountered seedlings were marked with a flexible aluminum tag and re-measured after 12 and 24 months (± 2 weeks). The survey was systematically done so to consider all the seedlings occurring in the hectares covered by the second year. Seedlings considered individuals that are clearly not just germinated the previous months. Each seedling and sapling was measured for diameter (1 cm above the ground), height (from the ground to the petiole base of the youngest leaf), and number of leaves present. Diameter was measured with plastic calipers to the nearest 0.1 mm, and height was measured with a measuring tape to the nearest 1 mm.

Characteristics of the microenvironment were recorded for each seedling and sapling. The distance to the nearest forest edge along water channels, lakes, rivers or swamps, was recorded as being either shorter or larger than 10 m. Although this is an arbitrary distinction between habitats that were not measured in their soil moisture or illumination characteristics, we assumed based in other works that characterize similar habitats (Kapos et al. 1997,) that differences between far and close this habitat might occur.

Analyses on the influence of light on growth and survival would be confounded if plants that had been mechanically damaged were included. Therefore, each seedling and sapling was examined for marks of external damage. The following categories were used: a) plant alive and apical meristem undamaged; b) plant alive but suffering from physical damage (apex dry, broken or covered by a fallen tree trunk), c) plant killed by a fallen tree trunk, and d) plant killed by other causes. Sometimes a plant was not found during re-measurement even after extensive searching. If its exact location could be inferred from the presence of the aluminum tag or other landmarks, it was assumed dead and assigned to category c or d, as appropriate. Plants that were alive but physically damaged (category b) were excluded from the analyses where growth was related to light, and those that had been killed by falling debris (category c) were excluded from analyses where survival was related to light. Twelve seedlings had to be excluded from all analyses because their exact locations could not be found, and another twelve because they had been accidentally cut by a machete.

The young successional forest had clearly received river sediments during the 1999 floods, which introduced an error into the height measurements. From 1998 to 1999, 3% of the seedlings and saplings that appeared healthy (no signs of physical damage) were reduced in height more than 2 cm, and from 1999 to 2000, 8% did. These plants were excluded from the analyses where growth in height was related to light, as it is unlikely that such reduction in height could occur without the plants having suffered from either unrecorded mechanical damage or sedimentation.

The light conditions experienced by the sub-sample of the seedlings and saplings (208 individuals selected to represent the different diameter size classes) were quantified using hemispherical photographs. Photographs were taken at the height of the seedling apex in November 1998, November 1999 and November 2000 in mature and young successional forest. A Minolta camera with a fish eye lens at 180° was used, and the photos were taken on black and white Kodak Tri X Pan 400 ASA film. Negatives were scanned at 256-level gray scale. The digital images were converted to positives and thresholded before analysis so that the gray of leaves was converted to black and the light gray or white of the sky to white. Thresholding was done by measuring three times the same image and getting the mean of that measurements. The program Whinphot (Hans ter Steege, Utrecht University) was used to compute % openness, % openness from zenith to 45°, and Indirect Site Factor. Because these three measurements were highly correlated and gave essentially

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identical results, only the results obtained with % openness are reported. The number of photos taken declined from one year to the next due to seedling mortality.

Data analysis

Several studies have shown that survival and competitive ability are strongly correlated with plant size (Veneklaas and Poorter 1998). To avoid confounding effects of initial plant size, and to try to clarify whether the effect of light varies in seedlings and saplings of different sizes, the *Dipteryx* plants were divided into four diameter classes: 1-4.9 mm, 5-9.9 mm, 10-19.9 mm and 20-30 mm. The first two size classes are considered seedlings and the last two saplings. The size classes were usually analyzed separately. Very few seedlings of the smallest size class were found in young successional forest, and very few saplings of the largest size class were found in late successional and mature forest, so these were excluded from some of the analyses.

To see if light levels changed among years, light levels received by each *Dipteryx* size class in each forest type were compared. In mature and young successional forest, light measurements were available for three years, so a Kruskal-Wallis test was run. In late successional forest, light measurements existed for two years, so a Mann-Whitney U test was used.

Survival

Logistic regression was performed to analyze the influence of light on survival. As seedling size may influence survival as well, but the sample size was not sufficient to analyze the four seedling size classes separately, additional logistic regressions were performed using the three measures of seedling size (diameter, height and number of leaves) as explanatory factors. All these analyses were done for young successional and mature forests separately using the sub-sample of seedlings for which light measurements were available. To evaluate to what extent seedling size and light conditions co-varied, Pearson's correlation was calculated between them.

Besides, the importance of the number of leaves for survival for each seedling size class in each forest type was assessed for the extensive sample with a Mann-Whitney U test. The extensive sample was also used to compare the survival of seedlings that were close to vs. far from forest edge (in mature forest only) with the chi-square test.

Growth

Growth was measured as the change in plant size (with diameter, height, and number of leaves used as alternative measures) between two observation events (1998-1999, 1999-2000 or 1998-2000). Comparisons of growth between years were done with a Mann-Whitney U test. Plants that bore signs of mechanical damage and those that were suspected of mechanical damage (height reduction >2 cm) were excluded from the analyses involving growth in height. The percentage of seedlings with meristem damage, a factor that reduces measurable growth, was calculated.

The effect of light on growth (in diameter, height and number of leaves) for the whole study period (1998-2000) and each year separately (1998-1999 and 1999-2000) was analyzed with a linear regression. The effect of initial size was analyzed in the same way with linear regression, and for the second observation year, a linear regression analysis was also carried out to test whether growth in 1999-2000 was affected by the previous year's growth. The residuals of this regression were then regressed on light levels in the second year to analyze if the differences in growth between the two years could be explained by light conditions.

Linear regression was also used to test whether a change in light levels was reflected in a change in growth. Average light level for each one-year interval (1998-1999 and 1999-2000) was computed as the arithmetic mean of the measurements taken in the beginning and in the end of the time interval, and these values were used to calculate the change in light level from the first to the second year. Similarly, growth for each year was calculated from the size measurements in the beginning and the end, and the difference between these was used as a measure of change in growth.

The relative effects of light, initial diameter and initial number of leaves on growth were analyzed with multiple linear regression with backward elimination. The backward elimination

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procedure enters all of the variables into the model in a single step, and then removes one at a time until all variables that remain in the model are statistically significant at the $P < 0.05$ level.

For the extended sample, Mann-Whitney U tests were used to compare the growth of seedlings close to and far from the forest edge.

Results

Size of seedlings

The mature and late successional forests differed from young successional forest in the relative abundances of *Dipteryx* seedlings and saplings of different sizes (Table 1). The proportion of individuals larger than 10 mm in diameter was less than 20% in mature and late successional forest, but more than 60% in young successional forest. Distribution of size classes was different between young successional and either mature or late successional (Chi-square test $P < 0.001$) but was similar between mature and late successional ($P = 0.66$).

Light characteristics

The proportion of seedlings that received light levels higher than 3% differed among years and forest types. In mature forest, 9-21% of the seedlings experienced mean light levels of more than 3% openness, whereas in young successional forest, 13-67% of the seedlings did (Fig. 1a). Median light levels for all seedlings in mature forest were 2.28% in 1998, 1.89% in 1999 and 2.15% in 2000. In young successional forest, they were 2.58% in 1998, 1.92% in 1999, and 3.5% in 2000. These include measures of light for all seedlings (alive and dead) in each year.

Mean light levels received by seedlings/saplings of different sizes in each forest type were in general low and always less than 4% openness, except for the larger diameter classes in young successional forest (Fig. 1b). Light levels for each size class also varied among years: in 1999, lower mean light levels were received by plants > 5 mm diameter in mature and young successional forest (Kruskal-Wallis test, $P < 0.01$), and by plants < 5 mm diameter in late successional forest (Mann-Whitney U test, $P < 0.01$).

Change in % openness received by seedlings in mature forest from one year to the next showed 74 and 35% of the them have had a reduction in it, while only 0% and 1% of seedlings in mature forest have had an increase in % openness of more than 4% from 1998 to 1999 and from 1999 to 2000 respectively (table M). No increase in light in more than 2% for any seedling in late successional forest from 1999-2000 occurred. In young successional forest only 1% and 3% have had an increase in 4% openness from 1998 to 1999 and 1999 to 2000 respectively. This indicates that a very small portion of the seedling population of this study has the opportunity to get an increase of light of more than 4% from one year to the next. Sample size for this analysis includes all measurement of light for two consecutive years, included those of seedling that might have died the second year or were excluded because broken.

In mature forest, there was no correlation between the light levels experienced by *Dipteryx* seedlings and their diameter or height in either 1998 or 1999, but there was a positive correlation between the number of leaves and light levels in both years. In young successional forest, the situation was different: number of leaves was not correlated with light levels in either year, but both diameter and height were correlated with light levels in 1998 (Table 2).

Survival

In the sub-sample with light measurements, *Dipteryx* mortality was clearly lower in young successional forest than in mature forest and late successional forest (Table 3). G-test results of the mortality of seedlings between years showed that there was no significant difference between

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forests in mortality for most of the diameter classes and years, except for the 1-4.9, 5-9.9 and 10-19.9 mm diameter classes from 1999 to 2000, where more seedlings than expected died in late successional forest ($P < 0.05$, 0.05 and 0.0001 , respectively). No significant differences were found in seedling mortality within size classes between years 1998-1999 and 1999-2000, except that in mature forest, mortality of the 1-4.9 mm diameter class seedlings was more than expected in 1998-1999 ($P < 0.05$).

Physical damage by trunks falling over the seedlings or saplings was observed to cause mortality in 3% or less of the individuals in all forest types. Survival was higher for large plants than for smaller plants in all three forest types (Fig. 2).

In general, plant size was a better predictor of survival than light conditions. Logistic regression of survival on light was statistically significant in 1998-1999 but not in 1999-2000 in young successional forest, but not significant in either year in mature forest (Table 4). This can be compared with logistic regressions of survival on initial plant diameter and initial plant height, which were statistically significant in both observation years in mature forest, and also the logistic regression of survival on initial number of leaves was significant in 1998-1999. In young successional forest, logistic regressions of survival on initial plant diameter and initial plant height were statistically significant in 1998-1999, but not in 1999-2000. Initial number of leaves did not explain survival in young successional forest in either year.

When analyzing the data on the extended sample for each of the four plant size classes separately, number of leaves in seedlings (either 1-4.9 mm or 5-9.9 mm diameter) that survived was significantly higher than number of leaves in seedlings that died in all forest types during 1998-1999 ($n \pm SD = 3.5 \pm 1.7$ vs. 2.8 ± 1.4 , $P < 0.01$ Mann Whitney U test.; 4.5 ± 1.8 vs. 2.9 ± 1.7 , $P < 0.05$ and 3.4 ± 1.4 vs. 2.4 ± 2 , $P < 0.05$) but not during 1999-2000. Being close to a forest edge was advantageous for survival in mature forest in 1998-1999 (Chi-square test, $P = 0.029$) but not in 1999-2000 when all size classes were analyzed together; when the analysis was done for each size class separately, no effect was found.

Growth

In general, *Dipteryx* seedlings and saplings (extensive sample) grew little during one year, and even negative growth was observed in all size classes. Over the entire two-year study period (1998-2000), mean annual growth in diameter was 0.4 mm in mature forest and 0.5 mm in young successional forest. Mean annual growth in height was 57 mm in mature forest and 82 mm in young successional forest (seedlings with meristem damage excluded). In late successional forest, average growth over one year (1999-2000) was 0.2 mm for diameter and 55 mm for height. Mean annual growth in diameter varied between 0.1 mm and 2 mm and mean annual growth in height between 16 mm and 273 mm for the different diameter classes and years (Fig. 3). The largest mean growth was observed in young successional forest, where growth in diameter and height peaked among saplings in the largest size class (20-30 mm diameter). Number of leaves remained essentially constant in the seedling population; median change in the number of leaves in both forest types was zero. Meristem damage was observed in all forest types in 4-9% of the seedlings each year.

When the growth patterns were analyzed in more detail, differences were found both between the two observation years and among the four plant size classes (for the extensive sample; comparisons were not done if any of the categories had less than three seedlings). When there was a difference between years, growth in diameter was higher in 1998-1999 than in 1999-2000 as in mature forest for the 1-4.9 mm and 5-9.9 mm diameter classes, and the 5-9.9 mm diameter class in both successional forests and the 10-19.9 mm class in young successional forest ($P < 0.01$, Mann-Whitney U test). For seedlings in all forests combined, growth in diameter was greater in 1998-1999 than in 1999-2000 ($P < 0.001$) (Fig. 3). Growth in height varied less among years; only the 10-19.9 mm and 20-30 mm diameter classes in young successional forest (Fig. 3) grew significantly more ($P < 0.001$) in 1998-1999 than in 1999-2000.

Linear regression analyses showed that growth in both diameter and height of *Dipteryx* seedlings and saplings were often significantly related to light levels, with higher light levels

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leading to more rapid growth. This was especially the case in mature forest, where the regression coefficients of both initial and mean light levels were always statistically significant, and usually explained more than 15% of the variation in growth (Table 5). In young successional forest, in contrast, most regressions of growth on light were not significant. The regressions of number of leaves on light levels were mainly not significant. Initial diameter was rarely correlated with growth in those seedlings and saplings for which light measurements were available (Table 5). Initial number of leaves, on the other hand, turned out to be a relatively good predictor of growth in both mature and young successional forest, with plants with more leaves growing more in diameter and height (Table 5). Interestingly, all regression coefficients between initial number of leaves and change in the number of leaves were negative, i.e., plants with many leaves lost leaves and plants with few leaves added new leaves.

In mature forest, growth in the first year was a relatively good predictor of growth in the second year for height ($R^2 = 18\%$, $P < 0.001$) and diameter ($R^2 = 19\%$, $P < 0.001$) but not for the number of leaves. In young successional forest, in contrast, only change in the number of leaves was predictable from previous year's change in the number of leaves ($R^2 = 44\%$, $P < 0.001$). For change in height, the regression coefficient was positive, but for change in diameter and number of leaves it was negative. When the residuals of these regressions were regressed against the light levels in the second year, the results obtained were very similar to simple regressions of growth on light.

To study if a change in light conditions between years might have promoted a change in seedling growth, the change in growth between the first and second observation year was regressed against corresponding change in light. In young successional forest, the regression coefficient was positive and statistically significant for the change in the number of leaves on change in light ($R^2 = 9\%$, $P = 0.025$), but not for change in diameter and for change in height. In mature forest, no statistically significant regressions were found.

Multiple regression analyses showed that the relative influence of light, initial diameter and initial number of leaves on seedling growth varied with forest type and observation year. In most of the cases where two independent variables remained significant in the regression model, one of them was light and the other was number of leaves. This was the case in the regression models of growth in height in 1999-2000 ($R^2=32\%$, $P<0.001$) and change in number of leaves in 1998-1999, ($R^2=32\%$, $P<0.001$) in mature forest, and in the regression model of change in number of leaves in 1999-2000 ($R^2=33\%$, $P<0.001$) in young successional forest. Light and initial diameter remained together in the regression in just one regression model, that involving growth in height in 1998-1999 in mature forest ($R^2=49$, $P<0.001$). In two cases, none of the three independent variables was statistically significant (growth in diameter in 1998-1999 and change in number of leaves in 1998-1999, both in young successional forest). In all other cases, only one variable remained in the regression model, and the results were similar to those of the simple linear regressions (see Table 5).

In mature forest, seedlings occurring within 10 m of water bodies (channels, lakes, rivers, swamps) were significantly larger in diameter than seedlings further away ($n=88$ vs. 574, $U=31172$, $P=0.0004$, mean diameter in mm + SD= 8.17±4.5 vs. 6.67±3.38), but no difference in growth in either diameter or height was found. In late successional forest, there was no difference in size between seedlings close to and far from water bodies ($n=28$ vs. 101, $U=1652$, $P=0.1748$, mean diameter in mm + SD= 7.54±4.0 vs. 6.38±2.82).

Discussion

Survival and recruitment

In the present study, smaller seedlings were found to have higher mortality than larger seedlings in all forest types. This is in agreement with earlier studies (Turner 1990, Sizer and Tanner 1999, Delissio and Primack 2003). For *Dipteryx panamensis*, for example, 19% exponential annual mortality was observed for seedlings (≤ 1 cm in diameter) but no mortality was

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observed for individuals 1-10 cm in diameter (Clark and Clark 1992). Higher mortality was observed for the smallest seedlings in mature forest during 1998-1999, which may be due to the long (two months) drought during that year. Previous studies in tropical forests have found that for most tree species, mortality is higher during the dry season than during the wet season, especially when the dry season is exceptionally long or dry (Veenandaal et al 1995, Condit et al. 1996, Gerhart 1996, but see Poorter and Hayashida-Oliver 2000). Small seedlings tend to be more affected by drought than large seedlings or saplings (Gerhart 1996, Delissio and Primack 2003), probably because their root system is too superficial or not extensive enough to reach soil moisture in the deeper soil layers.

Most of the *Dipteryx* seedlings and saplings found in this study were small, and only about 1% of the saplings were 20-30 mm in diameter in mature and late successional forest, whereas 6% were of this size in young successional forest. The low density of large saplings is understandable, considering the long lifespan of other species in this genus. Ages of 330 years have been reported for *D. panamensis* (Clark and Clark 1992), and 1000-1200 years for *D. odorata* (Chambers et al. 1998). The *Dipteryx* population will remain at a stable level if each tree produces, on average, one offspring that survives to the reproductive age.

It is not possible to deduce if the seedlings in young successional forest will survive to reach the canopy, because rare events occurring once every decade may affect survival. If saplings of 20-30 mm diameter have already passed the critical "bottleneck" and suffer no mortality, as has been suggested for the congeneric *D. panamensis* (Clark and Clark 1992), the saplings will probably reach the canopy when the forest is in late successional stage. However, if the 19% exponential annual mortality in young successional forest persists, then fewer saplings will survive into the late successional forest. An anecdotic observation suggests that even treelets are still subject to mortality: in another young successional forest close to Cocha Cashu, around 70% of the treelets of several species died in the "el Niño" year 1998 (M. Sanchez, pers. comm.). The dry season in 1998 had both two months of drought and the lowest total precipitation of the years studied in the present paper, but more long-term measurements are needed to establish long-term survival patterns.

The importance of precipitation in general on the production (and possibly permanence) of leaves is well known: Poorter and Hayashida-Oliver (2000) found an increase of leaf number during the rainy season for the seedlings of three tropical tree species. Moreover, Hall et al. (2003) found that two of four species studied had higher leaf area ratios (leaf area/total dry mass) in moist soils than in dry soils. Although leaf area ratio is not the same as number of leaves, they are correlated. The relation of leaf area and survival of seedlings is even better established (Clark and Clark 1985, Poorter and Hayashida-Oliver 2000), and for *Dipteryx panamensis* it has been found that seedlings with smaller leaf area had higher mortality (Sterck et al. 1999). In our study, the number of leaves was related with survival only in mature forest in 1998-1999, a year with two months of drought.

In the present study, a relationship between light and survival was found only in young successional forest, and even there, only in the first observation year. However, a comparison of survival of seedlings (<1 cm diameter) of *D. panamensis* at La Selva showed that survivors had significantly higher indirect measures of light (mean crown illumination and number of crowns above) than those seedlings that died (Clark and Clark 1992). Another study of seedlings transplanted to successional forest, where a wider range of light levels occurred (0-7%), showed a positive effect of light on survival (Montgomery and Chazdon 2002). Similarly, studies involving two contrasting light environments, undestory and gaps, showed a higher survival in the latter for both *Dipteryx micrantha* (Cintra and Horna 1997) and *Dipteryx panamensis* (DeSteven and Putz 1984). The difference between our study and the others is probably due to the range of light and proportion of places with higher light intensities included in the studies; in the mature forest in our study, light intensity ranged from 0.53% to 14.66% (median 2.16%). This corresponds to light levels beneath closed canopy, as in gaps light levels can reach 10-30% of full sun (Canham 1990, Van derMeer 1998, Osunkoya et al. 1993, Osunkoya et al. 1994).

Borders of lakes and swamps resemble forest edges, where it has been found that tree mortality (Lawrence et al. 1998) and lateral light are significantly higher than in the forest interior (Kapos et al. 1997), especially within 10-25 m from the edges (Lawrence et al. 2001). In our study, individuals found at border habitats were larger than those in the forest interior, even though

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growth rates were similar. During 1998-1999, seedlings at the borders showed higher survival than seedlings in the interior, which suggests that the observed presence of larger saplings at the borders may be a result of different survival rates rather than different growth rates.

Growth

Interestingly, growth in *Dipteryx* seedlings and saplings was variable between forest and between years. The median growth in diameter for all seedlings and saplings was 0.8 mm in the first year and -0.1 mm in the second year, which is comparable to the six-year range in median annual growth for *Dipteryx panamensis* (seedlings: 0.1-0.8 mm, saplings 1-4 cm in diameter: 0.2-1.9 mm, Clark and Clark 1992). In the Clark & Clark (1992) study, the year with the lowest rainfall (1985-1986) had significantly higher growth (0.7-0.8 mm for <1 cm diameter) than the other years (0.1-0.5 mm, $P < 0.0001$), and was similar to the median diameter growth of *Dipteryx micrantha* in the present study during 1998-1999 (0.7 mm), an “El Niño” year. Clark & Clark (1992) suggested that light limitation in high rainfall years may have reduced growth. Another study (Condit et al. 2004) showed similar results: at two sites in Panama, growth in diameter of saplings (1-1.9 cm diameter) of ten species out of around eighty was significantly higher during “El Niño” in 1998-1999 than during other years (1995-2000). On those sites, the intensity of PAR (photosynthetically active radiation) was 5-10% higher during the “El Niño” year interval (December 1997-March 1998) than at other times.

In our study, annual precipitation, months of drought, light levels in the understory and seedling and sapling growth in mature forest were higher during 1998-1999 than during 1999-2000. Sufficient precipitation enhances leaf flush and root growth, which enables the plants to survive the dry season better (Kitajima 1996, Poorter and Hayashida-Oliver 2000). Dry months induce some trees to drop their leaves and open the canopy (Condit et al. 2000). It is not possible to say if the combination of higher annual precipitation and number of months of drought have produced the higher growth observed during 1998-1999.

In young successional forest, light was mostly not related to growth in diameter or height. Together with the fact that light levels are higher in young successional forests than in mature forests (Nicontra et al. 1999), this suggests that either light is not as important for seedling growth in successional as in mature forests, or that other factors, such as water availability, transpiration or desiccation, override its effects. In both forest types, initial number of leaves explained growth best.

Interestingly, a change in the number of leaves was not common for the set of seedlings/saplings occurring in mature forest, where the majority of the population were small plants. In young successional forest, however, where larger seedlings existed (and therefore a wider range of number of leaves was found), a change in the number of leaves between years occurred and was associated with change in light levels.

This work shows that light being of importance for seedlings/sapling survival and growth have different responses not only in different forest types, but also between years. Light, being variable spatially was also found to be variable temporarily, at a scale of two year comparison. Forest of different successional stages having different light levels and probably also other characteristics result in different growth. In these spatially and temporarily variable environments plants should adapt to tolerate or take advantage of this range of variation in light along its life.

Factors that influence growth of seedlings and saplings, such as light, initial size and initial number of leaves, can change at different time scales, understanding this variability is essential to understand the scales at which we should visualize growth. For example, while light might vary at a yearly or seasonal time scale, number of leaves might either be very stable or dependent on seasonal rain. In the long run growth is the result of these interplay of factors.

Variation in growth among years along its life have been documented for *Dipteryx panamensis* as well for other species (Clark and Clark 1992, Connell and Green 2000). For shade tolerant plants performing so slow growth per year and being this growth dependent also in other variables such as leaf number, relations between light and growth need probably to be assessed at a longer time scale. The knowledge of the ecology of early years have importance to understand plan demography in general and for forest management practices. Furthermore, it is important to

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consider variability in both space and time to make generalizations and predictions of forest dynamics.

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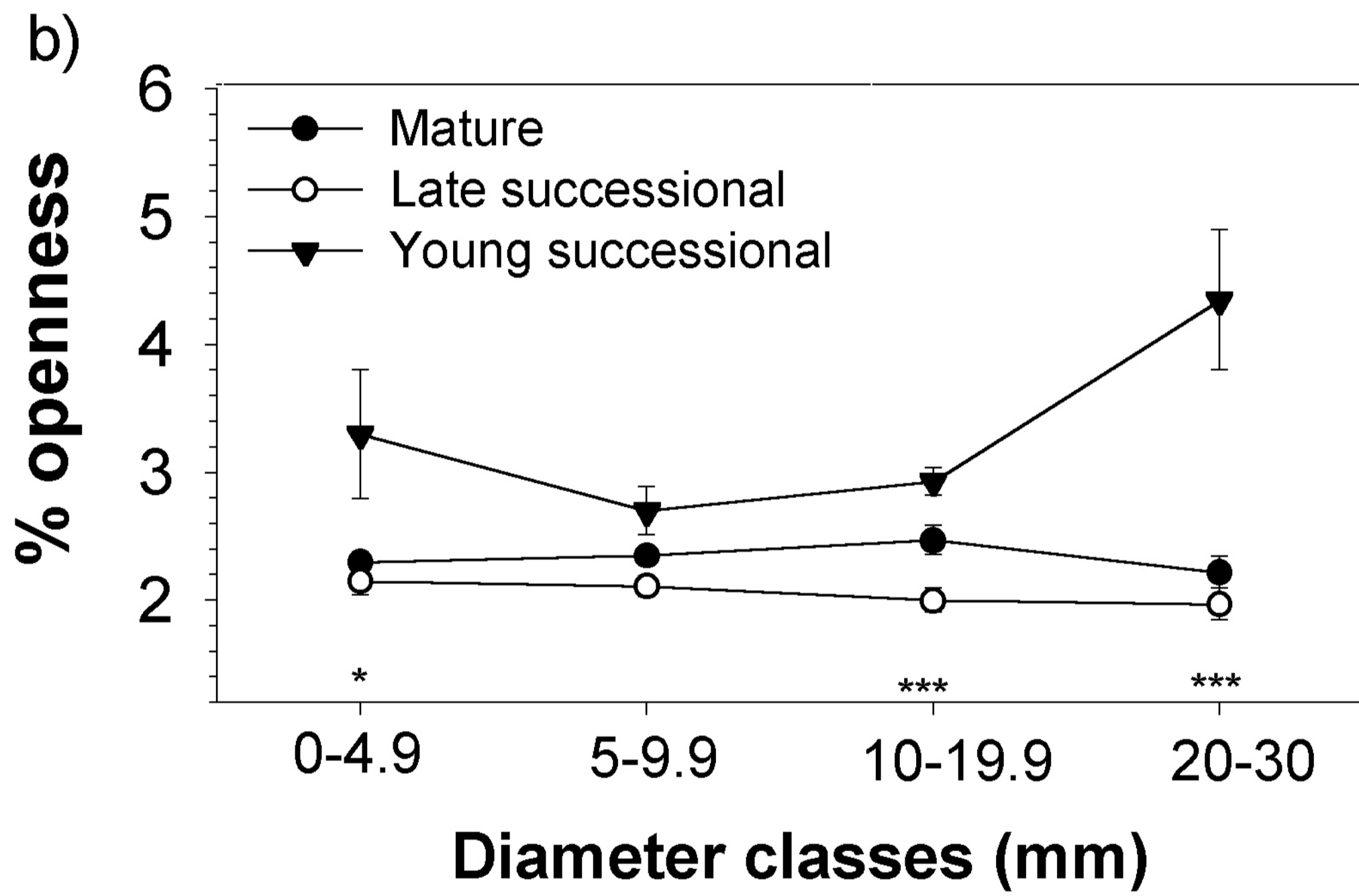
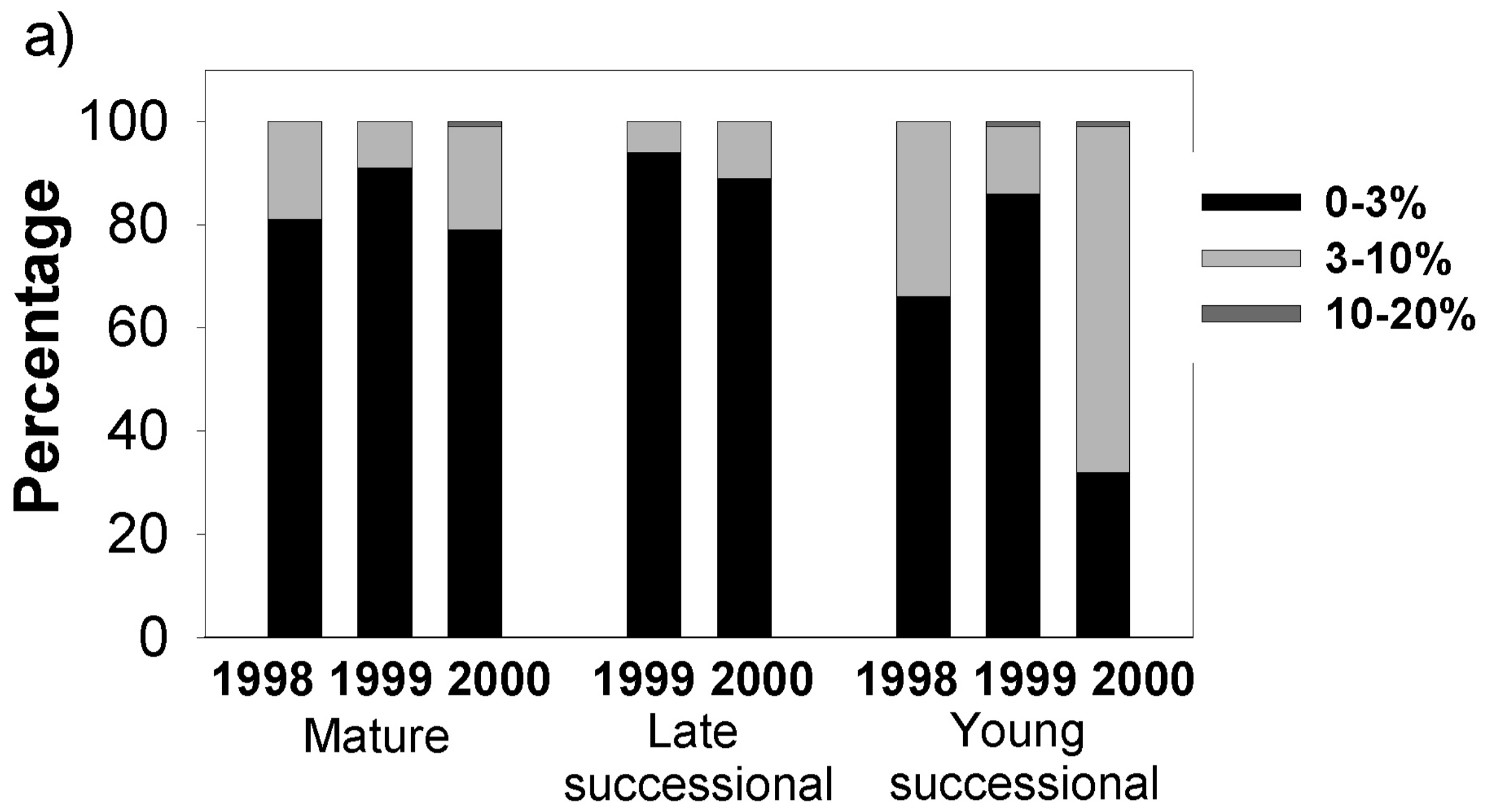
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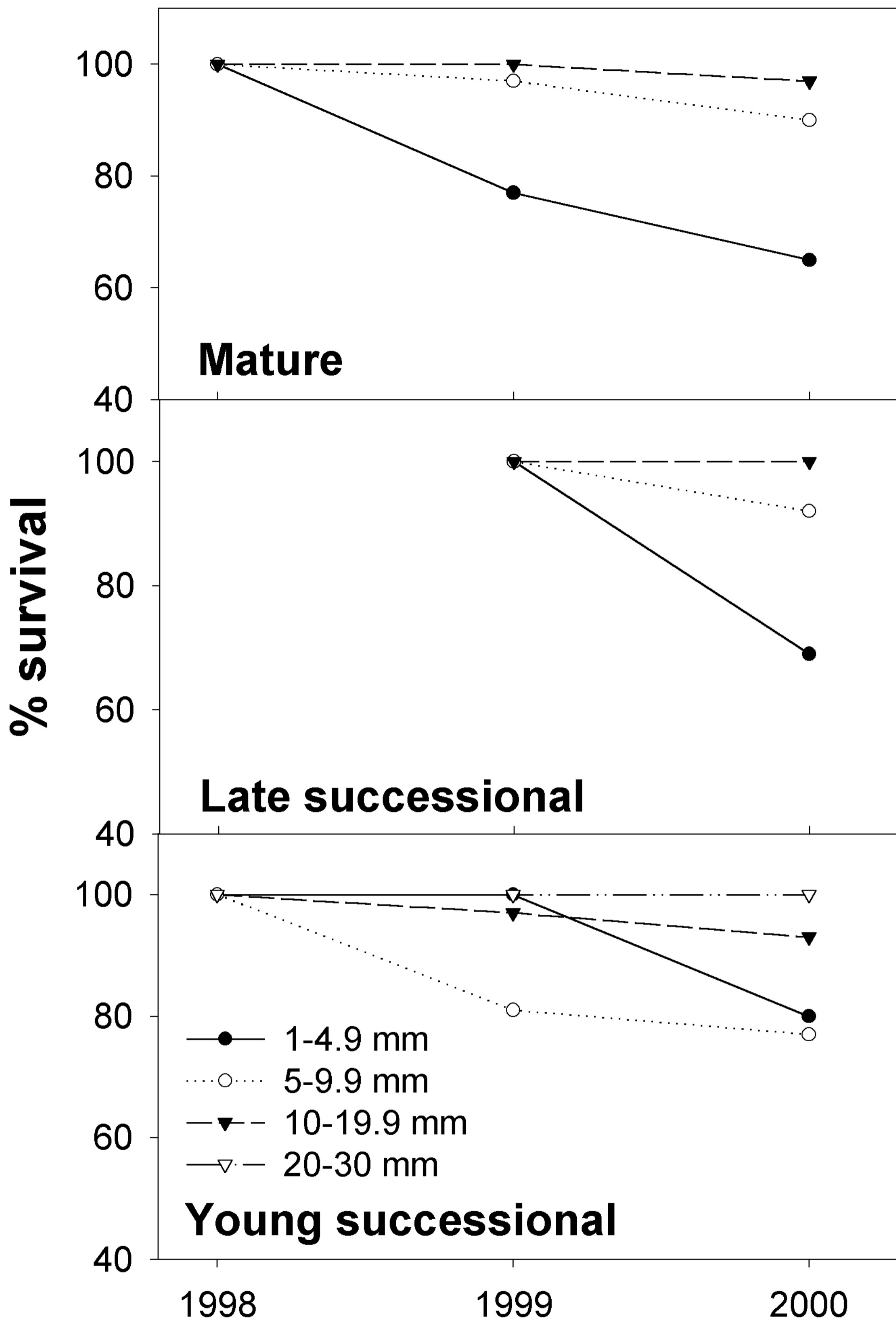
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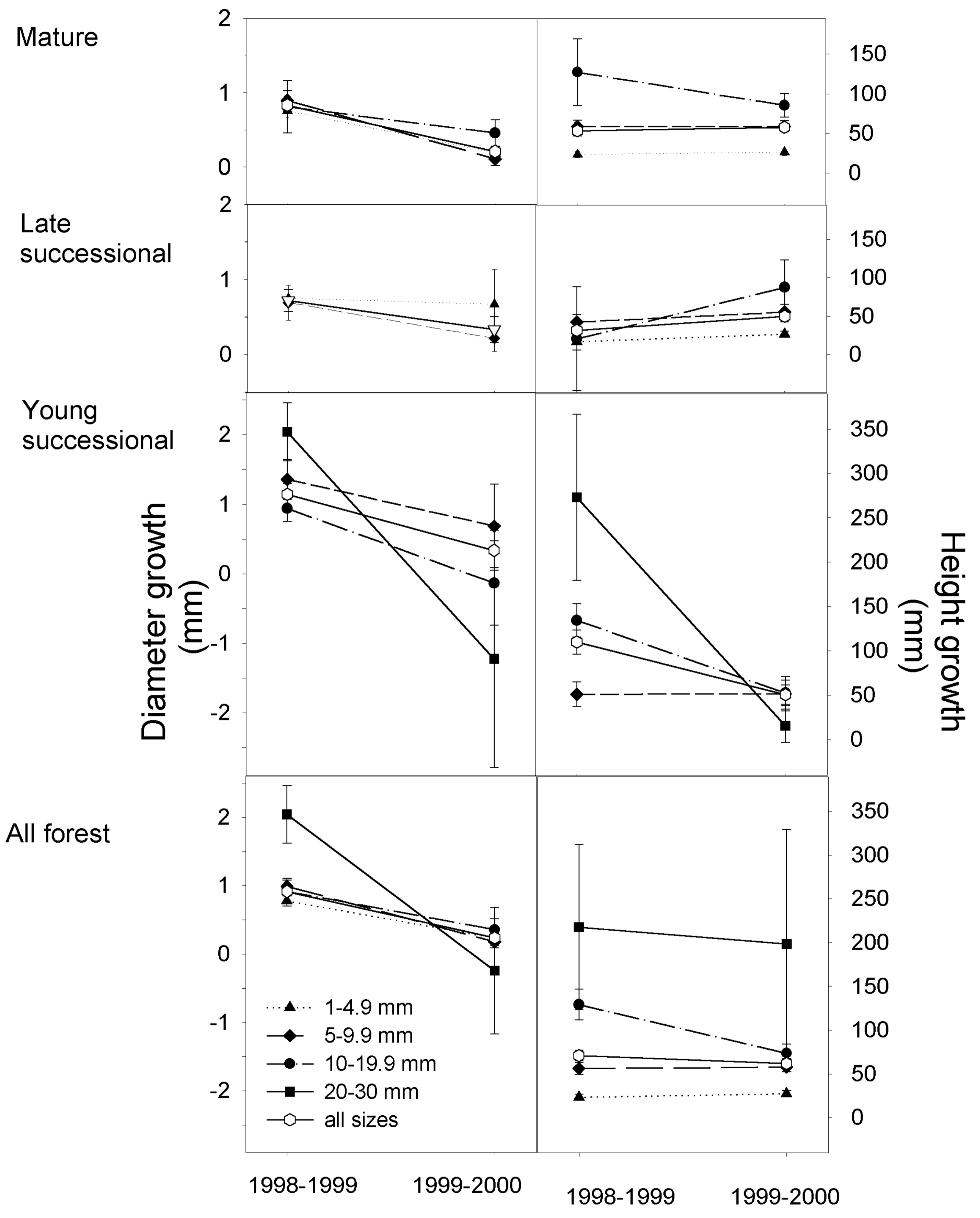
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