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Source: *Ecology*, Vol. 81, No. 2 (Feb., 2000), pp. 568-584

Published by: [Ecological Society of America](#)

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Accessed: 21/01/2014 13:22

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SEEDLING DYNAMICS OVER THIRTY-TWO YEARS IN A TROPICAL RAIN FOREST TREE

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Abstract. We examined patterns of seedling recruitment and their underlying mechanisms in a population of *Chrysophyllum* sp. nov. (Sapotaceae), a shade-tolerant canopy species in mature tropical rainforest in Queensland, Australia. We considered spatial scales ranging from 1 m² to 1 ha, and temporal scales ranging from 1 to 32 yr. Over the 32-yr study period there were six episodes of very high seedling recruitment (masts) at intervals ranging from 4 to 10 yr. Less than 2% of new recruits were found in the nine censuses in other years. We found no significant correlations between the numbers of seedlings per census and either seasonal or annual rainfall, number of dry months per year, or El Niño Southern Oscillation (ENSO) events but found two correlations with mean seasonal air temperatures in the years preceding flowering. There were long-term changes in abundance in both time and space. In 1965 there were 163 seedling-sized plants in two dense patches, whereas in 1996, there were 4000 in 15 patches. Once a new patch became established, seedlings recruited there in each succeeding mast episode. Adult trees varied in their production of seedlings. Only 25% of the trees in the sample analyzed participated in all mast years; others had few seedlings for up to 28 yr before beginning to produce many seedlings. Seedlings were shade tolerant. They grew extremely slowly in the shaded understory, mean height only doubling in 27 yr. They were also quite long-lived; 6% of seedlings recruited in 1969 were still alive 27 yr later. There was little effect of natural enemies on seeds or seedlings.

We found weak positive and negative effects of density on seed germination, seedling mortality, and growth. Mortality rates of *Chrysophyllum* seedlings did not show any trends with time, nor with distance from conspecific adults. These results suggest that abundance of older stages is determined by recruitment as well as subsequent growth and mortality. Mortality rates of seedlings of species other than *Chrysophyllum* decreased with distance from adult *Chrysophyllum* trees. Under present conditions, the *Chrysophyllum* population may be increasing in relation to that of other species, perhaps leading to a reduction in tree diversity in this tropical rainforest.

Key words: *Chrysophyllum*; dispersal limitation; mastings; rain forest; recruitment, episodic; recruitment limitation; recruitment, seedling; supply-side ecology; tropical.

INTRODUCTION

The importance of studying ecological processes at several scales has often been emphasized (Grieg-Smith 1964, Allen and Starr 1982, Dayton and Tegner 1984, Wiens et al. 1986, Steele 1989, Wiens 1989, Levin 1992). The mechanisms that influence community dynamics operate at many scales of time and space, so studies at both small and large scales are needed to understand them. For example, observations made over short periods or in small areas may well miss effects of extreme events that occur rarely, or fail to detect

slow processes or mechanisms that affect large areas. Conversely, observations made only at long intervals or over large areas cannot resolve fine-scale temporal and spatial heterogeneity, nor detect the ecological mechanisms that produce these patterns. Some ecological mechanisms operate at time and space scales that differ from those of the patterns they produce; thus relatively short-lived weather events or sudden biological changes may have significant long-term effects (Connell et al. 1997a). In particular, when rates of change are very slow, or when crucial events occur only rarely (e.g., extremely strong storms or widely separated recruitment events), detecting their effects requires long term records, obtained either directly by following the fates of individuals, or indirectly from the historical or fossil records.

Long term studies assessing the establishment,

Manuscript received 4 December 1998; accepted 23 December 1998; final version received 15 January 1999.

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growth, and mortality of newly recruited seedlings are few in tropical forests (but see Connell et al. 1984, 1999, Hart 1995, Puig and Fabre 1997), despite their probable importance in influencing the population and community dynamics of tropical trees (Whitmore 1996). This paucity of studies is due in part to the difficulty imposed by the extreme variability of seedling dynamics in time and space. For example, many tropical species reproduce at irregular supra-annual intervals (Ashton et al. 1988, van Schaik et al. 1993, Newstrom et al. 1994, Hart 1995). Such masting patterns are revealed only after long-term study. The underlying causes of masting have been viewed as both a proximal response to weather conditions and as an ultimate evolved reproductive strategy (Sork et al. 1993). A likely proximal cue to masting and unusual reproductive events is temperature (Sork et al. 1993, Tutin and Fernandez 1993). For example, low minimum temperatures associated with the incursion of dry air masses into an otherwise aseasonal climate have been linked to masting events in Southeast Asia (Ashton et al. 1988). Several evolutionary advantages to masting have been proposed, e.g., the satiation of seed predators (Janzen 1969, Smith 1970, Silvertown 1980), more efficient pollination (Nilsson and Wastljung 1987, Norton and Kelly 1988, Smith et al. 1990), and delayed reproduction that allows a tree time to accumulate the resources needed to produce a large seed crop (Sork et al. 1993).

Seedling recruitment also varies over different spatial scales. Such variations may be due to processes that take place in the adult tree, or on the ground after seedfall. Thus individual adults may vary in their intensity of flowering, fruiting, and seed production over time; this may produce, at intervals, patches of seeds and seedlings near them. For example, seedlings of most pioneer species in Panama tended to be commoner in gaps close to conspecific adults, whereas seedlings of other species were further from those adults (Dalling et al. 1998). Seedlings may also be affected by local conditions on the ground, either physical, e.g., runoff in heavy rains, soil conditions, etc., or biological, e.g., treefall gaps, plant competitors, predators, herbivores, and pathogens.

How influential is seedling recruitment in determining the abundance of older life stages? In general terms, the size of a local population is determined by "supply-side" processes (recruitment, birth, and immigration) vs. mortality and emigration. Supply-side ecology (Lewin 1986) has featured prominently in marine ecology, and has led to a deeper appreciation of the roles of recruitment and dispersal in determining the distribution and abundance of local populations of marine organisms (e.g., Hjort 1914, Gulland 1982, Warner and Chesson 1985, Warner and Hughes 1988, Underwood and Fairweather 1989, and Caley et al. 1996). In terrestrial plant populations, recent theoretical (Tilman 1994, Hurlt and Pacala 1995, Hubbell 1997), and em-

pirical (Hamill 1986, Harms 1996, Dalling et al. 1998) studies have established that dispersal and recruitment limitation could be important determinants of local abundance and diversity. If rates of growth and mortality do not act in a density-dependent manner, and do not undergo trends over time, then a reasonable inference can be drawn that variation in abundance of older stages may be determined from the supply side, that is, by recruitment. However, if rates of growth and mortality are strongly density dependent, or show temporal trends, then even if recruitment were important in determining initial seedling abundance, any correlation between recruitment and the abundance of older stages would be destroyed (Warner and Hughes 1988).

We have been studying the dynamics of all tree species at a rainforest site in northeastern Australia for >30 yr, with particular emphasis on the dynamics of the smallest size classes, especially newly recruited seedlings (Connell et al. 1984, 1999). In this paper, we concentrate on *Chrysophyllum* sp. nov. (Sapotaceae), the commonest species of canopy tree (≥ 10 cm diameter at breast height) on the study plot, comprising 9.5% of the basal area and 8.7% of stems. We describe the minimum size at sexual maturity, and the rates of recruitment, growth, and mortality of newly established *Chrysophyllum* seedlings, as well as of saplings and trees, at spatial scales ranging from 1 m² to 1.7 ha, and at time scales from 1 to 32 yr. We also document temporal variation in seedling production by individual adult trees.

Using these data, we tested hypotheses concerning temporal and spatial variation in recruitment, growth, and mortality. Hypotheses concerning proximal cues to masting were tested by examining relationships between seedling numbers and long term records of rainfall and air temperatures, during several periods in the plant's life history: the time before flowering, during flowering and fruit development, and during seed germination and early seedling survival. We also looked for evidence concerning some of the ultimate evolved mechanisms that have been proposed. To test for the existence of supply-side effects, we analyzed the growth and mortality of seedlings and saplings for density dependence, both at the scale of small quadrats, and in relation to distance from conspecific adult trees, and in addition looked for long-term trends in mortality rates. Lastly, to set *Chrysophyllum* into context with other common species on the study plot, we compared their recruitment and changes in abundance to those of *Chrysophyllum* over three decades in seedlings, saplings, juvenile trees and adults.

METHODS

Study species

Chrysophyllum is a canopy tree endemic to the rainforests of northeastern Australia. (This species has not been formally described, and is referred to as *Chry-*

sophyllum sp. (=RFK/3144) in the rainforest tree key of Hyland and Whiffen (1993); Connell et al. (1984) referred to it as *Planchonella* sp. nov.) Most distributional records are from granitic soils between 15°42' and 17°5' S latitude and elevations from 600 to 1300 m above sea level, but it is also known to occur near sea level on alluvial soils. *Chrysophyllum* reproduces as a canopy or subcanopy tree, with small (<5 mm) bisexual flowers occurring in axillary or ramiflorous fascicles; they are probably pollinated by animals. The large (up to 6 cm diameter) fleshy fruits contain between one and three seeds (mean \pm 1 SD, 1.15 ± 0.42 seeds, $N = 275$), which range in dry mass from 0.2 to 6.9 g (2.4 ± 1.4 g, $N = 275$); investment in dispersal tissue (percentage of the total dry mass of the fruit that is fleshy tissue) is 57%. The species is quite shade tolerant, judged by the longevity of seedlings and saplings in the shaded understory. Trees have flowered on the study plot in January in the past four years; fruits become mature by the following September and fall in October through December. Cassowaries (*Casuarius casuarius*) and some small mammals (e.g., the musky rat kangaroo *Hypsiprymnodon moschatus*) may disperse a few seeds, but other than by fruits rolling downhill, seed dispersal appears to be minimal.

Levels of predispersal and postdispersal seed predation also appear to be very low. Only 9% of 316 seeds in the seedfall that produced the 1995 mast seedling crop showed signs of attack by boring insects, and seed damage by vertebrates was rare. Further, seeds damaged by insects or vertebrates were still able to germinate if the embryo was left intact. The main period of germination is from January to April, with a few seeds still germinating in June. Germination is hypogeal (sensu Ng 1978). The seed coat is very thin, and seeds show little or no dormancy. Seedling recruitment is episodic; as we will show below, virtually all seedlings that were recorded during the 32 yr study established in just six recruitment pulses, hereafter termed "mast years."

Study area and census methods

The Davies Creek study site (17°05' S, 145°34' E, 830 m elevation) is located on the western slopes of the Lamb Range, mountains covered with continuous rainforest on the northeastern edge of the Atherton Tableland, Queensland, Australia. The soil is derived from highly weathered granite, and annual rainfall is ~3000 mm, most of which falls in a December–April summer wet season. Mean annual daily maximum and minimum air temperatures beneath the canopy are 22.1°C and 15.2°C. The 1.7-ha study plot lies on a slope facing west to southwest, and extends from a small creek to a ridge 50 m above. The plot includes three rain forest types, ranging from complex mesophyll and notophyll vine forests in the gully and lower slopes (these approximate types 1b and 5a, Tracey 1982), to simple notophyll vine forests (type 8) on the upper

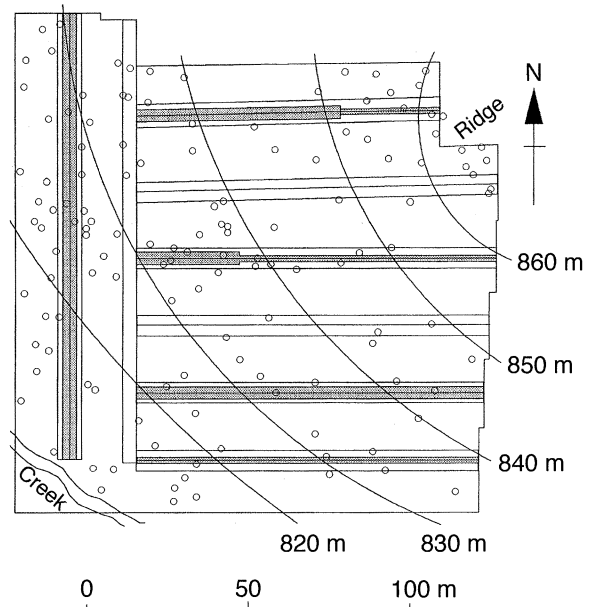


FIG. 1. Map of the study site, showing topography and transects. All trees ≥ 10 cm dbh were mapped on the entire map; the eight belt transects are where all the small trees, 2.5–9.9 cm dbh, were mapped; the shaded portions of five transects are where all the seedlings and saplings, <2.5 cm dbh, were also mapped. The circles indicate adult-sized *Chrysophyllum* trees. Elevations are shown at the end of each contour line.

slope and ridge. The canopy is 30–35 m tall, with emergent *Agathis atropurpurea* on the upper slopes. Unlike some other canopy species which occur in a narrow range of habitats on this plot, *Chrysophyllum* is common throughout the plot (Fig. 1).

The study plot and the forest surrounding it have never been significantly disturbed by humans. Australian aboriginal people never practiced agriculture (Flood 1995), so did not cut the rainforest for shifting cultivation, as occurs in rainforests in many other tropical regions. The local area has been protected from logging by the Queensland Department of Forestry since the early 1950's, when access roads were first constructed for selective logging to begin in the general area. At that time, the study plot and the forest surrounding it were set aside as an undisturbed research site (Volck 1968, Nicholson et al. 1988). The entire forested mountain range is now completely protected as part of a large World Heritage area. The forest has had a low rate of canopy gap formation during the study period; the mean percentage of the plot area opened in canopy gaps between 1963 and 1995 was 0.4%/yr (SE = 0.18); gaps have occupied a maximum of 3% of the plot area at any one time (Connell et al. 1997b).

In 1963, we measured, tagged, identified, and mapped all trees ≥ 10 cm dbh on the entire 1.7-ha plot. At the same time we also mapped all trees >2.5 <10.0 cm dbh along several belt transects 6.1 m wide, cen-

tered on survey lines, that were 20.1 m apart; these transects occupy 30% of the area of the plot (Fig. 1). All seedlings and saplings (except lianes and climbing palms) from 2 cm in height to ≤ 2.5 cm dbh were first mapped in 1965 along narrower portions (1.8 or 3.6 m wide) of some of these same belt transects; these occupy 9.6% of the plot area (Fig. 1). Thereafter, all new seedling recruits (those that had established on the standard belt transects since the previous census, and survived to the census date) were mapped, measured in height, identified, and tagged, in the period of August to October of 1969, 1971, 1974, 1978, 1981, 1983, 1988, 1990, 1991, 1993, 1995, 1996, and 1997, and in March 1986 and December 1994. Recruits were also censused on smaller portions of the permanent transects in 1976 and 1992. Mortality or damage of all previously tagged plants was assessed in censuses conducted in the period of August to October of 1969, 1971, 1974, 1978, 1981, 1983, 1986, 1988, 1990, 1992, 1996, and in February 1967, December of 1980 and 1994, and January 1986. The sizes of all survivors were remeasured in the censuses of 1978, 1986, and 1992. Thus the interval between censuses of new recruits ranged from 1 to 4 yr, for mortality from 2 to 4 yr, and for growth from 2 to 13 yr (for those first mapped in 1965). All censuses for recruitment, growth, and mortality have been repeated on precisely the same mapped areas, ensuring accuracy in temporal comparisons. Seed density was estimated by counts in quadrats (0.84 m²) in December 1990 and 1994. The positions of 235 seeds were mapped in December 1994 on these quadrats, and their germination and survival were noted between 2 February and 21 April 1995.

Recruitment at the scale of the whole plot

Aging seedlings.—Because there was variation in the interval between censuses, to ensure accuracy in comparisons among censuses we calculated the number surviving to age 2.5 yr in all censuses (this was the age of new recruits in our first census in 1969). To do this we needed to estimate the age of all *Chrysophyllum* recruits. In seven recruitment censuses the age of recruits was known, either because a census had been made in the previous year, or we had seen seedlings germinating earlier. In the other eight censuses where age was unknown, we estimated the age of seedlings using age-specific mortality rates calculated from the two cohorts of 1986 and 1991, for which we knew the survival schedule from early life. For each of these eight censuses we calculated the rate of “initial survival” over the period between the initial mapping and the next mortality census thereafter. The probable age of recruits in each of these censuses was estimated by assuming that it corresponded to the mean age of those portions of the 1986 and 1991 survivorship curves that most closely matched this initial survival. Using the survival schedules of the 1986 and 1991 cohorts, we

then calculated the number of seedlings surviving to age 2.5 yr in all censuses.

Variation in time.—We investigated two of the many possible causes of temporal variation in seedling recruitment, namely the effects of changes in rainfall and air temperature. We used weather data in years corresponding to periods of the plant's life history, as follows: (1) the year immediately preceding the census in August to October when almost all the seedlings were first mapped; this corresponds to the period when seedfall, seed germination, and early survival of seedlings were occurring; (2) the year previous to (1), which corresponds to the period of flowering and subsequent fruit development; (3) two years previous to (1), corresponding to the year before flowering; (4) three years before (1), corresponding to two years before flowering.

For each of these four yearly periods, we performed a stepwise linear multiple regression using the number of seedling recruits (standardized to 2.5 yr of age) in each of the 14 recruitment censuses of 1971 to 1997, for which we also had sufficient weather data, compared against five rainfall variables and four temperature variables. The four temperature variables were the means of the daily maximum or minimum air temperature for either the dry season (May through September), or the wet season, (November through March), for each year. Air temperature data were available for March 1968 to July 1998, from the meteorological station at Walkamin (594 m elevation, 23 km to the southwest of the study plot). Air temperatures at Walkamin and beneath the canopy at Davies Creek, from July 1994 to July 1998, were significantly correlated: Davies Creek Maximum Temp. = $1.62 + 0.72 \times \text{Walkamin Maximum Temp.}$ ($r^2 = 0.66$, $df = 237$, $P < 0.001$); Davies Creek Minimum Temp. = $1.41 + 0.85 \times \text{Walkamin Minimum Temp.}$ ($r^2 = 0.85$, $df = 237$, $P < 0.001$).

The five rainfall variables were: annual total rainfall, mean monthly rainfall in the dry season, mean monthly rainfall in the wet season, the number of dry months (those with < 100 mm rain) per year, and the minimum Southern Oscillation Index (SOI) per year, taken from the monthly SOI indices over the period from October to the next September of each year (Quinn and Neal 1983, Philander 1990).

We used rainfall data from Atherton (elevation 775 m, 28 km to the southwest of the study plot), since rainfall there and at the study site is highly correlated. For 72 periods of 1–26 d in duration, between 28 February 1995 and 11 March 1996, when some rain was recorded at one or both stations, the regression equation is: Davies Creek rain = $1.52 + 2.14 \times \text{Atherton rain}$ ($r^2 = 0.83$, $df = 70$, $P < 0.001$). Since the average annual rainfall over the past 100 yr at Atherton is 1398 mm, this equation yields an average for the study plot of ~ 3000 mm per yr. The annual rainfall at Atherton was positively correlated with the annual SOI index

for the years 1951 to 1995 ($r^2 = 0.19$, $df = 43$, $P < 0.01$). Since Ashton et al. (1988) found that masting in some species of rain forest trees in Southeast Asia was correlated with years of El Niño Southern Oscillation (ENSO) conditions, we also compared the years of mast and non-mast *Chrysophyllum* seedling crops with ENSO years, using the chi-squared test. During the study there were nine ENSO years (identified from the SOI index); these occurred in 1965–1966, 1969–1970, 1972–1973, 1976–1977, 1977–1978, 1982–1983, 1986–1987, 1991–1992, and 1993–1994 (National Oceanographic and Atmospheric Agency 1997).

Variation in space.—Seedling recruitment was spatially patchy; the boundaries of patches of dense seedlings along the transects were determined by eye, using computer-generated maps of seedling recruits at each census date. We determined the survival of seedlings in each individual patch for the four largest mast cohorts from 1969 to 1991, calculating the half-life empirically by interpolation from survivorship curves (Li et al. 1996).

Recruitment at the scale of individual adult trees

Size at sexual maturity and the size of fruit crops.—During a mast fruiting episode in October 1994, we measured the relationship between tree size, degree of illumination, and the size of the fruit crop. A total of 151 trees >2.5 cm dbh were scored on a six point scale for size of fruit crop, from none to “heavy.” The score was applied independently of their size; e.g., small and large trees could both be scored as having a heavy crop. We used the scoring system of Clark and Clark (1992) to assess crown illumination. The reproductive size threshold was calculated according to Thomas and Appanah (1995).

Variation in time among individual adults.—Mast years indicate synchrony in reproduction at the population level, but not all individual trees necessarily reproduce heavily in every mast year (Frankie et al. 1974, Bullock and Bawa 1982, Newstrom et al. 1994). We assessed whether individual trees did or did not participate in each mast year, by comparing their seedling production to the average of the other *Chrysophyllum* trees in that year. To do this, we first assumed that any seedling in the immediate vicinity of a reproductive-sized tree was likely to have been its own offspring, and further assumed that most of its offspring established within its “crown zone,” the area within twice the radius of its crown (in *Chrysophyllum*, crown diameter (in meters) = $2.14 + 0.13 \times (\text{dbh in cm})$; $N = 21$, $r^2 = 0.64$). These assumptions are reasonable given the fact that 92.3% of seedling recruits occurred within two crown radii of a *Chrysophyllum* adult, as discussed in the section: *Seedling recruitment at the scale of individual adult trees*.

Next, we identified those trees whose crown zones overlapped the seedling transects, but which were also isolated from other adult conspecifics such that their

crown zones either did not overlap, or the regions of overlap were very small. Any seedlings in the overlap area of the crown zones of two adult trees were not included in the analyses, because they could have come from either adult. For each mast year, for each of these isolated individuals, we then tallied the number of seedlings present on the area of the seedling transect that was overlapped by its crown zone. This area varied from tree to tree, since the area of transect encompassed by the crown zone of a tree depends upon its size and distance from the belt transect. To ensure an adequate sample size we included only those adults whose crown zone overlapped at least 7 m² of the transect, since this area was the minimum that contained ≥ 100 seedlings of all species combined. These calculations assume that a tree is vertical, with a circular crown centered on its base. Our analyses indicated that several trees produced very few seedlings during the study; these were checked in the field, and if they were leaning away from the transects, were excluded from further analysis, since their actual crown would not have overlapped the transect.

For each tree we calculated the proportion of seedlings in each year out of the total number recorded in the five largest mast years. (Due to constraints of sample size, the 1971 mast year was not included in these analyses.) Since the total number of seedling recruits sampled on the entire plot varied among the five mast years, we standardized the observed proportion for each tree in each year by the following equation: [(proportion for tree A)_{*t*} – (proportion for all trees combined)_{*t*}] ÷ (proportion for all trees combined)_{*t*}, where *t* refers to a particular mast year. We used a quotient of < -0.70 as the threshold to infer that an individual had had an unusually low seedling production in that year, i.e., that it had “missed” participating in that mast year.

Growth and mortality of seedlings and saplings

We calculated annual relative mortality rate as $(\ln N_{t_2} - \ln N_{t_1}) / (t_2 - t_1)$, in which *N* refers to the number, and *t*₁ and *t*₂ (with units in years), are the initial and final census dates, respectively (Harper 1977, Swaine and Lieberman 1987, Shiel and May 1996). Ln stands for a natural log. Growth was calculated as $(H_{t_2} - H_{t_1}) / (t_2 - t_1)$, where *H* refers to the height of the seedling or sapling. To look for trends in mortality over time, for each mast year cohort we calculated the mortality rate of seedlings within a short age span. For each age group, we regressed the mortality rate of each mast year cohort against its initial year. Regressions used the following data: for mortality of seedlings of ages 0.5–2.5 yr, data were available from five mast cohorts from 1971 to 1995; for seedlings of ages 2.5–4.5 yr, data from five mast cohorts, 1969 to 1991, and for ages 3.5–5.5 yr, data from three mast cohorts, 1969 to 1978. We also calculated the half-life of seedling year classes empirically by interpolation from survival curves (Li

et al. 1996). We measured recruitment by growth into the two size groups, >2.5 <10.0 cm dbh, and ≥ 10.0 cm dbh at each census.

To determine whether rates of mortality and growth of *Chrysophyllum* seedlings and saplings were density dependent, we did two types of analysis. First, at the scale of small quadrats, we regressed these rates against the density of their conspecifics in quadrats. We used two different measures of conspecific density; (1) the number of seedling recruits in each quadrat from the single cohort being analyzed (the 1978, 1986, and 1991 mast recruitment years), and (2) these recruits plus any others surviving from previous years. To obtain sufficient sample sizes we used quadrats of 6.7 m², and a minimum of six seedlings per quadrat for growth, and 15 for mortality. We also tested for density-dependent mortality in older classes of seedlings and saplings of unknown age mapped in 1965. Because the densities of the latter were lower than those of recruits, to obtain sufficient sample sizes we used quadrats of 28 m², with a minimum of five plants per quadrat.

Second, since density dependence can also apply to the interaction between seedlings and adults, we calculated the distance of each seedling recruit from the nearest conspecific adult. Because large adult trees probably exert their influence over a greater distance than do smaller ones, we expressed this distance in units of the radius of the crown of the particular adult that was nearest to it. We calculated the numbers and mortality of seedlings of *Chrysophyllum* and that of all other species combined, in classes of increasing distance from *Chrysophyllum* adults. The purpose of the group of other species was to serve as a control, since adult *Chrysophyllum* were so common and widespread (Fig. 1) that most seedlings of other species would occur fairly close to them. Dalling et al. (1998) used the same comparison for seedlings of pioneer species in Panama. We used the seedlings of other species rather than randomly-placed points, since the former occur only in those sites that could possibly be occupied by seedlings. Annual mortality rates were calculated for each census year class over the interval between the initial mapping and the first census thereafter; in the present analysis the rate for each class of distance from adult *Chrysophyllum* was the mean of these annual rates over all year classes.

The performance of Chrysophyllum relative to other species

To place *Chrysophyllum* in the context of the entire rainforest tree assemblage, we compared changes in its recruitment and abundance to those of the other tree species on the study plot, in each of the following categories: (1) the total numbers of seedling recruits that appeared between 1965 and 1996, and (2) changes in abundance between 1965 and 1994, within each of the following five size classes: (≤ 0.3 m ht., >0.3 <1.0 m ht., 1 m ht. <2.5 cm dbh, 2.5 <10 cm dbh, and

≥ 10 cm dbh). To assess the degree of synchrony of recruitment of *Chrysophyllum* with that of other species, we correlated its number of seedling recruits at each census with those of 16 other species, either individually, or as a group, using Kendall's Concordance Coefficient (Siegel 1956). These 16 species were chosen as the ones most likely to have had supra-annual episodic recruitment, judged from the high variation in their abundances among the censuses (i.e., a CV > 100 , and a range in abundance of >50). We also compared the CV of *Chrysophyllum* with that of 45 other species that had >100 seedling recruits between 1965 and 1996.

RESULTS

Seedling recruitment at the scale of the whole plot

Variation in time.—The *Chrysophyllum* population on the study plot recruited seedlings episodically at supra-annual intervals between 1965 and 1997 (Fig. 2). Six censuses (in 1969, 1971, 1978, 1986, 1991, and 1995) represented mast episodes, when 98.3% of all new *Chrysophyllum* recruits were recorded. Based either on direct observation in four mast years, or on our calculations of the age of the recruits in 1971 and 1976, the years when these recruits actually germinated were 1967, 1971, 1976, 1986, 1991, and 1995, with an average interval of 5.6 yr (1 SE = 1.1). We are confident that our records showing very poor recruitment in the years between these mast episodes are accurate, given that the censuses were closely spaced, and *Chrysophyllum* seedlings have very good survival (as discussed in the section: *Growth and mortality of seedlings and saplings*). The number of *Chrysophyllum* seedlings present on the plot increased substantially during the study period (Fig. 3). Only 163 *Chrysophyllum* of seedling size (≤ 0.3 m in height) and unknown age were mapped in 1965. Thereafter, the total numbers of seedling-sized plants present gradually increased. At each mast episode the numbers rose, then fell sharply as the young seedlings died. Since the rise during each mast episode exceeded the following decline (except for the mast of 1971), the total numbers gradually rose. By 1996 the total had reached 4000 seedling-sized plants, greater than a 24-fold increase since 1965 (Fig. 3).

With regard to the proximal causes of episodic recruitment in *Chrysophyllum*, in the stepwise multiple regression analyses of each of the four life history periods analyzed, we found only two significant relationships between the numbers of seedlings in the 14 censuses from 1969 to 1995, and any of the rainfall and temperature variables tested. First, the mean maximum temperatures in the summer season one year before flowering were negatively correlated to numbers of seedlings ($r^2 = 0.336$, $P = 0.024$, $df = 12$). Second, in the winter season two years before flowering, the mean minimum temperature and seedling numbers



FIG. 2. Numbers of seedling recruits of *Chrysophyllum* that became newly established between censuses since 1965. The data are plotted on the year of germination of the seedlings; numbers refer to seedlings at age 2.5 yr.

were positively correlated ($r^2 = 0.30$, $P = 0.042$, $df = 12$). In neither of these analyses did adding another independent variable in the next step significantly increase the coefficient of determination. Also, we found no relationship between the nine ENSO years that occurred during the study period (1965–1996) and years of mast seedling numbers.

Variation in space.—Seed fall and seedling recruitment were often dense and patchy in the mast years. In December 1990, seed density was $6.7 \pm 11.3/\text{m}^2$ (mean ± 1 SD; range 0–86, $N = 126$), and in December 1994, seed density was $14.5 \pm 47.7/\text{m}^2$ (range 0–242,

$N = 110$). The ratio of 1 SD/mean was 1.7 in 1990, and 3.3 in 1994, indicating a patchy distribution of seeds in both years. Of 235 individual seeds mapped in December 1994, 79.6% germinated between 2 February and 21 April 1995, and 81.3% of these germinants were still surviving at the latter date.

Newly germinated seedlings reached a maximum density of $140/\text{m}^2$ in 1995, with densities of $>25/\text{m}^2$ covering tens of square meters in extent. Since new seedlings were 5–20 cm in height, in mass recruitment years their leaves often covered the ground almost completely. At each succeeding episode of mass recruitment, dense patches of recruits appeared in new locations. (In all cases, a few seedlings were present at these locations in previous years.) In 1965, 74% of all existing seedlings (≤ 0.3 m) were concentrated in two patches (Fig. 4). During the first masting episode in 1969, four more dense patches appeared in new locations. Patches continued to appear in new locations at each succeeding masting episode until 1991, when there were 15 patches; no new patches appeared in 1995, although new recruits appeared at all of the 15 locations where patches had occurred earlier (Fig. 4). Thus once a patch appeared, dense recruitment usually continued there in succeeding mast years.

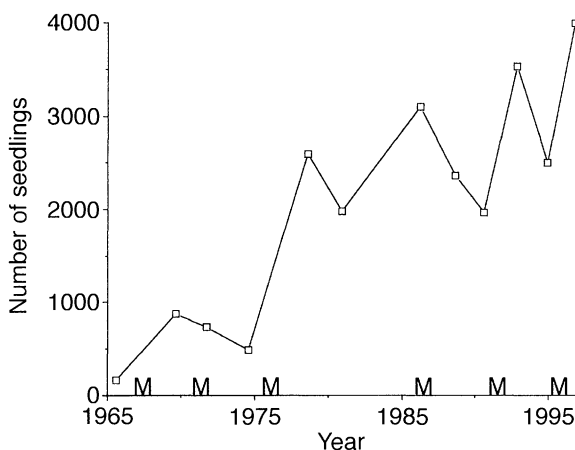


FIG. 3. The gradual increase in density of live *Chrysophyllum* seedlings on the standard census transects through time. The numbers in 1965 refer to those ≤ 30 cm in height. The values for 1980 and 1992 are slight underestimates. The letter M indicates a mast year.

Seedling recruitment at the scale of individual adult trees

Size at sexual maturity and the size of fruit crops.—Individual trees varied in the size of their fruit crop produced during the mast year of 1995. The threshold of reproductive size in October 1994 was 10.5 cm dbh; no trees smaller than this had any fruit, whereas 87%

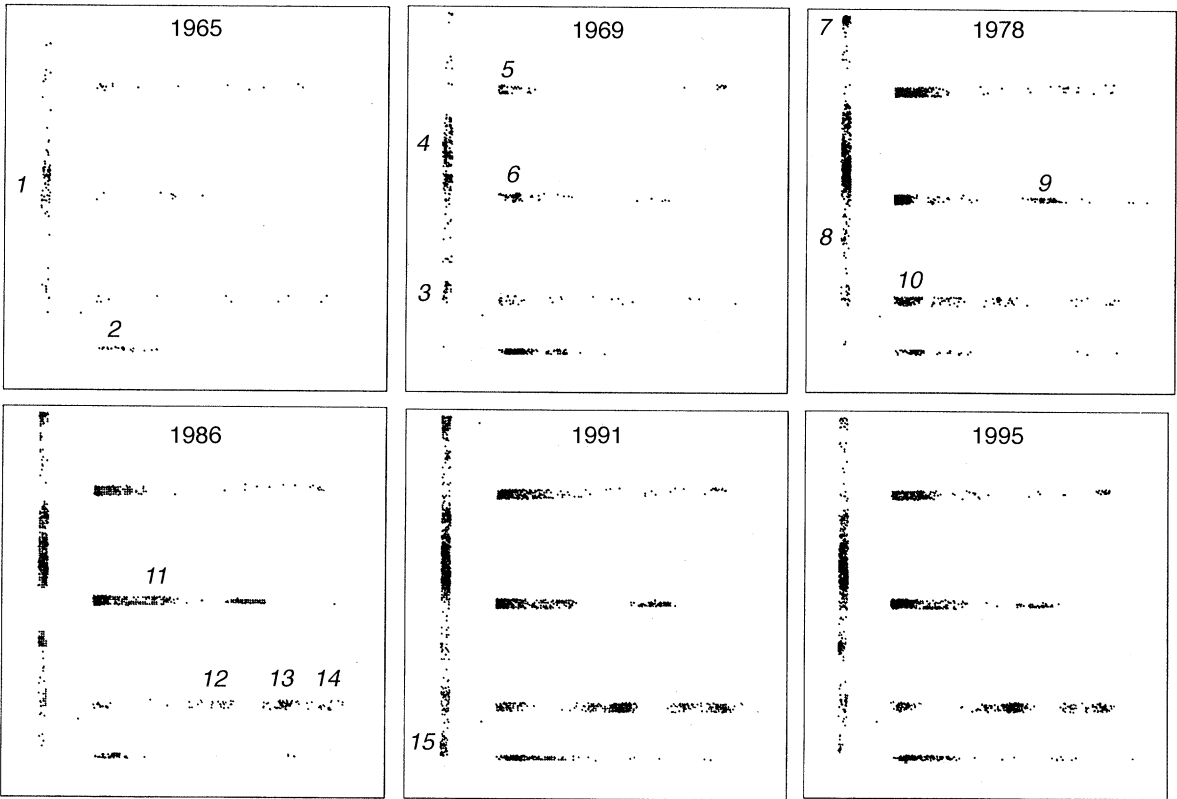


FIG. 4. The distribution of *Chrysophyllum* seedling recruits on the belt transects (see Fig. 1) in mast years. Each map shows only those seedling recruits that appeared for the first time in that year's census. The 1965 map shows the patches of seedling-sized *Chrysophyllum*, of unknown age, present at the initial mapping. The dense patches are numbered as they appeared from 1965 to 1991.

of trees >10.5 cm dbh had some fruit, although some large trees had few or no fruit (Table 1). A multiple linear regression analysis showed that the relative size of the fruit crop was highly positively correlated with

tree size, but less so with crown illumination index once the effect of size was removed (Table 1).

Variation in time.—Twenty adult trees were sufficiently isolated from other conspecific adults, and close

TABLE 1. Fruiting vs. tree size and crown illumination.

Tree size class (dbh; cm)	Number of trees	Fruiting index		Number of trees in each size class with the following fruiting indices					
		Mean	1 SE	0	1	2	3	4	5
a) Fruiting index (range 0 to 5) for different-sized trees									
2.6–10.4	46	0.00	0.00	46	0	0	0	0	0
10.5–19.9	39	1.62	0.19	10	6	13	9	1	0
20.0–29.9	25	2.40	0.19	2	1	8	13	1	0
30.0–39.9	20	2.70	0.26	1	2	4	9	3	1
40.0–49.9	13	2.91	0.19	0	0	1	9	2	1
≥50.0	8	2.75	0.53	1	1	0	3	3	0
b) Multiple regression: fruiting index vs. tree size and crown illumination index, df = 147									
		Coefficient							
Independent variable		Mean	1 SE		<i>t</i>			<i>P</i>	
Intercept		−0.12	0.28		−3.31			0.0012	
Crown index		0.64	0.17		3.77			0.0002	
Diameter (dbh)		0.12	0.01		9.06			<0.0001	
Crown index × dbh		0.005	0.005		−4.72			<0.0001	

TABLE 2. Number of seedlings produced by individual adult trees of *Chrysophyllum*, during each of five mast years; dates indicate the year seedlings germinated.

Tree no.	Size†	Number of seedlings on the standard transects produced by each tree in each mast year						No./m ²	Relative seedling production [(% observed - % all trees combined) ÷ (% all trees combined)]					Longest interval between masts	
		1967	1976	1986	1991	1995	Total		1967	1976	1986	1991	1995	Dates‡	Length (yr)
93	54.2	3	45	9	11	28	96	1.3	-0.65	1.44	-0.38	-0.62	0.09	76-86	10
259	32.3	8	13	6	26	9	62	7.7	0.46	0.09	-0.36	0.38	-0.45	76-86	10
720	38.0	38	29	18	26	33	144	18.2	1.98	0.04	-0.17	-0.40	-0.13	76-86	10
980	50.1	7	38	4	31	7	87	4.0	-0.09	1.28	-0.69	0.16	-0.69	76-86	10
7431	26.7	3	3	24	7	7	44	1.7	-0.23	-0.65	2.63	-0.48	-0.40	76-86	10
418	25.1	4	56	53	35	23	171	26.1	-0.74	0.70	1.06	-0.33	-0.49	65-76	11
7035	42.9	0	4	4	16	22	46	4.2	-1.00	-0.55	-0.42	0.17	0.77	65-76	11
7636	32.3	3	42	50	18	43	156	6.5	-0.78	0.41	1.14	-0.62	0.03	65-76	11
936	44.5	10	54	1	10	17	92	2.3	0.22	2.04	-0.93	-0.64	-0.29	76-91	15
995	24.3	2	18	3	45	31	99	3.9	-0.77	-0.06	-0.80	0.49	0.19	76-91	15
716	44.5	39	2	7	7	6	61	5.3	6.19	-0.83	-0.24	-0.62	-0.63	67-86	19
1075	30.7	3	3	56	27	9	98	6.0	-0.65	-0.84	2.79	-0.09	-0.65	67-86	19
733	12.1	24	8	0	1	8	41	1.4	5.56	0.01	-1.00	-0.92	-0.25	76-95	19
1090	29.1	0	6	13	49	46	114	4.0	-1.00	-0.73	-0.24	0.40	0.54	65-86	21
201	45.3	1	3	1	45	12	62	1.5	-0.82	-0.75	-0.89	1.39	-0.27	65-91	26
1008	34.8	3	2	5	163	108	281	13.1	-0.88	-0.96	-0.88	0.90	0.46	65-91	26
728	10.5	6	3	2	5	43	59	4.4	0.15	-0.73	-0.77	-0.72	1.75	67-95	28
469	20.2	0	3	2	6	4	15	1.8	65-97	32
875	15.4	0	1	0	0	2	3	0.2	65-97	32
7472	23	0	1	3	0	1	5	0.2	65-97	32
Number of seedlings:															
		154	334	261	527	459	1735								
Percentage of total seedlings:									8.87	19.24	15.05	30.38	26.45		

Notes: The numbers underlined in columns 10-14 indicate the years when a tree produced a much lower proportion of seedlings than the average for all trees in that year. Note that seedling numbers refer only to those on the standard transects, not to the total production by the tree. The numbers of seedlings were standardized to age 2.5 yr.

† Size is reported as dbh (cm) in 1963.

‡ Endpoint years of interval (e.g., "76-86" indicates mast years in 1976 and 1986).

enough to the census transects, for their seedling productivity to be analyzed. Of these, three trees (No. 469, No. 875, and No. 7472) had very few seedlings mapped beneath their crown areas in the period from 1965 to 1997, indicating that they had probably contributed almost no seedlings for at least 32 yr (Table 2). The five trees listed first in Table 2 had no strikingly low years among the five mast years included in the analyses, so the longest interval between successful mast years was the 10-yr period between the masts of 1976 and 1986. The other 12 trees had some significantly low years, when in effect they missed a mast year. Some trees missed two or more mast years in succession, then produced many recruits in the subsequent masts (e.g., No. 1090, No. 201, No. 1008, and No. 728, Table 2). Among these, the tree with the longest interval between masts was No. 728, 1967-1995, 28 yr.

These 17 trees were highly synchronized when data on numbers of seedling recruits from 13 census years are included in the analysis (Kendall's Coefficient of Concordance $W = 0.655$, $\chi^2 = 126$, $df = 12$, $P < 0.001$), but less so when only the five largest mast seedling years were analyzed ($W = 0.232$, $\chi^2 = 14.8$, $df = 4$, $P < 0.01$). Thus the synchrony among these

trees was probably due to the high variation in numbers among years.

Variation in space.—The great majority of *Chrysophyllum* seedlings were very close to adult conspecifics; only 7.4% were beyond two adult crown radii, and none were beyond six radii (Fig. 5). Because *Chrysophyllum* adults were common and widespread on the plot, most seedlings of other species were also close to adult *Chrysophyllum*. However, in contrast to *Chrysophyllum* seedlings, 48.8% of the seedlings of other species were beyond two crown radii from an adult *Chrysophyllum*, ranging up to 50 radii away (Fig. 5).

Growth and mortality of seedlings and saplings

Growth.—*Chrysophyllum* seedlings grew extremely slowly in the shaded understory. The mean height of seedlings that germinated in 1967 and survived until 1996 increased from 17.5 ± 1.1 cm (mean ± 1 SE, $N = 26$) in 1969 to 34.9 ± 3.5 cm in 1996, only doubling in 27 yr. Similarly slow growth was observed in a larger sample ($N = 408$) that germinated in 1986: the average height of seedlings increased from 19.2 ± 0.3 to 22.9 ± 0.3 cm from 1986 to 1992.

Mortality.—*Chrysophyllum* seedlings are quite long

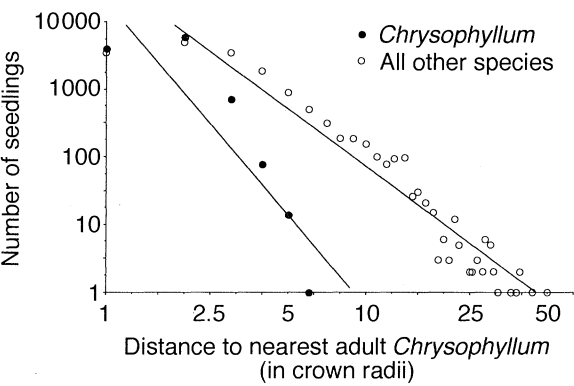


FIG. 5. Distance from the nearest living adult *Chrysophyllum* for all seedlings of *Chrysophyllum* and for the set of seedlings of all other species that appeared between 1965 and 1995. Note log scales. The units of distance are multiples of crown radii; they are scaled to the size of each adult tree. Regression equations: for *Chrysophyllum* seedlings, $\log(\text{number of seedlings}) = 4.38 - 4.54 \times \log(\text{distance to nearest living adult } Chrysophyllum)$, $r^2 = 0.786$, $N = 6$, $P = 0.0187$; for seedlings of all other species, $\log(\text{number of seedlings}) = 4.67 - 2.83 \times \log(\text{distance to nearest living adult } Chrysophyllum)$, $r^2 = 0.913$, $N = 22$, $P = 0.0001$.

lived; 10% of seedlings (≤ 0.3 m) of unknown age mapped in 1965 were alive 31 yr later, and 6% of those newly recruited in 1967 and mapped in 1969 at age 2.5 yr, were still alive 27 yr later (Fig. 6). The 1986 mast cohort was mapped soon after germination; its half-life from age 0.1 yr was 5.5 yr. Survival varied among the different mast seedling cohorts. Beginning at age 2.5 yr, the 1978 year class had higher survival to age 10 yr than the other cohorts, but in its older years its survival was poorer than the 1969 and 1971 cohorts (Fig. 6). Mortality in individual patches also varied among year classes, as shown by their half-lives,

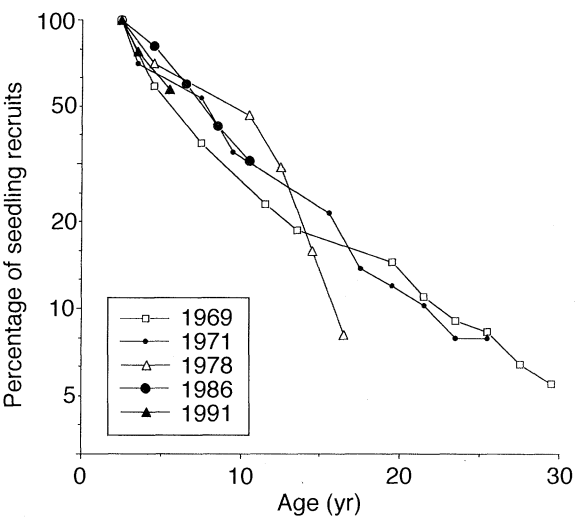


FIG. 6. Survival of seedling recruits of *Chrysophyllum*, from five mast years. The years indicate when the recruits were initially mapped; the survival curves all begin with the number of seedlings aged 2.5 yr. Note log scale on y-axis.

which measure survival only during the younger years. The patches in the 1978 year class had much longer half-lives than those of any other year class (Table 3). Survival varied spatially among the different patches of a given year class, half-lives ranging 2 to 5-fold. However, there was more variation among years within a patch than among patches within a year, judging by the coefficients of variation shown in Table 3.

When the mortality rates of seedlings of the same age span among different mast year cohorts were regressed against the year of their first mapping, there were no trends with time. The coefficients of determination from linear regressions of annual mortality

TABLE 3. Survival of *Chrysophyllum* seedlings in patches from four years of mass recruitment.

Patch no.	Patch age in 1991 (yr)	Patch area (m ²)	Half-life (mo)				Mean	cv
			1969	1978	1986	1991		
1	26.1	67.0	25.0	106.5	76.1	52.2	64.9	53.4
2	26.1	50.2	40.0	99.1	nd	10.2		
3	22.1	16.7	37.2	75.1	17.3	54.6	46.1	53.5
4	22.1	39.1	19.4	145.4	56.0	36.8	64.4	87.0
5	22.1	44.6	19.8	97.6	39.8	40.5	49.4	67.9
6	22.1	33.5	48.4	124.0	47.1	44.4	66.0	58.7
7	13.1	33.5	...	76.9	53.5	48.0		
9	13.1	27.9	...	93.1	23.6	26.2		
10	13.1	44.6	...	96.4	nd	28.2		
11	5.6	78.1	64.1	47.3		
12	5.6	50.2	53.4	nd		
13	5.6	39.1	nd	nd		
14	0	37.9	53.3		
15	0	94.9	54.9		
Statistics for patches 1–6								
Mean			31.6	108.0	47.3	39.8		
cv			37.9	22.4	45.7	40.2		

TABLE 4. Tests of intraspecific density dependence in seeds, seedlings, and saplings.

Regression equation: Rate = $a + b \times \log(\text{density})^\dagger$							
Time period	a	b	N	r^2	P	Age at start (yr)	Density dependence
A) Seed germination [$\log(\%$ germination, Dec. 1994–Apr. 1995) vs. no. seeds/0.84 m ² in Dec. 1994]							
	1.006	0.313	24	0.033	>0.10	1	none
B) Relative mortality per year							
Cohorts of newly recruited seedlings							
Density of that cohort of seedlings only							
1978–1980	0.83	5.66	33	0.059	>0.10	2	none
1986–1990	25.02	−7.46	36	0.176	0.01	0.1	positive
1991–1994	10.67	4.01	52	0.066	>0.05	1	none
Density of all seedlings present							
1978–1980	−2.47	7.55	33	0.094	>0.05	2	none
1986–1990	24.38	−6.35	36	0.181	0.01	0.1	positive
1991–1994	9	4.61	52	0.106	<0.02	1	negative
Older seedlings, mapped in 1965 (≤ 0.3 m in height)							
1965–1971	40.7	0.22	8	0.027	>0.10	unknown	none
1971–1993	82.3	−2.32	8	0.001	>0.10	unknown	none
Saplings, mapped in 1965 (> 0.3 m in height, < 2.5 cm dbh)							
1965–1971	−11.3	26.7	15	0.39	<0.02	unknown	negative
1971–1993	20.2	27.3	15	0.097	>0.10	unknown	none
C) Growth (height; m/yr)							
Cohorts of newly recruited seedlings							
Density of that cohort of seedlings only							
1986–1992	38.42	−11.46	26	0.01	>0.10	0.1	none
1991–1996	69.47	−26.24	28	0.31	<0.01	1	negative
Density of all seedlings present							
1986–1992	3.15	−0.136	26	0	>0.10	0.1	none
1991–1996	13.46	−4.44	28	0.213	<0.02	1	negative

Note: See *Methods: Growth and mortality of seedling and saplings* for methods of calculating rates of growth and relative mortality.

\dagger Density = no. seedlings or saplings per quadrat.

rate vs. year from 1969 to 1991 were as follows: for the age class 0.5–2.5 yr, $r^2 = 0.34$ ($N = 5$), for ages 2.5–4.5 yr, $r^2 = 0.20$ ($N = 5$), and for ages 3.5–5.5 yr, $r^2 = 0.18$ ($N = 3$). None were statistically significant ($P > 0.10$).

Density dependence

To investigate supply-side effects, we looked for evidence of density dependence in seed germination, seedling survival and growth (Table 4). Initial seed density had no effect on survival to germination. In six tests of the effects of density of conspecifics on mortality of newly recruited seedlings (cohorts of 1978, 1986, or 1991) we found two positive effects (mortality decreasing with increasing density), and one negative effect, but density explained relatively little of the total variation on survivorship (all $r^2 < 0.20$, $P < 0.05$). We found no density-dependent effects in two tests with seedlings of unknown age mapped in 1965, but with small saplings mapped in 1965, mortality increased with increasing density in one of the two periods analyzed. Growth decreased with increasing density in quadrats in the cohort of newly recruited seedlings of

1991, but not in that of 1986 (Table 4). There was no significant trend in mortality of *Chrysophyllum* seedlings with increasing distance from conspecific adult trees, but in the group of all other species combined, mortality of seedlings decreased significantly with increasing distance from adult *Chrysophyllum* trees (Fig. 7).

Performance of *Chrysophyllum* relative to other species

Chrysophyllum had the most recruits of any species during the 32-yr study, and was the commonest species in the three smallest size classes when they were first mapped in 1965 (size classes ≤ 0.3 m ht.; $> 0.3 < 1$ m ht.; $1 \text{ m ht.} < 2.5 \text{ cm dbh}$). By 1994, it had maintained its rank as the commonest species in the first two of these size classes, and ranked second in the third size class. In the small tree size class ($2.5 < 10 \text{ cm dbh}$) it ranked fourth in both 1963 and 1994. *Chrysophyllum* was the commonest species among trees $\geq 10 \text{ cm dbh}$ in both 1963 and 1994.

There was no significant synchrony of recruitment among the group of 16 species (that included *Chry-*

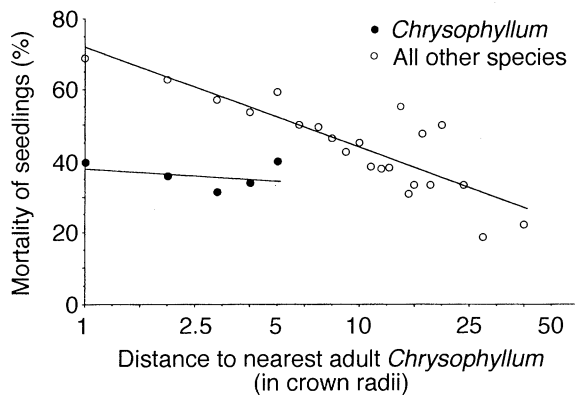


FIG. 7. Annual mortality rates of seedlings for *Chrysophyllum* and for the set of all other species, in relation to their distance to the nearest living adult *Chrysophyllum* (units as in Fig. 5). Regression equations: for *Chrysophyllum* seedlings, (% mortality of seedlings) = $37.70 - 3.55 \times \log(\text{distance to nearest living adult } Chrysophyllum)$, $r^2 = 0.069$, $N = 5$, $P = 0.670$; for seedlings of all other species, (% mortality of seedlings) = $72.03 - 28.36 \times \log(\text{distance to nearest living adult } Chrysophyllum)$, $r^2 = 0.726$, $N = 21$, $P = 0.0001$. To ensure an adequate sample size, we combined the number of seedlings of species other than *Chrysophyllum* at distances from 30.1 to 50 crown radii. Note log scale on x-axis.

sophyllum) with the most variable recruitment (Kendall's Concordance Coefficient $W = 0.08$, $N = 14$ censuses, $P > 0.05$). Recruitment was significantly positively correlated to that of *Chrysophyllum* in only one of these 16 species (*Cryptocarya grandis*, Lauraceae; $r^2 = 0.75$, $N = 14$, $P < 0.01$). The recruitment rates (number of seedlings/census) of species that had produced many seedlings were all quite variable. The cv of the 46 species that had at least 100 seedling recruits between 1965 and 1996, ranged from 55 to 269. With a cv of 145, *Chrysophyllum* ranked 14th in variability among the 46 species.

Long-term changes in abundance of *Chrysophyllum*

Seedling-sized plants increased in abundance 24-fold over three decades (Table 5). This was accompanied by a 1.8-fold increase in both the saplings and juvenile trees, and in adults, a decrease of 14% in numbers and 16% in basal area (Table 5). There were fewer seedlings than saplings in 1965, but by 1996, seedlings were 10 times more abundant. Saplings remained 12 times as abundant as juvenile trees in both 1965 and 1996; the juvenile trees were 1.6 times as common as adult trees in 1963, and increased to 3.4 times as common as adults in 1996 (Table 5).

DISCUSSION

Variation in seedling recruitment at the population level: masting

Plants display a continuum of reproductive patterns, from species that flower almost continuously throughout the year, to others that reproduce in discrete episodes at intervals of several years (Janzen 1978, Silvertown 1980, Newstrom et al. 1994). Among the latter "masting" species, few show a "strict" masting pattern with no reproduction at all in the years between masts (Kelly 1994). Rather, most show at least some reproductive effort between masts, albeit at very low levels. Trees that show this pattern are species in several families in tropical rain forests in Southeast Asia (Ashton et al. 1988, Yap and Chan 1990), and several oaks in temperate forests in the United States (Sork et al. 1993, Koenig et al. 1994, Koenig and Knops 1995). Our seedling data indicate a similar phenomenon in *Chrysophyllum*; although more than 98% of all seedlings were recorded in six mast years, a few new seedlings were still recorded in the intervening years. Further, we have observed very low levels of flowering and fruiting during each of the four annual flowering seasons since the last mast fruiting in 1994 (P. T. Green, unpublished data). Several other species of Sapotaceae also mast in Southeast Asia (Appanah 1985, Ashton et

TABLE 5. Changes in abundance of the different size classes of *Chrysophyllum* over 32 yr.

Measure and size class	Size range	Abundance†		Change over time (ratio 1996/1963)	Transition between size classes (small/large)	
		1963 or 1965	1996		1963 or 1965	1996
Number (stems/ ha)						
Seedling recruits	≤0.3 m ht.	...	24 931			
Older seedlings	≤0.3 m ht.	1035	25			
All seedlings	≤0.3 m ht.	1035	24 956	24.3		
Saplings	0.3 m ht. to 2.5 cm dbh	1327	2 383	1.8	0.8	10.5
Juvenile trees	2.5–9.9 cm dbh	106	192	1.8	12.5	12.4
Adult trees	≥10 cm dbh	65	56	0.9	1.6	3.4
Basal area (m²/ha)						
Juvenile trees	2.5–9.9 cm dbh	0.23	0.34	1.5		
Adult trees	≥10 cm dbh	4.98	4.18	0.8		

† Abundance at the start of the study refers to 1965 for the seedlings and saplings, and to 1963 for juvenile and adult trees.

al. 1988). In contrast, another *Chrysophyllum* species, *C. albidum*, showed no evidence of masting behavior over a ten year period in a Ugandan rainforest (Struhsaker 1997).

Chrysophyllum is typical of many other masting species in that it is relatively large seeded, long lived, and slow to mature (Waller 1993), but may be unusual in that only two other studies have documented masting in a fleshy-fruited species (Norton and Kelly 1988, Herrera et al. 1994). However, our seedling recruitment and phenological data together suggest that most of the common canopy species at the present Queensland study site may show masting behavior, including the fleshy-fruited species *Cryptocarya angulata* and *Beilschmiedia bancroftii* (Lauraceae) (Connell et al. 1999). Further, the long intermast periods observed for *Chrysophyllum* may not be unusual in other species at this site; one wind-dispersed species, *Ceratopetalum succirubrum* (Cunoniaceae), has probably only masted twice since 1965 (Connell et al. 1999).

Both temperature fluctuations at critical periods and ENSO conditions have been suggested to be important cues to masting events in Southeast Asia (Ashton et al. 1988). However, few of our tests of these hypotheses revealed any significant relationships between seedling production by *Chrysophyllum* and weather, neither as annual or seasonal rainfall, including dry periods and ENSO episodes, nor as mean seasonal air temperatures. Only two relationships between numbers of seedling recruits and mean seasonal air temperatures were significant, both applying to the years before flower initiation; none were significant during flowering, fruiting, seed germination, or seedling survival. Also, there were no significant interactions between effects of any two of the independent variables. The results of Sork et al. (1993) caution against searching for a single environmental factor that is correlated with masting events. However, our analyses have tested for two of the factors that could be considered as likely to affect long term variation in seedling recruitment. That variations in temperature in the years before flowering could affect subsequent flowering of *Chrysophyllum* is reasonable, since variation in weather in the year before flowering has been shown to affect its initiation in temperate beech and pine forests (Matthews 1955, 1963, Maguire 1956). Masting of *Chrysophyllum* shows almost no synchrony with other species at the study site. This contrasts with the synchronous masting of many species in several families in rainforests in Southeast Asia (Appanah 1985, Ashton et al. 1988). This suggests that cues to masting may be more general and less species specific in Southeast Asian rainforests than elsewhere.

With regard to evolved mechanisms, the predator satiation hypothesis (Janzen 1969, Smith 1970, Silvertown 1980) predicts that seeds (and seedlings) suffer relatively low levels of mortality in mast years, and this seems to be the case in *Chrysophyllum*; fewer than

10% of seeds in the 1994 mast year showed evidence of attacks by boring insects, and seed survival to germination was almost 80%. However, we would need comparable data on the few seeds or seedlings occurring in non-mast years to fully evaluate this hypothesis for *Chrysophyllum*. Similarly, to evaluate the pollination hypothesis fully (Nilsson and Wastljung 1987, Norton and Kelly 1988, Smith et al. 1990), data on levels of outcrossing and seed set in mast vs. non-mast years are required. Lastly, to test the resource accumulation hypothesis (Sork et al. 1993) would require long term monitoring of a tree's carbohydrate reserves (C. D. Canham, *personal communication*).

Variation in seedling recruitment by individual adults

Herrera (1998) has suggested that variation among individuals in their reproductive schedules forms the basis for variability in all reproduction at the population level. He pointed out that wherever annual variability in seed production had been studied in detail, the proximate biological causes at the population level stemmed from supra-annual variation among individual adult trees in their annual rhythm of fruit and seed production. For example, Wheelwright (1986) found that individual trees varied from year to year in fruit production in a Costa Rican rainforest. There was little synchrony in reproduction among 12 trees of one species over a seven year period, and the mean size of each year's crop was correlated with the number of trees fruiting that year. Further, Tapper (1996) found that among 76 individual *Fraxinus excelsior* trees in Sweden, some flowered only once in 13 years, whereas one tree flowered in all 13. In the present study, 25% of the trees in the sample analyzed participated in all mast years, whereas others had few seedlings for up to 28 yr before beginning to produce heavily. These latter trees were large enough at the beginning of the study to have produced seeds and seedlings, so the long delay in seedling production was not because they were still growing to a mature size. Herrera (1998) found great variation in synchrony in reproductive effort among individual trees, based on studies 4–12 censuses in length; Kendall's coefficient of concordance ranged from 0.019 to 0.653. For trees of *Chrysophyllum* over 14 censuses, the coefficient was 0.655, at the upper limit of the examples cited by Herrera (1998). Clearly, for *Chrysophyllum* and some other species, there is great variation among individual trees in their degree of participation in any particular masting event.

Variation in seedling abundance in space and time

Seedlings became established in patches in new locations in each successive mast year for several reasons. First, some individual adults did not begin producing many seedlings until the later mast years, and since their seedlings tended to become established very near them, these clumps appeared at later mast years.

Second, influences of postdispersal events (dispersal after seedfall, germination, predation on seeds and seedlings, etc.) probably also played a role in their spatial distribution. Although *Chrysophyllum* seedlings were very dense near conspecific adults, seedling mortality did not change with increase in distance from these adults. In contrast, seedlings of other species had higher mortality nearer adults of *Chrysophyllum* than further away (Fig. 7). This latter pattern could be due either to a deleterious effect of the adult tree on seedlings of other species, or to competition with *Chrysophyllum* seedlings that were particularly dense near the adults. An analysis on this study site (Connell et al. 1984) showed that interactions between neighboring seedlings of the same species had more deleterious effects than those between different species. This suggests that the pattern in Fig. 7 is more likely to be due to the influence of adults than of seedlings of *Chrysophyllum*, but further investigation is clearly warranted.

Densities of seedlings in masting species should also show temporal fluctuations, with high density after a mast fruiting, followed by a gradual decline as seedlings die during the intermast period. Studies of three successive masts of *Parashorea tomentella* in Sabah (see Fox 1972 in Whitmore 1975) indicated that the population of seedlings fluctuated between 2000 and 6000 per ha over 9 yr. In extreme cases, seedling density may fall nearly to zero between successive masts, as seems to be the case in some Dipterocarpaceae in Malaysia (Whitmore 1975), and in *Phillyrea latifolia* (Oleaceae) in southeastern Spain (Herrera et al. 1994). The number of living *Chrysophyllum* seedlings on our permanent transects did show fluctuations with the masts, but the declines after each mast were less than the increases during it, so the total number has increased gradually over more than three decades, from 163 seedlings in 1965, to >4000 in 1996.

One possible explanation for this gradual increase is that the reproductive potential of the *Chrysophyllum* population has also gradually increased over the 30 yr study period. (We define the reproductive potential of a tree population as the maximum number of seeds that can be produced by all adults on the plot.) Such an increase in reproductive potential may have occurred because: (1) there was an increase in the number of reproductive-sized trees on the plot over the study period, or (2) existing trees grew substantially during the study period, increasing their potential for seed production through increases in biomass. We reject explanation (1); although a small number of trees have indeed grown to a reproductive size during the study period, the total number of reproductive-sized trees decreased by 14% over that period. We also reject explanation (2), because the total basal area of adult *Chrysophyllum* has decreased by 16% over the past three decades. We conclude that the increase in seedling density over 30 yr cannot be attributed to an increase in

the reproductive potential of the adult *Chrysophyllum* population on the plot.

Instead, we suggest that an increase in the degree to which the reproductive potential is realized is a more likely explanation, based on two lines of evidence. First, some trees began producing many seedlings after long periods of low production (Table 2), and second, new dense seedling patches appeared in each new mast year, located up to 50 m from patches formed in previous years. We suggest that the mechanism underlying these changes may be an increase in the strength of the cue or cues that trigger mass flowering, acting on the variation among individual trees in their sensitivity to these cues. As the strength of the cues increased over time, they gradually captured a larger proportion of the less sensitive individuals at each successive mast period. In essence, we are suggesting that instead of an increase in the reproductive potential of the adult population, the environmental trigger that stimulates flowering has changed in such a way as to increase the degree to which this potential is realized. That such a mechanism is plausible has been shown by Augspurger (1982), who identified the specific cue for flowering in *Hybanthus prunifolius* (rain after a period of drought), and showed that variation in the strength of the cue (total rainfall) produced similar variation in the number of flowering individuals.

The relative longevity of *Chrysophyllum* seedlings has also undoubtedly contributed to the remarkable increase in seedling density during the study period. It is widely accepted that the seedlings of many tropical rain forest species suffer relatively high rates of mortality. Fifty percent of the species studied by Li et al. (1996) had half-lives of less than 3.5 months, and only 20% of species had half-lives greater than 12 mo; none exceeded 41 mo. In contrast, the 1986 cohort of *Chrysophyllum* seedlings (followed from the age of 0.1 yr) had a half-life of 66 mo. Given that the mean interval between mast years is 67 mo, a high proportion of seedlings survive the interval, so contributing to the gradual increase in the total standing crop of seedlings from 1965 to 1996. Large initial seedling size, the ability of browsed seedlings to resprout new shoots (Harms and Dalling 1997 and *personal observation*), and the fact that mammalian herbivores cause little seedling mortality (T. Theimer and C. A. Gehring, *unpublished data*) are probably the major determinants of their longevity.

Our long-term data raise the possibility that *Chrysophyllum* seedling populations may fluctuate cyclically, at a frequency measured in decades. The 24-fold increase in seedling density indicates that the past 32 yr period has been an extremely favorable one for the recruitment of *Chrysophyllum* seedlings. By analogy, the very low density of seedlings at the beginning of the study suggests that the period prior to 1965 was unfavorable for seedling production. We calculate that, if recruitment were to cease at this point and mortality

remained at the present rate, the present crop of *Chrysophyllum* seedlings would take about 26 yr to drop to the original 1965 level. Since *Chrysophyllum* was the commonest species in the seedling stratum in 1965, it would have dominated the seedling stratum of a large portion of this rain forest plot for ~50 yr. Clearly, the time scale of change of even the smallest life history stage of this species on this site is quite long. Whether this scale is exceptional or routine cannot be judged at present, since we know of no other decades-long studies of seedling dynamics. However, given the "reverse-J" distribution of size classes in *Chrysophyllum* (Table 5), it seems clear that its seedling recruitment has been abundant over temporal scales of several hundred years, despite the decades-long fluctuations we have suggested here.

*Relative importance of recruitment vs. mortality:
supply-side ecology*

Will this dramatic increase in the abundance of seedlings be expressed in the future as an increase in the number of adults on the plot? In more general terms, what is the relative importance of recruitment, vs. growth and mortality, in determining the abundance of rain forest trees? Evidence comes from several demographic studies using matrix transition probabilities to explore the sensitivity of population growth rates to changes in transition probabilities between different size classes. Some have suggested that, while the population growth rates of several tropical species are relatively insensitive to changes in the transition probabilities of seeds to seedlings, or seedlings to small saplings, they are quite sensitive to variations in these transitions among older stages (e.g., Piñero et al. 1984, Peters 1991). These studies suggest that supply-side effects may not be important in some tropical plant species.

We assessed the relative importance of recruitment vs. growth and mortality by looking for evidence of density-dependent growth or mortality in the younger life stages. The presence of such evidence suggests that recruitment would probably not strongly influence the abundance of the older life stages. We found evidence of density dependence of mortality and growth in six of 14 tests for *Chrysophyllum* seedlings and saplings in quadrats. However, mortality did not change with distance from conspecific adult trees. These results suggest that supply-side effects as well as subsequent growth and mortality of seedlings and saplings, determine the abundance of the older life stages.

*Maintenance of the high relative abundance of
Chrysophyllum in the rain forest assemblage*

Will the *Chrysophyllum* population maintain its position as one of the commoner species on the plot? Its extremely high recruitment rates during the study period suggest that it will continue to maintain its high relative abundance, unless environmental conditions

change in ways that cause its recruitment to decrease. The age structure or size structure of populations give clues to their future trends. DeSteven (1994) measured the population size structure of three species of rain forest trees in Panama; the species with higher proportions of smaller sizes had increasing adult populations, and vice versa. Over the past three decades the size and age structure of the *Chrysophyllum* population has shifted toward relatively more smaller, younger stages with the adult stage decreasing slightly (Table 5). The direction of these changes indicates that, if rates of growth and survival do not begin either to decrease, or to act in a strongly negative density-dependent fashion in the future, the adult population of *Chrysophyllum* is more likely to increase than to continue to decrease. The finding that seedlings of species other than *Chrysophyllum* have higher mortality nearer adults of *Chrysophyllum*, but that conspecific seedlings do not show this pattern, would suggest that *Chrysophyllum* should increase at the expense of other species. Since it is already one of the dominant species, such a tendency would result in a reduction in species diversity in this forest.

ACKNOWLEDGMENTS

We thank the many people who have helped us over the past 35 years. Special thanks are due to J. G. Tracey and L. J. Webb, who helped start the project and keep it running, and who, with M. D. Lowman in the later years, were responsible for most of the identifications. C. D. Canham, C. A. Gehring, T. Theimer, E. W. Schupp, V. L. Sork, J. G. Tracey, and D. Westcott read the manuscript and W. R. Black, L. P. Goldwasser, M. J. Keough, I. R. Noble, and S. C. Schroeter also gave statistical and programming assistance. I. Davies wrote the programs that have kept the data base accurate and allowed it to be displayed in maps. The research has been supported since 1962 by grants from the U.S. National Science Foundation; the current grants are DEB 95-03217 and DEB 98-06310. It has also been supported by I. R. Noble of the Ecosystem Dynamics Group, Research School of Biological Sciences, Australian National University, Canberra, Australia.

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