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Effects of seedling size, El Niño drought, seedling density, and distance to nearest conspecific adult on 6-year survival of *Ocotea whitei* seedlings in Panamá

Abstract We present an analysis of the long-term survival of two cohorts of seedlings of the tropical canopy tree *Ocotea whitei* (Lauraceae) on a 1-ha plot of mature, lowland moist forest on Barro Colorado Island, Panamá. In 1980, we counted an even-aged cohort of seedlings that germinated in 1979, then measured and tagged survivors in 1981. We also measured and tagged a second, smaller cohort of seedlings that germinated in 1981. We followed the subsequent survival of all seedlings through 1985. Seedling mortality was phenotypically, temporally, and spatially non-random. Important correlates of non-random mortality included: (1) seedling size and age, (2) an El Niño drought, and (3) biotic neighborhood. Larger and older seedlings survived better than smaller and younger seedlings, respectively, and the El Niño-related drought of 1982–1983 was associated with elevated mortality rates. Seedling density, which was strongly correlated with the proximity to the nearest conspecific adult, increased mortality. The observed mortality patterns suggest that processes consistent with the Janzen-Connell hypothesis operate during the recruitment phase of *O. whitei* population dynamics. However, the processes causing the observed density- and distance-dependent mortality may vary with factors such as total seed number, seedling size, and climatic variation, making it difficult to determine whether time-integrated seedling-to-adult spacing mechanisms other than self-thinning operate on a given plant population. After 6 years in the hectare studied, survivors remained densest and most numerous underneath the adult trees. We conclude that only long-term demographic data, collected at a variety of scales on a variety of species, will ultimately answer the question: do Janzen-Connell effects contribute substantially to structuring tropical forests?

Introduction

Non-pioneer trees in mature forests spend many years, even decades, as seedlings and small saplings in the understory (Clark and Clark 1985; Canham 1989; De Steven 1994; Hubbell 1998; Connell and Green 2000). Over such long periods of time, many factors such as physical stress, attack by pathogens and pests, and competition lead to the death of most seedlings, and determine which individuals recruit into larger size classes. Non-random survival may produce plant spatial distributions different from those predicted by random thinning of the seed-rain. Furthermore, natural selection occurs when survival is non-random with respect to genotypes. Evaluating the nature and extent of non-random effects on seedling survival is the basis for assessing the evolutionary and ecological processes important in structuring forest communities.

Mortality of tropical tree seedlings is usually greatest in the first year, decreasing to a much lower, nearly constant mortality rate after several years (Clark and Clark 1985; Schupp 1988a; De Steven 1994; Gerhart 1996). Seedling mortality is frequently spatially non-random, with per capita mortality greatest where seedlings are at high density or close to conspecific adults (see Clark and Clark 1984; Hammond and Brown 1998 for reviews). Plant density and the distance to the nearest conspecific adult are two of the most cited correlates of non-random mortality of seedlings and may be caused by intraspecif-

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ic competition, by density-dependent attack by pathogenic or herbivorous organisms, or by adult trees acting as pest reservoirs (Janzen 1970; Connell 1971; Augspurger 1984, 1990; Clark and Clark 1984; Westoby 1984; Hamill and Wright 1986; Gilbert 1995; Gilbert and De Steven 1996; Barone 1998; Webb and Peart 1999; Harms et al. 2000). Such non-random attack by pests may also increase susceptibility to other stresses that would normally not have a density or distance-to-adult component, such as drought (Gerhardt 1998).

Seedling size and climatic events may also influence the relative importance of different mortality agents. For example, larger plants may be more tolerant than small ones to pests (Marquis 1984; Clark and Clark 1985; Howe 1990), regardless of higher pest pressure at higher host densities. Under crowded conditions, larger plants may out-compete smaller neighbors for resources (Weiner 1990). Additionally, climatic events such as droughts or exceptional rains associated with El Niño-Southern Oscillations may predispose seedlings to damage from pathogens from which they might otherwise suffer little damage (Brooks and Ferrin 1994; Scherm and Yang 1995; Wiersma et al. 1997). Long-term monitoring of cohorts of seedlings along with environmental variables can suggest which processes or interactions among processes are most important in the recruitment of seedlings into larger size classes.

A non-pioneer tree of tropical moist forests that experiences non-random mortality is *Ocotea whitei* Woodson (Lauraceae). On Barro Colorado Island (BCI), Panamá, *O. whitei* juveniles (individuals 1 cm≤dbh<30 cm, where dbh=diameter at 1.3 m) experience greater mortality closer to conspecific adults (individuals 30 cm≤dbh) and at higher densities than at greater distances or lower densities (Gilbert et al. 1994). Mortality is associated with a canker disease, is non-random, and can shift the spatial distribution of juveniles (a decade or more old) away from conspecific adults, thus favoring those individuals that initially dispersed farther from the parent tree (Gilbert 1993). We know little, however, about mortality processes in *O. whitei* in the first few years of life. *O. whitei* produces large fruit crops on a supra-annual cycle (although flowers are produced by at least some individuals in most years) (S.J. Wright, unpublished data), and seed germination takes place synchronously at the beginning of the wet season, exemplifying the "rapid-rainy syndrome" of Garwood (1983). The distinct cohorts of seedlings produced by *O. whitei* are well suited to long-term studies on the effects of multiple, potentially interacting factors on seedling survival.

In this study, we compared the relative importance of environmental conditions and individual characteristics of seedlings on non-random seedling mortality in structuring the local sapling population of *O. whitei*. We expected that larger and older seedlings should have a survival advantage over smaller ones and that seedlings growing at high densities or close to conspecific adults suffer greater rates of mortality than those found at low densities or farther from the parent in the first years after germination. Finally, we examined the effect of climatic variability on seedling mortality, particularly due to a severe drought associated with the 1982–1983 El Niño-Southern Oscillation.

Materials and methods

We conducted this study on the 50-ha Forest Dynamics Project (FDP) permanent census plot in the semi-evergreen tropical moist forest of BCI in the Republic of Panamá. The FDP plot was established in 1980 and four complete censuses of all trees and shrubs ≥1 cm dbh have since been completed (Hubbell and Foster 1983, 1992). The climate on BCI is seasonal, with a 4-month dry season from December to April, with periodic extreme droughts associated with El Niño events (Leigh et al. 1982; Windsor 1990; Wright et al. 1999).

Abundant seed production by *O. whitei* occurred in 1979 on BCI (S.P.Hubbell, personal observation). S.P.H. mapped the seedlings of *O. whitei* across 1 ha of the FDP plot in January 1980, by counting all live and dead 8-month-old seedlings in each 1×1 m quadrat of a square 1-ha area with its southwest corner at FDP plot coordinate 760, 230. This hectare contained three reproductive adult *O. whitei* trees, clustered in the central 40×40 m subplot. The next nearest conspecific adult to any of the adults within the focal hectare was >50 m distant. The total number of seedlings (alive plus dead) in 1980 was considered to be the number of seedlings alive in 1979. A minor fruiting event occurred in 1981, but no other fruit production was recorded for *O. whitei* within the focal hectare throughout the remainder of the study. D.N.H. measured the height, counted the number of extant leaves, and tagged all surviving seedlings of the 1979 cohort and of the newly germinated seedlings in 1981, and followed the fate of the tagged seedlings and remeasured them each year through 1985. Seedling height and leaf number were highly correlated (Spearman rank correlation=0.41, $P \leq 0.0001$, n=5,030, in 1981), so we used leaf number as a measure of seedling size throughout. We subsequently conducted analyses on two separate cohorts of seedlings: those that germinated in 1979 (cohort 79) and those that germinated in 1981 (cohort 81). Locations and sizes of individuals of *O. whitei*≥1 cm dbh were available from the FDP records. Voucher specimens from this species on BCI have been deposited in the BCI herbarium (D. DeSteven specimens no. 8 and no. 9, 29 March 1981 and 6 April 1981, identified by R. Foster in 1995).

For each seedling, we examined the probability of mortality in each year with respect to (1) seedling age, (2) seedling size, (3) density of conspecific seedlings, (4) distance to the nearest conspecific adult, and (5) precipitation, using the logistic regression analysis procedure of SAS 6.12 (SAS Institute, Cary, N.C.). We fit the full five-parameter logistic model for seedling mortality, including only those individuals surviving at the start of the intercensus interval. We tested the effects of seedling age (years since 1979 or 1981 germination), size (number of leaves, measured at the start of each interval), density (total number of live cohort 79 and 81 seedlings within the 1-m^2 quadrat of the focal individual at the start of the interval), distance of the quadrat of the focal individual to the nearest conspecific adult, and the total precipitation during that interval. Our full logistic model includes all non-interaction terms. We determined the best-fit model and the relative contribution of each of the parameters to seedling mortality by repeating the logistic analysis for all possible reduced models, and assessed the contribution of each parameter by likelihood ratio tests, where G=-2log$L_{reduced}$-(-2logL_{full}), where G is distributed as χ^2 with 1 df, and the parameters in the reduced model are a subset of the parameters in the full model (Kleinbaum 1994).

To further examine the effect of seedling size on long-term survival, we grouped those cohort 79 seedlings alive in 1981 into four size classes (based on number of leaves in 1981) and tested for differences in their mean survival times using the log-rank χ^2-test of homogeneity among groups of the Kaplan-Meier product-limit survival analysis (Lee 1992) using JMP 3.2 (SAS Institute,

Table 1 Rainfall data for Barro Colorado Island, Panamá, during the period of *Ocotea whitei* seedling censuses. Data are compiled for each intercensus interval, from mid-census date to mid-census date. An El Niño-associated drought occurred in 1982–1983 and was preceded by an unusually wet year in 1981. Data from Table A1 of Windsor (1990)

|	Intercensus interval				
	1 March 1980– 30 June 1981	1 July 1981– 30 June 1982	1 July 1982– 30 June 1983	1 July 1983– 30 June 1984	1 July 1984– 30 June 1985
Total rainfall (mm)	3,917[a]	3,297	2,021	2,641	2,635

[a] This intercensus interval was 16 months long; all others were 12 months long

Cary, N.C.). Data for the survival analysis were months to mortality beginning with the 1981 census (when sizes were first recorded); data were tagged as right censored for individuals that survived until the end of the study.

Results

Within the censused 1-ha plot, 13,096 seedlings of cohort 79 remained standing as live or dead stems in 1980, when they were mapped to 1-m^2 quadrats. This is therefore a lower-bound estimate of the number of seeds produced in 1979 by the three adult *O. whitei* found within the 1-ha area. An additional 532 seeds fell and produced seedlings within the focal hectare in 1981; these seedlings constitute cohort 81. Of the original cohort 79 seedlings, only 184 (1.4%) remained alive in 1985 [and only 4 (0.75%) of cohort 81 seedlings]. For the surviving cohort 79 seedlings, plants had a mean of 13.0±10.3 leaves (maximum=72) in 1985.

Annual mortality varied greatly between cohorts and among years, ranging from 6.5 to 92.8% of seedlings (Fig. 1). The first year of existence for each cohort and the El Niño year were the two 1-year periods of highest mortality for both cohorts. Cohort 81 suffered its highest annual mortality rates during the first 2 years; the second year included the El Niño drought (Fig. 1A). Cohort 79 also suffered more than 50% mortality in its first year, but mortality was highest in the fourth year, during the El Niño drought (Fig. 1A).

The El Niño drought of 1982–1983 was one of the most severe of this century, and was associated with a longer-than-average dry season and lower-than-average total rainfall on BCI (Table 1; Leigh et al. 1989; Condit et al. 1992, 1995; Hubbell and Foster 1992). The drought was associated with very high mortality (88%) in both cohorts, with the mortality of cohort 79 nearly double that of the previous wet year (Table 1, Fig. 1B). The highest mortality for cohort 79, and the second highest for cohort 81 occurred during the drought year (Fig. 1B).

Effects of precipitation and seedling age, size, density, and distance to conspecific adults

Logistic analysis of the full five-parameter and all reduced models indicated that the best model for probability of seedling mortality includes all parameters except
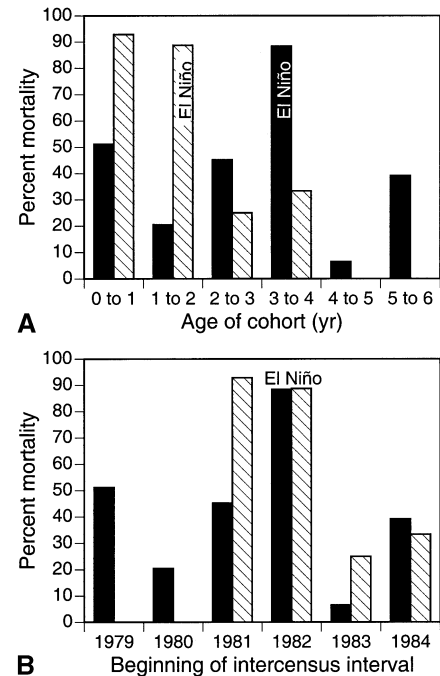
Fig. 1 Observed mortality of seedlings in the 1979 (*solid bars*) and 1981 (*hatched bars*) cohorts of *Ocotea whitei* by age of cohort (**A**) and year (**B**). **A** Insets indicate the 1982–1983 El Niño-associated drought. **B** Mortality is calculated as the percentage of stems dying from the census year indicated to the following census

distance to conspecific adult (Table 2). By removing each parameter individually from the full model, and comparing each four-parameter model to the full model using the likelihood ratio test, we found that age, seedling size (leaf number), density, and precipitation each contribute significantly to determining the probability of mortality ($P \leq 0.005$). In further reduced models, we found that distance to conspecific adult does contribute significantly to explaining mortality, but only when seedling density was not included in the model, due to the correlation between distance and density (cohort 79 seedling density was negatively correlated with distance from adult; $r = -0.55$, $P \leq 0.0001$, $n = 1,242$; 1980 data). Stepwise logistic regression (SAS 6.12) selected the same four-parameter best-fit model (not shown). The best-fit model was:

logit(probability of mortality)=10.583-0.003(rain)-0.173 (leaves)+0.014 (density)-0.811 (age)

Table 2 Log likelihood ratio test of each four-parameter reduced logistic model compared to the full five-parameter model. For each model *i*, the –2 log likelihood value for the model including an intercept is presented, together with the likelihood ratio test for each reduced model compared to the full model 1, where $G=-2\log L_i-(-2\log L_1)$, and the associated *P*-value for χ^2 with $df=1$. All measured plants from cohorts 79 and 81 were included in the model (*NS* not significant)

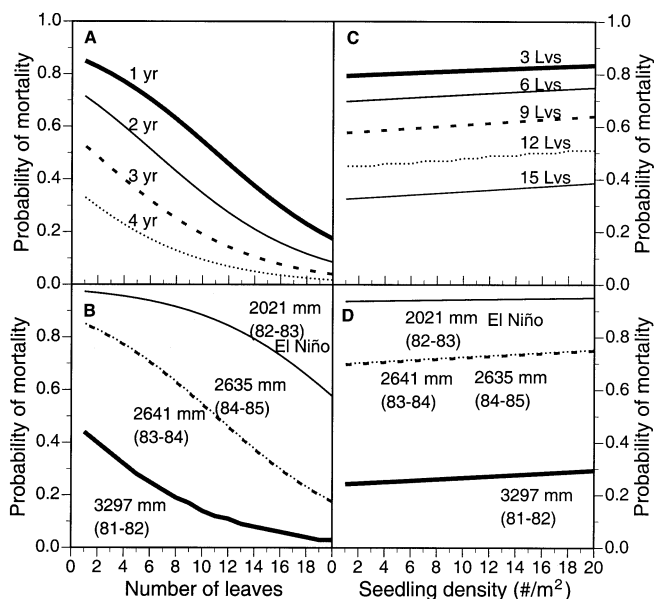| Model	Parameters					–2 log *L*	G	P
1	Rain	Leaves	Density	Distance	Age	8,844.0	0.0	–
2	Rain	Leaves	Density		Age	8,845.4	1.4	NS
3	Rain	Leaves		Distance	Age	8,868.9	24.9	<0.005
4	Rain	Leaves	Density	Distance		9,115.7	271.7	<0.005
5	Rain		Density	Distance	Age	9,362.4	518.4	<0.005
6		Leaves	Density	Distance	Age	10,383.3	1539.3	<0.005

Fig. 2A–D Interacting effects of precipitation and seedling age, size, and density on mortality of *O. whitei* seedlings, as described by the best-fit four- parameter logistic regression logit(probability of mortality)=10.583-0.003(precipitation)–0.173(leaves)+0.014 (density)-0.811 (age). Probability of mortality=$e^{(\mathrm{logit}(p)}/(1+e^{\mathrm{logit}(p)})$. **A** Effects of seedling size (number of leaves) and age [precipitation=2,641 mm, density=4.11 seedlings/m² (mean for 1981)]. **B** Effects of seedling size (number of leaves) and precipitation (density=4.11 seedlings/m², age=1 year). **C** Effects of seedling density and seedling size (precipitation=2,641 mm, age=1 year). **D** Effects of seedling density and precipitation [leaves=6 (median for 1981), age=1 year]
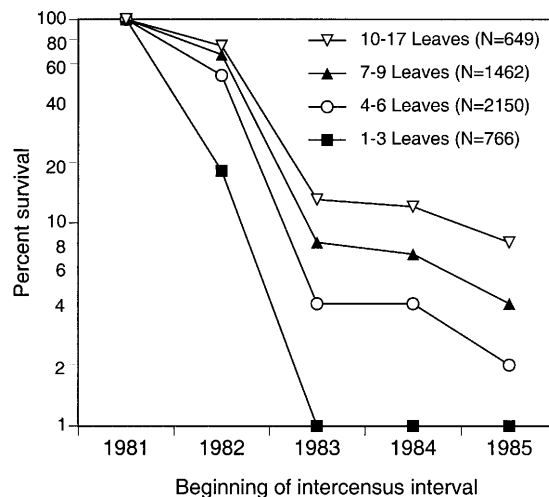

Fig. 3 Long-term survival of *O. whitei* seedlings from the 1979 cohort according to seedling size in 1981. Only seedlings alive in 1981 were included. Shown is survival of seedlings with 1–3, 4–6, 7–9, and 10 or more leaves in 1981

producing a concordance of predicted probabilities and observed responses of 80.1%. Inspection of the terms of this model indicate that, as expected, larger and older plants have lower probabilities of mortality (negative coefficients), and as predicted by the Janzen-Connell model, seedlings at high densities have a greater probability of mortality. Additionally, mortality was greater in drier years. Only distance from conspecific adults did not contribute significantly to predicting mortality, because the effect of distance was subsumed in the effect of seedling density.

To explore how these terms interact to affect seedling mortality, we calculated the expected mortality under the observed range of seedling characteristics and environmental conditions (Fig. 2). The two primary determi-

nants of seedling mortality were clearly precipitation and seedling size. Larger plants had a greater probability of survival regardless of their age, and among plants of a given size, older plants had greater survival than younger plants (Fig. 2A). Larger plants had greater survivorship in all years, but the effect of the El Niño drought in 1982–1983 overshadowed the effect of seedling size: in the 3 non-drought years, the largest seedlings suffered <20% mortality, whereas the same-sized seedlings suffered almost 60% mortality during the drought (Fig. 2B). Increasing seedling density lead to greater mortality regardless of plant size (Fig. 2C) or precipitation (Fig. 2D), although at the high mortality rates experienced during the El Niño drought, the contribution of density-dependent mortality was minimal.

Seedling size was an important predictor of survival over both the long and short term. Because larger seedlings were more likely to survive over the short term and because larger plants in one year were also likely to be the larger plants in the following year (e.g., number leaves in 1981 vs number leaves in 1982 for cohort 79, Spearman rank correlation *r*=0.51, *P*=0.0001, *n*=2,754), seedling size in 1981 influenced which seedlings survived the entire interval from 1981 to 1985 (Fig. 3).
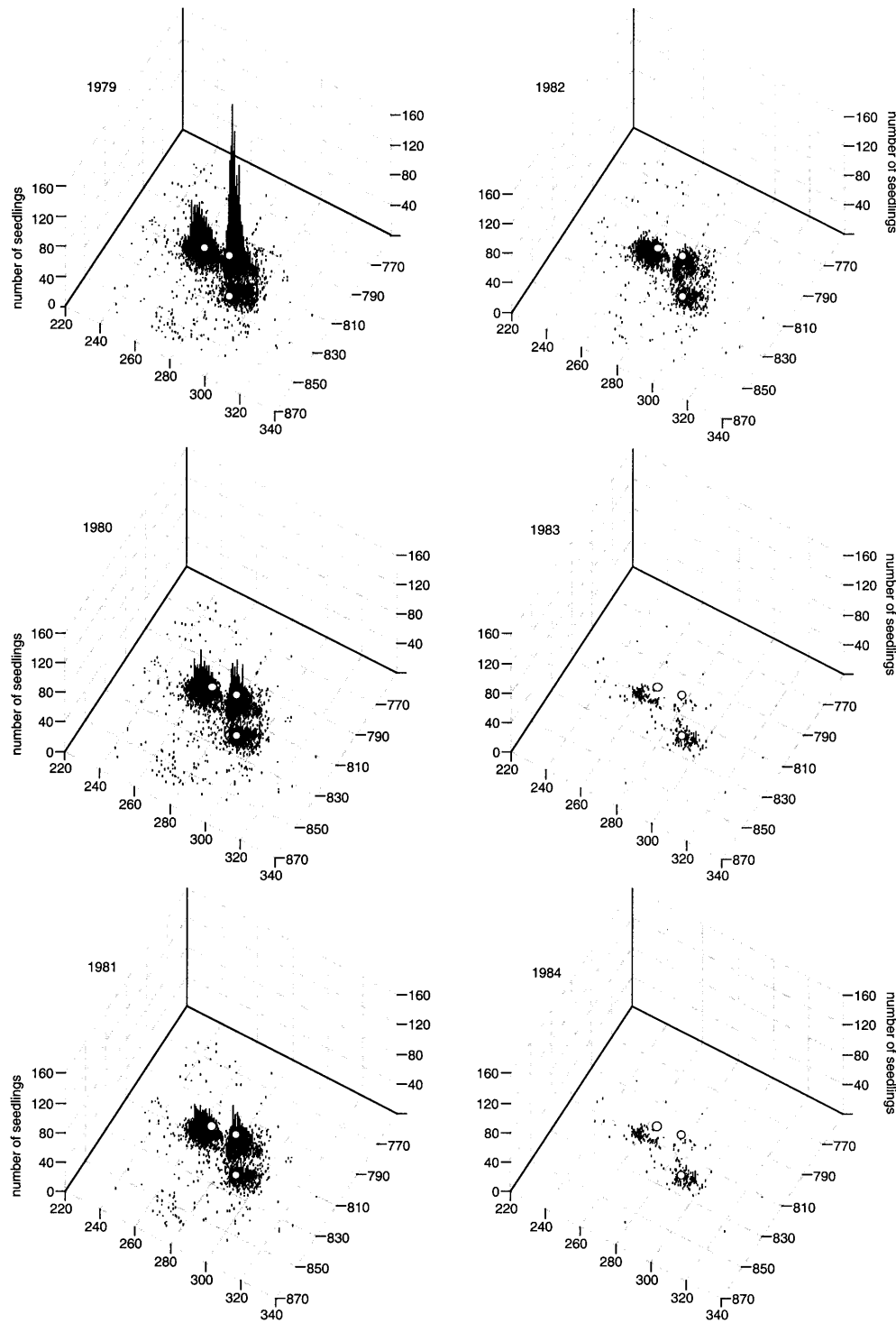
Fig. 4 Distribution of cohort 79 seedlings of *O. whitei* in each census year in the 1-ha study plot. An additional 10 m on all sides is included in the figure to avoid obscuring plants that fell on or near the edge of the 1-ha area. The *x*-axis (to the right of vertical) indicates the distance north from the southern border of the 50-ha FDP plot, and the *y*-axis (to the left of vertical) indicates the distance east from the western border. The southwest corner of the 1-ha area is at coordinates 760, 230. The *z*-axis is the number of seedlings per 1 m^2. High seedling densities are associated with the location of three adult *O. whitei* (*open circles*). The lowermost corner of each map is the northeast corner of that map

Kaplan-Meier product-limit survival analysis showed highly significant differences in survival probabilities across seedling size classes (log-rank $\chi^2=600.9$, $df=3$, $P\leq0.0001$), with mean estimated survival times increasing with plant size (Fig. 3). Indeed, plants with >10 leaves had a 72% longer mean survival time than plants with only 1–3 leaves [mean survival time 14.5±0.2 months (1–3 leaves), 19.7±0.2 months (4–6 leaves), 22.4±0.3 months (7–9 leaves), and 25.0± 0.5 months (10 or more leaves)]. Over the long term, of

the 174 cohort 79 seedlings still alive in 1985 (and with complete data), 33% had been among the largest 10% (by number of leaves) of seedlings in 1981, whereas only 7.5% of the 6-year survivors were from the smallest quartile in 1981.

Because seedlings occur at greater densities closer to adults, the greater mortality associated with either distance or density should shift the spatial distribution of a cohort away from parent trees (Augspurger 1983). Such patterns were observed in 1981–1983, and this non-random mortality changed the distribution pattern of cohort 79 seedlings around adult *O. whitei* (Fig. 4). In 1979, 50% of all seedlings were within 7 m of an adult, but by 1983, this distance had increased to nearly 9 m. The main reason for the observed shift was the disproportionate mortality of seedlings within 6 m of an adult (where seedlings were at highest densities), a distance approximately double the average crown radius of an adult *O. whitei* (mean crown radius=2.7 m for a 30-cm dbh adult; O'Brien et al. 1995). By 1984, it was apparent that seedlings in areas distant from adults and at low seedling density had a greater probability of long-term survival than those at high density, directly beneath adults (Fig. 4). Nevertheless, more than 90% of seedlings were found within 13 m of an adult in all years, and despite the patterns of mortality that shifted the recruitment curve away from adult trees, most survivors after 6 years were still found within two crown diameters of the adults that produced them.

Discussion

In this study, mortality of *O. whitei* seedlings was phenotypically, temporally, and spatially non-random. Larger seedlings survived 1-year census intervals better than did smaller seedlings, even under the pressure of the El Niño drought. That greater size confers an advantage to tropical understory plants is apparently a general phenomenon, with greater survival for larger seedlings in moist to wet (Clark and Clark 1985; Schupp 1988b) and dry (Gerhardt 1996) tropical forests, as well as more rapid recovery of growth from herbivory damage in larger plants (Marquis 1984). The cumulative effect of size-enhanced survival highlights the importance of genetic or environmental effects on initial seedling size for the long-term survival of tropical tree seedlings.

El Niño drought effects on mortality overshadowed or exacerbated the effects of seedling size or age, with mortality approaching 90% for both 1979 and 1981 cohorts during the drought (Fig. 1). El Niño events have been suggested to be important to fruit production (Wright et al. 1999) and to the growth and survival of juvenile and adult trees on BCI (De Steven 1989; Condit et al. 1995). Low soil moisture is a correlate of increased mortality in seedlings of at least one tree species on BCI (Howe 1986, 1990; Fisher et al. 1991). Drought conditions associated with El Niño events may therefore be important for the performance of seedlings on BCI; these data are the first to demonstrate such an effect.

First-year mortality rates for the 1979 and 1981 cohorts differed considerably, with cohort 81 suffering much greater mortality. Such variation in first-year mortality is also known for several other species on BCI (De Steven 1994; Schupp 1988a). In the present study, there are at least three potential explanations for the difference. First, because the total 1979 seedling density was determined by counting live and dead seedlings in 1980, a large number of seedlings possibly died and decomposed or were removed by herbivores prior to the first census. This would result in underestimation of first-year mortality. We regard this as unlikely, however, because there was little evidence of advanced decomposition in any of the dead seeds or seedlings (S.P. Hubbell, personal observation). Moreover, the large seeds and tissues of most Lauraceae are rich in anti-fungal and anti-herbivore compounds, which are likely to slow decomposition rates (Adikaram et al. 1992; Himejima and Kubo 1992; Sanchez-Hidalgo et al. 1999).

Another possible explanation for the difference is that cohort 81 seedlings germinated in areas with an already high seedling density from cohort 79. If the density-dependent mortality found for cohort 79 was related to pest pressure, as it is for juveniles of this species (Gilbert et al. 1994), pathogens or herbivores may have already been at unusually high levels, leading to greater pest-related mortality in cohort 81 than in cohort 79. The *Phytophthora* canker disease that affects juveniles of *O. whitei* can affect small saplings (G.S. Gilbert, unpublished data), but we do not know how much seedling mortality in the current study can be attributed to this disease.

Finally, the first census for cohort 79 seedlings occurred approximately 8 months after seeds fell, whereas the first census for cohort 81 was 12 months after seed fall (Table 1). The greater time for accumulated mortality for cohort 81 is perhaps the most likely explanation for the apparent difference in first-year mortality between cohort 79 and cohort 81.

The spatial pattern of mortality of *O. whitei* seedlings is consistent with the predictions of the Janzen-Connell model for how plant pests can affect the spatial distribution of their hosts. In the model, plant pests that act with greater severity at high host densities or that spread to offspring from parent trees, cause disproportionately greater seedling mortality among seedlings close to parent trees than among seedlings dispersed to greater distances. This leads to a gradual shift in spatial distribution away from parents, as well as decreasing the spatial clumping of the populations. Although we do not know whether pests or pathogens were important in seedling mortality for *O. whitei* during the years of this study, both diseases and insect pests have been shown to behave in a manner consistent with the Janzen-Connell model for several host species in tropical forests, including *O. whitei* (Clark and Clark 1984, 1985; Augspurger 1990; Gilbert et al. 1994). Distance to nearest adult was not included in the best-fit logistic regression model because the high correlation between distance and

density means that most of the information included in distance measurements was included in seedling density. However, when density was left out of the model, distance was a significant contributor to the regression.

Mortality caused by processes that are not inherently density dependent, such as falling branches or rooting peccaries, may possibly have made spurious contributions to the observed patterns of density-dependent mortality. This could have happened if such disturbances occurred randomly with respect to high- and low-density areas, resulting in higher per capita probabilities of mortality where individual disturbance events affect many near neighbors in high-density areas, but very few individuals in low-density areas. The large sample size and long-term nature of this study should buffer the analyses from a substantial influence of such density-independent disturbances. Nevertheless, elucidating the causes of the observed density-dependent mortality requires additional experimental studies.

Mortality that is dependent on seedling size, density, or distance to adults is important in determining which seedlings will survive to recruit into larger size classes. The resulting population and community structure is distinct from that which would result from random survival of dispersed seeds. In addition, natural selection may favor characters such as disease resistance or increased tolerance to herbivory, through non-random mortality of seedling genotypes. However, events like the severe El Niño drought may lead to mortality that is independent of pest distribution or seedling size and age, temporarily overwhelming these non-random processes. Only long-term studies conducted in the field can determine the ultimate contribution of any one factor operating in concert, conjunction, or contrast to the combination of other factors determining which seeds ultimately become reproductive adult trees.

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