Tropical Rainforests

PAST, PRESENT & FUTURE

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Dynamics of Seedling Recruitment in an Australian Tropical Rainforest

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ABSTRACT

We have measured seedling recruitment in all the common tree species, at several scales in time and space, over a 39-year period in a tropical rainforest in North Queensland, Australia. This forest has probably never been disturbed by humans. It has a higher tree density and basal area than most rainforest study plots in other regions. Among the factors determining the abundance, distribution, and diversity of trees in forests, initial seedling recruitment is important, because it determines the initial abundance of each species. We found that some common species produced few seedlings, while others produced enormous numbers at very long intervals, ranging up to a decade or more between bouts of recruitment. Few species produced seedlings regularly and evenly. Commoner species had more variable recruitment than did rarer species. To explain the enormous variation in recruitment that we have observed, we have begun to measure the dynamics of the stages preceding recruitment; for example, flowering, fruiting, germination, and initial seedling establishment. The greatest losses seem to occur between the initiation of fruit development and the germination of seeds, rather than earlier, during flowering and pollination, or later, during early survival of seedlings. A controlled field experiment indicated that ground-dwelling mammals and birds reduce rates of seed survival and of seedling recruitment and survival. Some of these effects may happen when these animals mix and move ground litter, as well as when they disperse seeds and feed on seeds and seedlings. Our analyses of long-term trends in population dynamics indicate that, during the period of growth to maturity, rates of growth and mortality rarely act in a frequency-dependent manner. This finding suggests that, if these rates do not change significantly over time, the species composition of the future generation of adult trees may be determined by the species composition of the present generation of seedling recruits: the adult community structure will be "recruitment-limited." Species diversity can be maintained if there is significant negative frequency dependence, with the commoner species having lower rates of recruitment, growth, or survival than the rarer species. Although negative frequency dependence was rare in older stages, it did occur during seedling recruitment. This finding suggests that species diversity may be maintained by forces acting during the very early life stages (flowering, fruiting, seed germination, or initial seedling establishment), which determine the species composition of the seedling recruits. We plan to investigate whether negative frequency dependence occurs during these younger life stages, or as a result of the activities of ground-dwelling vertebrates that affect the abundance of seeds and young seedling recruits.

INTRODUCTION

The abundance and distribution of tree populations is determined by rates of supply (seedling recruitment) and of loss (mortality). However, most studies of forest population dynamics have tended to neglect the supply side of the equation. Yet seedling recruitment determines the initial abundance of each species, setting the stage for all future events in the community dynamics of the trees. Over time, the surviving shade-tolerant seedlings create a mosaic of juveniles of various ages and sizes, known as "advanced regeneration," which serves as a template for the next generation of mature trees.

This idea is not new. Janzen (1970) and Connell (1971) proposed that, in mature tropical rainforests, spatial patterns of mortality of seeds and seedlings determine the species composition of the understory vegetation, which, under some circumstances, can determine that of the older stages. Evidence exists that supports this viewpoint: Uhl et al. (1988) found that 4 years after gap formation in an Amazonian rainforest, 97% of trees taller than 1 m in small gaps had existed as advanced regeneration before the gaps had formed; in a larger gap, 83% of trees taller than 2 m had originated as advanced regeneration. Brokaw and Scheiner (1989) observed that "creation of a gap in the canopy acts on patterns already established in the understory of the closed phase," and believed that these results "suggest the need to explore pervasive processes unrelated to discernible gaps." Connell (1989) observed that "the selection that takes place beneath the closed canopy has a great influence on the suite of species available to take advantage of the short burst of light in a gap."

Recognition of the paucity of studies of recruitment has stimulated an emphasis on "supply-side ecology" (Lewin 1986). Studies of supply-side ecology focus on the degree to which the distributions or abundances of species in a population or community are limited by dispersal or recruitment, relative to the degree to which they are limited by mortality. To date, most studies of supply-side ecology have dealt with limitation of abundance or distribution by recruitment in single-species populations of marine animals (Hjort 1914; Gulland 1982;

Warner and Chesson 1985; Warner and Hughes 1988; Underwood and Fairweather 1989; Caley et al. 1996), or with dispersal limitation of spatial patterns of seedlings in single-species populations of terrestrial plants (Augspurger 1983, 1984a, 1984b; DeSteven 1994; Clark, Macklin, and Wood 1998; Dalling and Wirth 1998; Silvera, Skillman, and Dalling 2003; Dalling, Swaine, and Garwood 1998). Some of the studies have analyzed several species at the same site, but have not compared their relative abundances.

In contrast to these studies of how dispersal limitation affects the spatial distribution of plants in single-species populations, this chapter addresses the question of the degree to which seedling recruitment affects the relative abundance of species in a multispecies assemblage of plants. Will the relative abundance of species of recruits in a community be passed on with little or no change to the future adult generation? It can be, if rates of growth and mortality during the period of growth to adulthood are not frequency-dependent (i.e., if growth or mortality rates do not vary as a function of the abundances of the different species). In that case, the relative abundances of species will probably not change as recruits grow to adulthood; the adult species composition of the community will be "recruitment-limited." In contrast, if growth and mortality in the period between recruitment and adulthood are frequency-dependent, then the relative abundances of adults of each species will probably not accurately reflect that of the recruits; the adult species composition of the community will not be recruitment-limited. (Such inferences require the assumption that rates of growth and mortality remain constant over time.) Apparently, few other studies have addressed the role of recruitment limitation at the community level. The only one we are aware of is that of Hubbell (1997a), who suggested that dispersal limitation might determine the diversity of the tree community in a Panamanian rainforest.

In this chapter we discuss the long-term patterns of variation in seedling recruitment of all tree species at a tropical rainforest study plot in North Queensland, Australia, over a period of 39 years. We also discuss some of the mechanisms underlying the observed variations in seedling recruitment. Finally, we describe two recent investigations of the life stages preceding the age at which the seedlings are first recorded in our long-term censuses and of the effects of vertebrate animals on the seedlings. We have carried out our study over a long period with the aim of documenting recruitment patterns that take place at both short and long time scales. The length of the study also increases the probability of assessing the effects on the tree populations of rare events (e.g., severe storms, droughts, fires, floods, population peaks of herbivores or pathogens, extremes of reproduction or recruitment), and of detecting gradual trends against the noisy background of short-term variations in environmental conditions or population fluctuations, which can have long-lasting effects on community structure and dynamics (e.g., Woods 1989; Hubbell and Foster 1992; Marshall and Swaine 1992; Meggers 1994; Nascimento and Proctor 1994; Nelson et al. 1994; Reader and Bricker 1994; Condit, Hubbell, and Foster 1995, 1996c; Newbery, Prins, and Brown 1996; Magnusson, Lima, and de Lima 1996; Swaine 1996; Walsh 1996b; Harms and Dalling 1997; Dalling, Swaine, and Garwood 1997; Dalling and Denslow 1998; Dalling, Swaine, and Garwood 1998; Schnitzer, Dalling, and Carson 2000; Dalling and Hubbell 2002; Dalling et al. 2002; Daws et al. 2002; DeSteven and Wright 2002; Pearson et al. 2002).

CHARACTERISTICS OF THE DAVIES CREEK FOREST PLOT

Since 1963 we have monitored tropical rainforest dynamics at Davies Creek, 17°05′ S, 145°34′ E, in North Queensland, Australia (Connell 1971, 1989; Connell, Tracey, and Webb 1984; Connell and Green 2000, 2001). The study area is a single plot 1.7 ha in area at 800 m elevation. Measurements at the plot indicate that it has an annual rainfall of about 300 cm. The means of the daily maximum and minimum air temperatures inside the forest over the past 3 years were 22.1°C and 15.2°C, respectively. The soils are relatively infertile and are derived from granite bedrock.

In 1963, all trees greater than 10 cm DBH on the entire 1.7 ha plot were mapped, tagged, measured, and identified; there were 1,426 such trees of 123 species. A similar census was done for all medium-sized trees between 2.5 and 10 cm DBH on permanently marked belt transects constituting 30% of the area of the plot and extending throughout it (see fig. 2 in Connell, Tracey, and Webb 1984 for a map of the transects).

This tropical rainforest site is unusual because it apparently has never been subject to cutting by humans. Our evidence for this is twofold: First, Australian aboriginal peoples were not farmers and entered these forests only to hunt and gather, so there was no cutting of trees for shifting cultivation, as occurred in many other tropical rainforests (Flood 1995). Second, many of the common large trees at Davies Creek are highly desirable timber species and would have been among the first to be cut if European timber cutters had logged the forest (R. Keenan, Queensland Department of Forestry [QDF], personal communication). The area has been protected by the QDF since 1952 as a plot for monitoring growth, surrounded by a buffer zone; it is now completely protected in a World Heritage Area.

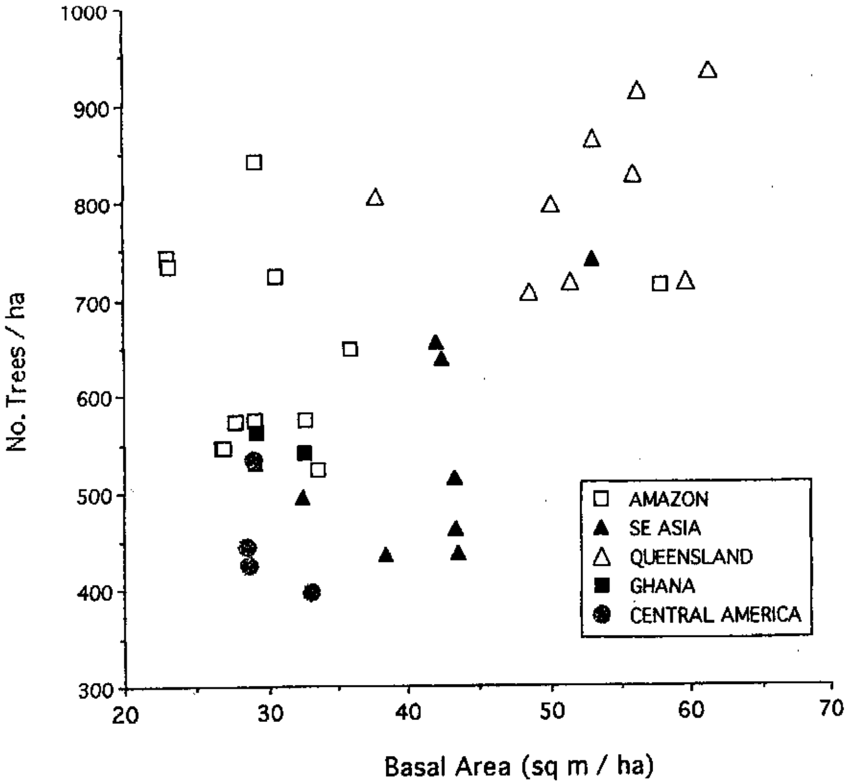

Figure 23.1 Density (no. of trees/ha) and basal area (m²/ha) of trees greater than 10 cm DBH in study plots in various regions of the world. (Data from Nicholson, Henry, and Rudder 1988; Lieberman et al. 1990; Phillips et al. 1994; J. H. Connell, unpublished data.)

The abundance of trees greater than 10 cm in diameter at breast height (DBH) in most of the rainforests sampled in North Queensland is greater than that found elsewhere in the world, both in density (number/ha) and biomass (basal area/ha) (fig. 23.1, table 23.1). The species richness (number of species/ha) is less than that found in the large continuous rainforest regions of Southeast Asia, Africa, and South America, but similar to that of other regions on the fringes of those central regions, such as Central America and Ghana (fig. 23.2, table 23.1).

The dynamics of trees greater than 10 cm DBH at Davies Creek are slower than those at two other well-studied rainforest sites, at La Selva, Costa Rica (D. Lieberman et al. 1990; Lieberman and Lieberman 1987), and Gunung Palung, Borneo (C. Webb, unpublished data). The annual rates of mortality, stem growth, and opening of the canopy by treefalls are all lower at Davies Creek than at those two sites (table 23.1; canopy gaps as defined by Brokaw 1982).

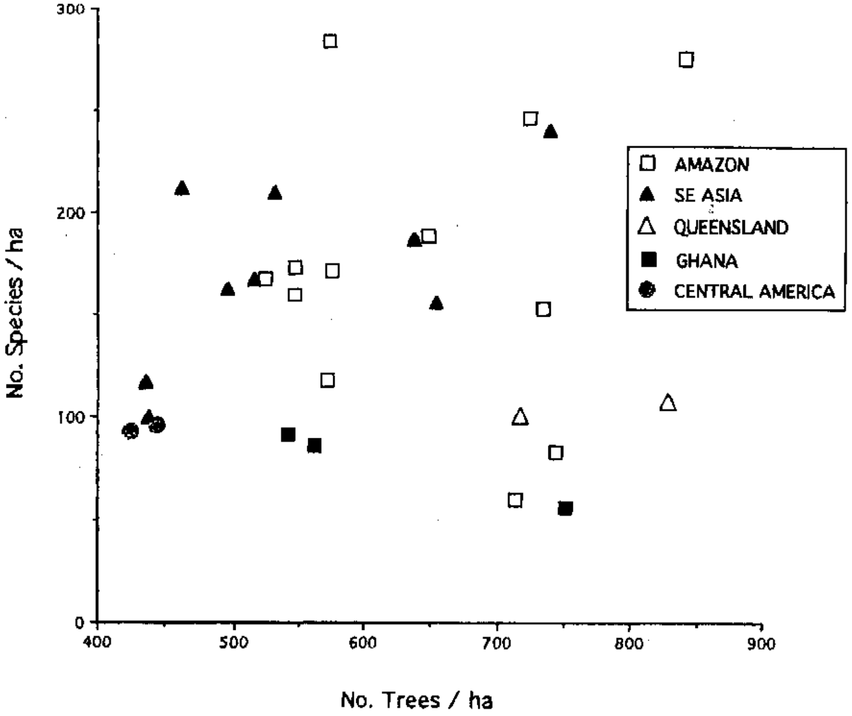

Figure 23.2 Species richness (no. species/ha) and density (no. trees/ha) of trees greater than 10 cm DBH in study plots in various regions of the world. (Data from Nicholson, Henry, and Rudder 1988; Foster and Hubbell 1990; Lieberman et al. 1990; Phillips et al. 1994; J. H. Connell, unpublished data.)

It has been suggested that turnover of trees greater than 10 cm DBH has increased over the past 20–40 years in a high proportion of tropical rainforests of the world (Phillips and Gentry 1994). Phillips and Gentry estimated turnover as the mean of mortality and recruitment by growth; since mortality and recruitment were highly correlated in their analysis, either can suffice as a measure of turnover. We calculated the turnover in our tropical plot, measured as annual mortality rate of trees greater than 10 cm DBH, applying the equation used by Phillips and Gentry. Since we had measured mortality at fifteen censuses, but recruitment by growth at only three censuses, mortality was clearly the better

Table 23.1 Comparisons of abundance and diversity and rates of mortality, growth, and treefall gap formation for trees greater than 10 cm DBH in rainforest study plots at Davies Creek, Queensland, Australia, Barro Colorado Island, Panama, La Selva, Costa Rica, and Gunung Palung, Borneo

	Davies Creek	BCI	La Selva	Gunung Palung
Statics				
1. No. stems/ha	716	536	450	638
2. Basal area (m²/ha)	59.7	28.6	30.1	42.5
3. No. species/ha	101	92	92	187
4. No. species/500 stems	93		103	
Dynamics				
5. % mortality/yr	0.69		2.03	1.1
6. Stem growth (DBH, mm/yr)	0.5		2.65	0.74
7. Gap formation rate (% area/yr)	0.4	0.73	0.96	

Sources: J. H. Connell, unpublished data, for Davies Creek; Lang and Knight 1983; Hubbell, Condit, and Foster 1990 for BCI; D. Lieberman et al. 1985, 1990; Lieberman and Lieberman 1987; Phillips et al. 1994 for La Selva; C. Webb, unpublished data, for Gunung Palung.

measure to investigate long-term trends in turnover in our study. In contrast to Phillips and Gentry, we found no evidence of a rising trend in turnover (as indicated by mortality) at our tropical plot from 1963 to 1996 (fig. 23.3).

SEEDLING RECRUITMENT

Long-Term Patterns of Variation

In 1965, all saplings and seedlings less than 2.5 cm DBH, including all sizes down to tiny, newly germinated seedlings, were mapped and tagged on permanently marked narrower transects, which constitute 9.6% of the total plot area and are nested within the transects for medium-sized trees. Thus, all woody plants except vines were mapped, the smaller size classes along transects located throughout the map of large trees. This arrangement ensured that the seedlings produced by the majority of adult trees on the plot would be adequately sampled in subsequent censuses. At intervals of 1 to 4 years thereafter, the survival of all previously mapped and tagged individuals was checked, and in addition, all newly recruited seedlings that had germinated and survived in the interval since the previous census were mapped, tagged, measured, and identified on precisely the same permanently marked transects used in the original mapping. These censuses of new recruits, which were done twenty-one times between 1965 and 2002, provide information about the temporal and spatial variation in seedling recruitment of all species of trees. In addition, all trees taller than 6 m on one portion of the plot have been censused by the QDF since 1952; this record of 45 years of continuous monitoring is one of the longest in any tropical forest (Phillips and Gentry 1994). Details of topography, census dates, and weather patterns are given in Connell, Tracey, and Webb (1984) and Connell and Green (2000).

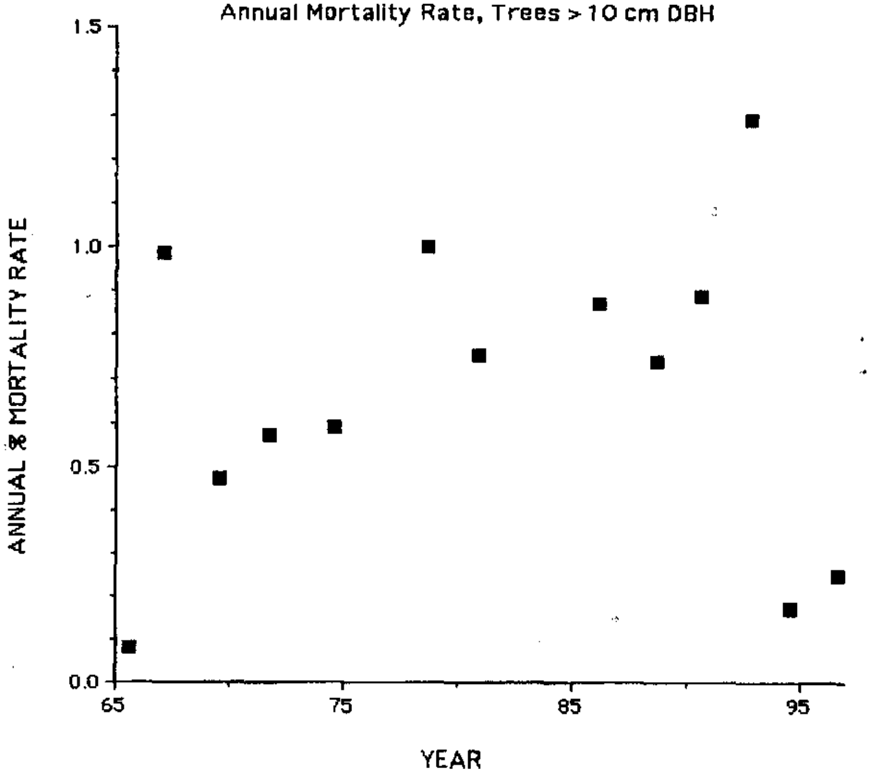

Figure 23.3 Changes over time in the annual mortality rates of trees greater than 10 cm DBH at the Davies Creek study plot. There was no significant correlation between the two variables.

Recruitment of seedlings in our standard periodic censuses was extremely variable within and among species. Of the 121 species that had at least two adults on the study plot in 1963, some have had little seedling recruitment over the past 31 years, while others have had high recruitment. For the 46 species for which we had a sufficient sample size (> 100 seedlings in all censuses combined), there was considerable temporal variation in recruitment within species: the coefficient of variation of the logarithm of the number of recruits per census ranged from 21 to 387. This variation is especially evident in the commonest species (fig. 23.4).

To see whether the recruitment of different species was synchronized, we analyzed concordance of recruitment among the 46 species with more than 100 seedlings across the fourteen censuses from 1969 to 1996 (Connell and Green 2000). The analysis found that there was a low but statistically significant degree of synchrony (Kendall's coefficient of concordance, $N = 46$, $W = 0.09$, $p < .01$). The reason for this synchrony in recruitment may be that environmental conditions in some years are favorable for recruitment for the majority of species, while those in other years are not (see also Wright, chap. 15 in this volume).

This synchrony does not apply to all groupings of species. We assessed the synchrony of recruitment among the sixteen species with the highest variation in recruitment rate (i. e., a CV of > 100 and a range of > 50); no significant synchrony was found (Kendall's coefficient, $W = 0.08$, $N = 16$, $p > .05$). Also, the five species ranked highest in numbers of recruits recorded between 1965 and 1996 were not significantly synchronized (Kendall's coefficient, $N = 5$, $W = 0.33$, $p > .05$). For example, figure 23.4 shows that the first three seedling peaks in *Chrysophyllum* sp. nov. and *Cardwellia sublimis*, between 1965 and 1985, were clearly synchronized, but that their peaks were quite unsynchronized over the next 11 years. This change in synchrony across decades illustrates the value of long-term records.

Over 39 years, seedling numbers varied over three orders of magnitude. For the 121 species that had at least two adults in 1963, the number of new seedlings mapped and tagged since 1965 has ranged between 1 and 12,677. In one common species, *Chrysophyllum* sp nov., the seedling numbers per census ranged from 10 to 3,900; 98% appeared in five peaks spaced at 4- to 11-year intervals (Connell and Green 2000). Of the five species with the most seedlings, all showed a similar pattern of markedly episodic recruitment (fig. 23.4). This pattern of sporadic occurrences of very heavy seedling recruitment, separated by relatively long intervals with few seedlings, is analogous to the "mast seeding" seen in some forest trees (Appanah 1985; Ashton, Givnish, and Appanah 1988; Yap and Chan 1990; Sork, Bramble, and Sexton 1993; Newstrom et al. 1994; Koenig et al. 1994; Wright, chap. 15 in this volume). Figure 23.4 shows this extreme variation in the five species with the most recruits in the period 1965–1996.

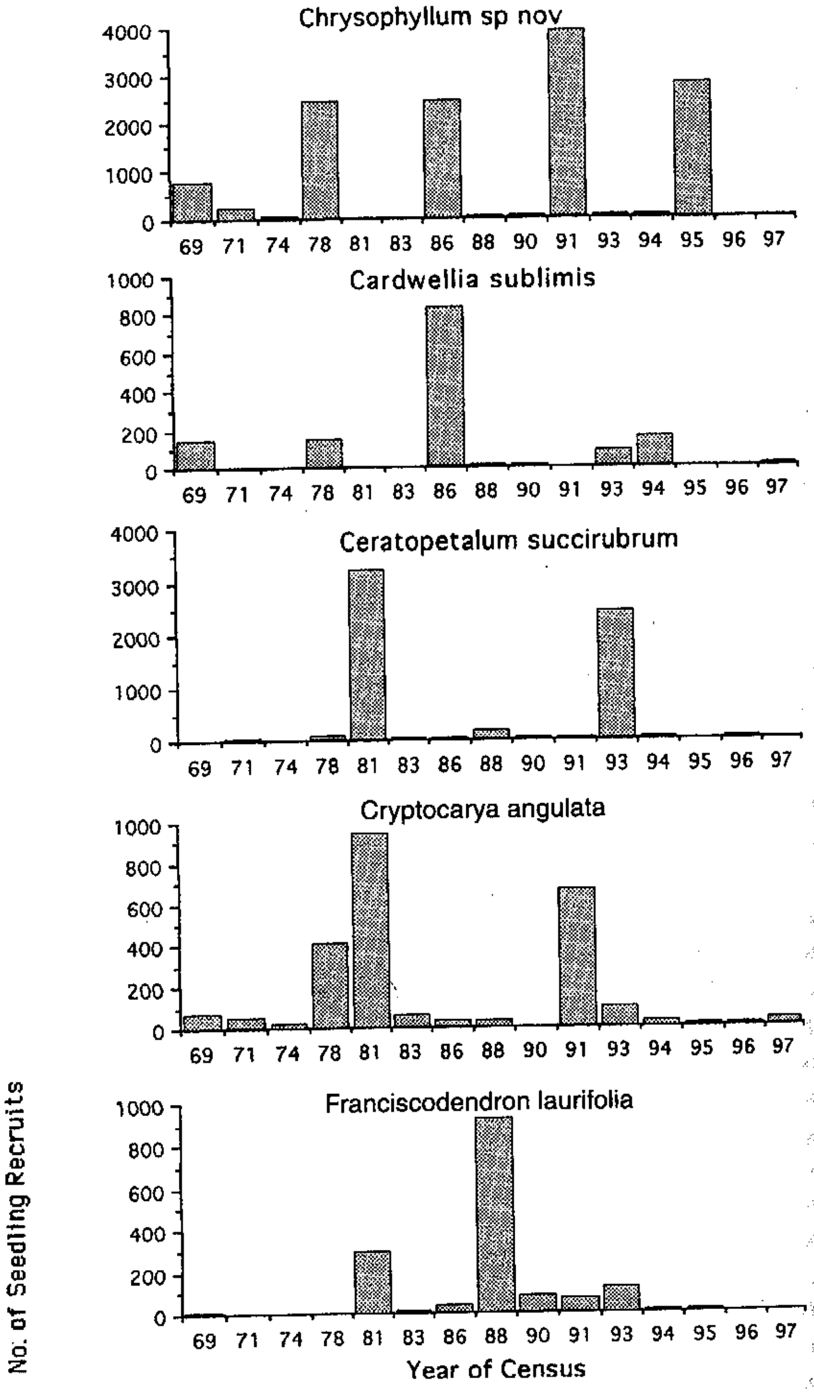

Figure 23.4 Seedling recruitment rates (no./yr) of five species with high numbers of recruits recorded on the permanent transects at the Davies Creek study plot between 1965 and 1996. Each point represents the rate over the period since the previous census; the first census was in 1965.

The fact that these five masting species were also among the commonest in the community suggests that variation in recruitment might be related to a species' abundance. To test this hypothesis, we looked for a correlation between variation in recruitment and abundance. There were thirty-five species that had some trees greater than 10 cm DBH, as well as a total of more than 100 seedling recruits, between 1965 and 1997. For these species, the correlation between the logarithm of the CV of number of seedlings per census and the number of trees was positive and significant ($r^2 = .215, p < .01$), as it also was when tree abundance was measured as basal area ($r^2 = .123, p < .05$). Thus the commoner species have relatively more variable seedling recruitment.

Recruitment Limitation: The Influence of Seedling Recruitment on the Relative Abundance of Species in the Adult Community

To what degree do variations in seedling recruitment affect future adult abundance? How well does the relative abundance of species among the present seedling recruits predict future adult species composition and diversity? If growth and mortality rates during the period of growth to adulthood are not frequency-dependent, and if those rates remain constant during that period, then the relative abundance of species of seedlings will not be altered significantly as they grow to maturity, and recruitment will have determined the relative abundance of species in the future adult community.

We analyzed our data for the occurrence of frequency dependence of growth or mortality (Connell, Tracey, and Webb 1984), but found it only rarely. At a small spatial scale, we found that the recruits of species with abundant seedlings were likely to occur in single-species clumps, with a high proportion of nearest neighbors that were conspecific, whereas the recruits of species with few seedlings tended to be intermingled with other species, with a high proportion of nearest neighbors that were not conspecific. This observation suggested that frequency dependence would be occurring if seedlings performed more poorly when their nearest neighbors were conspecific (as was the case in abundant species) than when their neighbors were not conspecific (as was the case in rarer species). Our analyses found frequency dependence in growth in four of twelve seedling year classes analyzed, but not in the other eight. Survival was frequency-dependent in thirteen of twenty year classes, but not in the other seven (see tables 7 and 8 in Connell, Tracey, and Webb 1984). Overall, frequency dependence was demonstrated in about half of these instances of interactions between juveniles.

In contrast, at larger spatial scales, for both seedlings and older stages, we found no significant evidence for frequency dependence of growth or mortality. At the scale of the whole study plot, neither seedling growth nor mortality varied with the abundance of conspecific adults, measured either by numbers or basal area (see table 4 in Connell, Tracey, and Webb 1984). Also, neither growth nor mortality rates varied in relation to the abundance of conspecifics of the same size class for nine classes ranging from seedlings to large trees (see tables 5 and 6 in Connell, Tracey, and Webb 1984). This evidence is also weak at a smaller spatial scale: in quadrats (1.8 m × 12.2 m), five of forty-four regressions of growth rate versus abundance, and three of twenty-two regressions of mortality versus abundance, showed frequency dependence; however, at a significance level of 0.05, one or two would have occurred by chance in this many comparisons (Connell, Tracey, and Webb 1984). No density dependence in seed germination was found in field experiments in which seeds of two species were placed in dense and sparse patterns.

Last, we tested the hypothesis that seedlings and saplings in close proximity to conspecific adults would have higher mortality than those farther away (Janzen 1970; Connell 1971). Since juveniles of species whose adults were commoner would be more likely to occur closer to conspecific adults than would those of rarer species, agreement with this hypothesis would constitute evidence for frequency dependence. The result of the analysis showed that, of 28 species for which we had a sufficient sample size, 6 had higher mortality close to conspecific adults (in a zone within 1.5 times the crown radius of a conspecific adult) than at an equal distance farther away, suggesting frequency dependence. Increasing the zone of proximity to 3 times the crown radius gave a larger sample size. In this analysis, of 64 species, 10 showed frequency dependence in mortality and 54 did not (see table 10 in Connell, Tracey, and Webb 1984). Also, little evidence of frequency dependence in survival was found in field experiments in which seeds of two species were placed beneath the crowns of either conspecific or non-conspecific adults (see table 12 in Connell, Tracey, and Webb 1984). Overall, the evidence for frequency dependence in either growth rates or mortality rates during growth to maturity was weak.

Mechanisms Underlying Variation in Seedling Recruitment: Events during the Life Stages Preceding Recruitment

As described above, many species with mature adult trees on the study plot did not have seedlings at every census. Species with mature adults may not have seedlings in a particular census for one or more of the following reasons: (1) no flowers were produced in the period since the last census because the cues stimulating flowering were less strong than the factors inhibiting it (pathogens, predators, or deleterious environmental conditions); (2) flowers were produced, but did not develop into fruit with viable seeds, for reasons such as very unequal sex ratios of dioecious trees or floral sex organs, too few flowers or pollinators, fruits developed without seeds (parthenocarpic fruits), or abortion of developing fruits; (3) viable fruit and seeds were produced, but were either destroyed on the tree by frugivores or parasites before maturation or were dispersed away from the study plot; (4) after maturation, viable seeds arrived on our standard transects, but either they were all destroyed on the ground by predators or parasites, or the local physical conditions in that year were not suitable for germination or establishment of seedlings; (5) seedlings became established, but early mortality was so high that no seedlings survived to appear in our next census.

We began a long-term phenology study to investigate these possibilities in a variety of species, with the aim of estimating the losses among the different life stages leading up to seedling establishment. Monthly since January 1995, we have observed the reproductive activity of two to ten sexually mature individuals (mean 6.7 trees/species) of 103 species. We observe the trees with binoculars from the ground, scoring activity on a six-point scale from 0 (no flowers or fruits) to 5 (masses of flowers or fruits). The score is scaled to the size of the individual adult. Each individual is observed from the same location in each survey so that the monthly observations are comparable. In addition, we have measured the abundance of newly germinated seedlings in monthly surveys, from September 1994 onward, on twenty belt transects of 1 m × 100 m each on and around the study plot. All new seedling recruits that have appeared during the preceding month are counted, identified, and removed, except for those species in which large numbers of seedlings germinated in the same month; for these, all are removed except for a sample, which is mapped and its survival followed.

Analysis of our first 2.5 years of phenological observations shows that, of the 103 species, 15% never flowered; for example, the common species *Ceratopetalum succirubrum*, *Chrysophyllum* sp nov., *Macaranga subdentata*, and *Xanthopyllum octandrum* all failed to flower. A further 7% flowered, but did not initiate fruit; the remaining 78% had both flowers and fruit. Of the species that were observed to initiate some fruit development, 65% never had newly germinated seedlings on our transects. Examples of such species are *Beilschmedia bancroftii*, *Elaeocarpus elliffii*, *Guettardella tenuiflora*, *Halfordia scleroxyla*, and *Rapanea achradifolia*. Survival from the newly germinated seedling stage to the next regular census was high; of the 34 species of newly germinated seedlings recorded between September 1994 and September 1996, 82% (28 species) were also found in one or the other of the two next regular censuses, in October of 1995 and 1996.

These data provide an estimate of the degree to which losses in each of the life stages might influence the high annual variation in numbers of seedlings recruited. Our results show that the greatest proportion of the losses seem to occur between the start of fruit development and the time of germination, rather than at an earlier or a later stage. (All of the 103 species had produced seedlings at least once during the previous 29-year period before the phenology study began in 1995, so it is clear that records longer than 2.5 years are needed to adequately characterize the early stages of adult reproduction and seedling establishment.)

For some species, the reasons for such reproductive failure are known. For example, *Halfordia scleroxyla* produced masses of fruits in 1995, but failed to recruit any seedlings thereafter, and we found that virtually all of these fruits were seedless; such parthenocarpic behavior is apparently rare among the species in this forest. *Elaeocarpus* spp. regularly flowered and fruited, but many of their seeds appeared to be destroyed by insect predators while still on the tree. For *Hylandia dockrilli*, only two new seedling recruits have appeared since 1965. This species is monoecious, and we have evidence of variable sex expression from one year to the next. The trees that have flowered in the past 3 years have done so almost exclusively as males; however, some of these had masses of seed remnants on the ground beneath their crowns, indicating a female function in some previous years. These remnants may indicate intense seed predation, which, combined with predominately male functioning, might account for the lack of seedling recruitment.

Mechanisms Underlying the Variation in Seedling Recruitment: Precipitation

A likely environmental factor affecting reproduction and recruitment is precipitation. To investigate this possibility, we used long-term rainfall data from Atherton, which is the nearest standard meteorological station to the study site and close to the same elevation. Rainfall data gathered simultaneously at the Davies Creek plot and at Atherton were highly correlated: for 72 periods of 1 to 26 days between February 1995 and March 1996, when some rain was recorded at one or both stations, the regression equation was Davies Creek rain = 1.52 + (2.14 * Atherton rain) ($r^2 = .83$, df = 70, $p < .001$).

We regressed the total number of recruits per year against rainfall totals for three periods: the entire year immediately preceding the census date (which was usually in September–October), or only during the winter (May–September) or the summer (November–March) of that year. Because flowering and fruit development in many species was observed up to 2 years before the census date, we also repeated these analyses using rainfall from 1 and 2 years before the census date for each of the above three periods. In none of these analyses was there a statistically significant correlation ($N = 14$ for each, all r^2 ranging from 0 to .17).

Another aspect of precipitation that has been found to be of importance to reproduction and recruitment of trees is the length of relatively dry periods (Augspurger 1982; Wright, chap. 15 in this volume). Following the suggestion of Phillips et al. (1994), we tallied the number of consecutive "dry" months (when rainfall was less than 100 mm/month at Atherton) in each year. Since there was sometimes more than one such period in a year, we calculated the average number of consecutive dry months, and also the total number of dry months, in each year. We regressed the total number of recruits per year against each of these variables for each of the 3 years preceding the census. Of the six regressions, two were significantly positive: the total number of dry months in the year ending 1 year before the census ($N = 14$, $r^2 = .35$, $p < .05$) and the average number of consecutive dry months in the year ending 2 years before the census ($N = 14$, $r^2 = .38$, $p = .02$). Thus, seedling recruitment seems to be greater 1 to 2 years after a relatively long dry period. These lagged effects are consistent with the reproductive patterns that we have observed in our phenology study; some species take 1 to 1.5 years from flowering to seedling germination. Our analyses suggest that a relatively dry period is favorable for flowering, fruit development, or survival of fruit until germination, and that such a dry period may be more important than total precipitation, annually or seasonally (see also Wright, chap. 15 in this volume).

Effects of Ground-Dwelling Vertebrates on Recruitment and Survival of Seeds and Seedlings

Ground-dwelling vertebrates can act as seed dispersers, seed predators, litter disturbers, and herbivores. In Australian tropical rainforests, four species of native rodents (*Rattus fuscipes, R. leucopus, Uromys caudimaculatus,* and *Melomys cervinipes*), the musky rat kangaroo (*Hypsiprimnodon moschatus*), and the long-nosed bandicoot (*Parameles nasuta*) include fruits and seeds in their diet and so have the potential to act as seed dispersers or seed predators. The red-legged pademelon (*Thylogale stigmatica*) and the musky rat kangaroo may be important herbivores. Several ground-dwelling bird species have the potential to affect the rainforest understory through their activities as either seed dispersers (the cassowary, *Casuarius casuarius*) or litter disturbers (the chowchilla, *Orthonyx spaldingii;* the orange-footed scrubfowl, *Megapodius reinwardt;* and the brush turkey, *Alectura lathami*) (Theimer and Gehring 1999).

In some tree species, lack of seedling recruitment may be due to the seeds being completely destroyed by animals on the ground before germination. Several large individuals of *Prumnopitys amara* and *Beilschmedia bancroftii* have flowered and produced large fruit crops, but few new seedlings have appeared in the monthly seedling surveys. Seed predation by white-tailed rats (*Uromys caudimaculatus*) is an important source of seed mortality for *Beilschmedia bancroftii* in North Queensland (Harrington et al. 1997), and the seedlings that do arise on our plot apparently do so from seeds cached below the soil surface by white-tailed rats (Theimer 2001).

We set up the following field experiment to assess the overall effects of ground-dwelling birds and mammals on seeds and seedlings. Sixteen pairs of plots, each 6.5 m × 7.0 m in size, were established in the vicinity of the long-term study plot. One member of each pair was fenced to exclude vertebrates, while the other member of the pair was fenced only along the upper side to control for the effects of reduction of litter washing downhill during heavy rains. The growth, mortality, and recruitment of seedlings (< 30 cm height) within these plots have been measured at 6-month intervals since April of 1996, with ground-dwelling vertebrates excluded since November 1996. Live trapping has indicated that mammal access to the exclosure plots has been reduced to about 1/7 of that on the control plots. Measurements of the depth of litter at twenty locations in each exclosure and control plot indicate that the variance in depth in the controls was 1.75 times that in the exclosures. Neither seedling recruitment nor seedling survival differed between the exclosure and control plots in the 6 months (April to November 1996) prior to fence closing, nor during the first 6 months after fence closing (November 1996 to April 1997), but both were significantly higher in the exclosure plots than in the controls over the next 6 months (April to November 1997) (recruitment: Wilcoxon signed ranks test: $Z = 2.84$, $p = .004$; survival: paired t-test, $t = -5.74$, $p < .0001$; fig. 23.5). To measure the intensity of seed predation directly, we placed seeds of *Beilschmedia bancroftii* in both exclosures and controls; after 1 year, 64% of the seeds were still present in the exclosures, whereas all had disappeared in the controls after only 4 months.

DISCUSSION

Our study of rainforest trees greater than 2.5 cm DBH has been carried out for 34 years, and our study of saplings and seedlings for 32 years. Several other long-term studies of rainforest trees were reviewed by Swaine, Lieberman, and Putz (1987) and Phillips and Gentry (1994); these studies ranged from 6 to 38

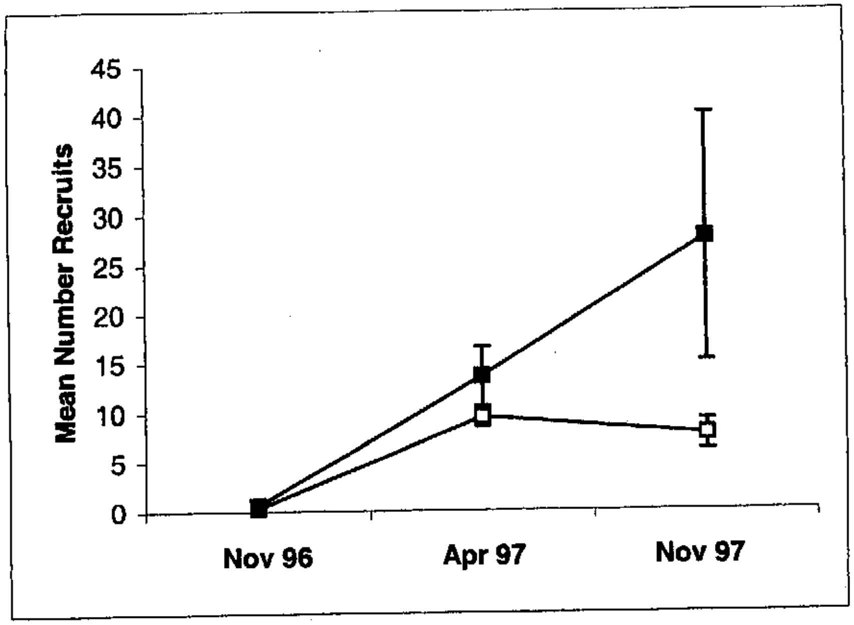

Figure 23.5 Rates of survival and recruitment of seedlings (mean ± 1 SE), in experimental plots at Davies Creek during the periods shown. The exclosures (represented by solid boxes) prevented entry by ground-dwelling mammals and birds; the adjacent controls (represented by open boxes) allowed entry. The exclosures were open for the first census period and closed for the last two.

years in length. Most of them used a minimum size of 10 cm DBH; three used minimum sizes of 3.2, 4.0, or 5.0 cm DBH. More recently, a few studies have established long-term plots that include smaller size classes (see reviews by Condit 1995; Lieberman 1996). To our knowledge, the present study has the longest record of dynamics of tropical rainforest trees less than 10 cm DBH.

The patterns of seedling recruitment among the many species on the study plot have been extremely complex during the past three decades. Most tree species did not produce seedlings every census, and sometimes there were long intervals of up to a decade between successive recruitments. Our phenological observations indicate that the absence of seedlings in a particular year could have been due to the an absence of flowering, or to flowering without subsequent fruit development. The largest proportion of the species began to develop fruit, but without seedlings subsequently appearing. Losses at this stage could have been due to fruits being destroyed on the tree at any stage in development, or to mature fruits never germinating after falling to the ground.

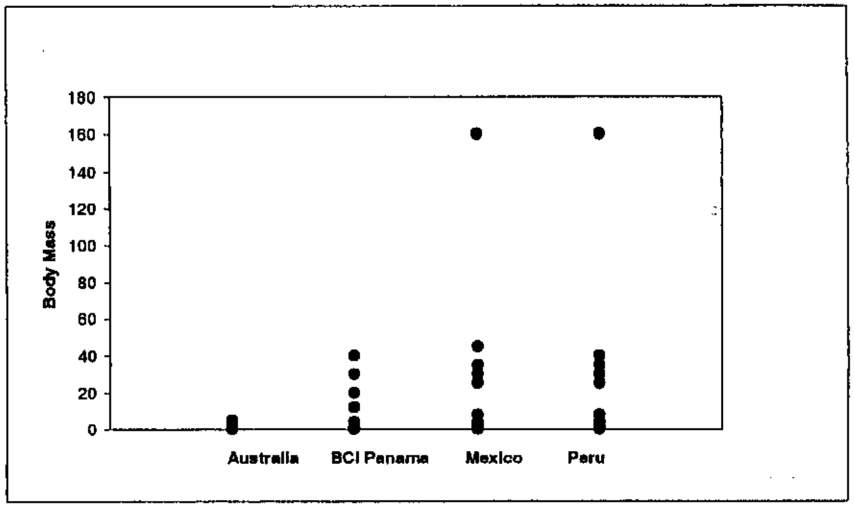

Figure 23.6 Body mass (kg) of ground-dwelling mammalian herbivores, seed predators, and seed dispersers that occur at four tropical rainforest sites: Davies Creek, Australia (T. C. Theimer and C. A. Gehring, unpublished data); Barro Colorado Island (BCI), Panama (Glanz 1990); Montes Azules, Mexico (Martinez-Gallardo and Sanchez-Cordero 1997); and Cocha Cashu, Peru (Janson and Emmons 1990).

Many studies of phenology have been done (see review in Van Schaik, Terborgh, and Wright 1993), and some have been long-term: Newstrom et al. (1994), for example, took 12 years of monthly phenological records in a Costa Rican rainforest. Two studies measured fruit fall (Foster 1982b) and seedling germination (Garwood 1983) in different years on Barro Colorado Island, Panama. However, the present study is, to our knowledge, the first to link phenological observations of flowering and fruiting to measurements of germination and early survival of seedlings during the same period on the same plot, with the aim of estimating losses among the different life stages leading up to seedling establishment.

Judging from the results of the field experiment designed to measure the effects of vertebrates, these losses may be due in part to attacks by vertebrates or to their disturbance of litter. Australian rainforest mammal communities have fewer large species than those in other regions (Eisenberg 1981); the absence of large ground-dwelling mammalian herbivores, such as tapirs, peccaries, and deer, is especially striking (fig. 23.6). Most of the smaller mammals act as seed dispersers and seed predators, with only the red-legged pademelon and the musky rat kangaroo feeding directly on seedlings. As a consequence of these differences, we predict that, in Australian tropical rainforests, vertebrate seed dispersers and seed predators should have a greater effect on the recruitment and mortality of tree seedlings than vertebrate herbivores. While seed-eating rodents consume the majority of fallen seeds, their scatter-hoarding behaviors may be the major avenue for the establishment of some seedling species in the face of heavy seed predation on our plot (Theimer 2001, 2003).

In addition to their roles as seed dispersers, rainforest vertebrates may also disperse mycorrhizal fungal spores, leading to indirect effects on seedling performance. Gehring, Wolff, and Theimer (2002) observed that vertebrate exclusion led to reductions in arbuscular mycorrhizal fungal diversity, which in turn reduced rates of seedling colonization by these fungal mutualists. Reductions in mycorrhizal inoculum are likely to influence seedling community dynamics because tree species in this rainforest vary in their dependence on mycorrhizal fungi for growth in the shaded understory (Gehring 2003).

Our field experiments suggest that litter-disturbing birds could have strong effects on seedling recruitment and mortality in Australian tropical rainforests. The effects of variation in litter depth on seedling establishment have often been demonstrated (Carson and Peterson 1990; Facelli and Pickett 1991; Facelli 1994; Molofsky and Augspurger 1992; Reader 1993; Cintra 1997). Since litter-disturbing animals increase the spatial heterogeneity of litter depth, they should promote the germination of a greater diversity of species of seeds than if they were absent. Theimer and Gehring (1999) documented that a common litter-disturbing bird on our plot, the chowchilla, created spatial variation in litter depth of magnitudes great enough to alter the germination success of three common tree species. Furthermore, seedling mortality due to litter disturbance by these birds was twofold to fivefold greater for two common species of seedlings than for two rarer species, suggesting that variation in susceptibility to this type of disturbance may affect plant community dynamics (Theimer and Gehring 1999).

Among the factors that determine the abundance, species composition, and diversity of trees in forests, we have concentrated on initial seedling recruitment, since it determines the initial abundance of each year's cohort. To measure the likelihood that the relative abundance of species in the seedling recruitment determines the relative abundance of species at the adult stage, we looked for evidence of frequency dependence during the period of growth from the seedling stage to adulthood. We found such evidence in about half the instances in which seedlings interacted with close neighbors (Connell, Tracey, and Webb 1984). However, in several other analyses of seedlings and older stages, growth and survival showed little relation to abundance of conspecific adults, density of individuals of the same size class, or proximity to conspecific adults. Given this evidence that growth and mortality in the period between recruitment and adulthood are only weakly frequency-dependent, we conclude that the species composition of older life stages may be determined by that of seedling recruitment.

Given the weakness of the evidence for frequency dependence in all stages from seedling to adult, could frequency dependence play a role in the maintenance of tree species diversity at our study site? It could, if the population dynamics of the early life stages that produce the initial recruits are frequency-dependent (in this context, we will use the term to refer only to negative frequency dependence; e.g., growth or survival rates that are lower in commoner than in rarer species). We found that the per capita recruitment rates of the group of species that reach maturity in the subcanopy and understory layers of the forest did exhibit negative frequency dependence (see fig. 5 in Connell, Tracey, and Webb 1984). In contrast, the group of species that mature only when they reach the canopy layer did not exhibit it. (This analysis used data from 1965–1980; a reanalysis using data from 1980–1997 reached similar conclusions: J. H. Connell et al., unpublished data.) In addition, some frequency dependence apparently occurs during later seedling growth and mortality due to interactions between the young seedlings.

Thus, the strongest evidence for frequency dependence at Davies Creek is confined to the earliest life stages. In contrast, in a plot on Barro Colorado Island, Panama, evidence of frequency dependence has been found in some older stages (Hubbell, Condit, and Foster 1990; Condit, Hubbell, and Foster 1992; Wills et al. 1997). The difference in these findings from the two sites could be due to differences in climate, tree species, tree abundance, and dynamics, as pointed out earlier (see figs. 23.1, 23.2, and table 23.1), or to the past history of the local forests. From our results at Davies Creek, we hypothesize that frequency dependence does occur in some species groups during the production of the initial seedling recruits—that is, during flowering, fruit development, seed dispersal, and seed germination—or during the early seedling period before the standard censuses are made. We plan to investigate these hypotheses, using the results from our phenology observations, as well as those from the field experiment measuring the effects of ground-dwelling vertebrates.

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The Theory and Practice of Planning for Long-Term Conservation of Biodiversity in the Wet Tropics Rainforests of Australia

NIGEL E. STORK

ABSTRACT

The Wet Tropics of Queensland World Heritage Area was established in 1988 to "protect, conserve, present, rehabilitate and transmit to future generations" the natural World Heritage values of the region—the evolutionary history of the rainforests, the superlative natural beauty of the area, and its unique and rich biological diversity. The region also has an important indigenous cultural heritage. The World Heritage Area was created against a preexisting set of land uses. Currently, there are more than 700 separate parcels of land within the World Heritage Area and many thousands of landholders whose land abuts it. Land uses varying from residential to agriculture, tourism, and forestry present many management problems and conflicting demands on the World Heritage Area. Creating short-term and long-term management goals for the conservation of biodiversity of the region is a complex task. Community consultation and support and expert and timely research are essential. Current problems include increasing demands for water from the World Heritage Area and continued forest clearing in adjacent lands. Immediate threats to biodiversity and other World Heritage values include feral animals, exotic weeds and other pests, and roadkills of cassowaries. In addition, globalization of trade is creating new problems with the unintentional transport of "hitchhiker" pest organisms. The consequences of climate change for different environments within the World Heritage Area are unknown. Determining the carrying capacities of particular areas and the limits of acceptable changes is fundamental to managing human uses. Research on the past and present dynamics of the Wet Tropics rainforests, on the current and past distribution of biodiversity, and new modeling of future scenarios should help managers to devise management plans to cope with future changes and threats.

INTRODUCTION

Sustainability had become the fundamental principle for decision making in natural resource management by the end of the twentieth century, but in reality it has been difficult to achieve, particularly in areas of the world that have only recently been developed. This is nowhere more true than in tropical forests,

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