HABITAT-SPECIALIZATION AND SEED DISPERSAL-LIMITATION IN A NEOTROPICAL FOREST

Kyle Edward Harms

A DISSERTATION
PRESENTED TO THE FACULTY
OF PRINCETON UNIVERSITY
IN CANDIDACY FOR THE DEGREE
OF DOCTOR OF PHILOSOPHY

RECOMMENDED FOR ACCEPTANCE
BY THE DEPARTMENT OF
ECOLOGY AND EVOLUTIONARY BIOLOGY

June 1997

ABSTRACT

Many theories exist for the maintenance of diversity in species-rich tropical tree communities. In Chapter 1 of this thesis I briefly review the past contributions to testing these theories made by the long-term Forest Dynamics Project (FDP) on Barro Colorado Island (BCI), Panamá. This chapter also sets the conceptual context for the investigations into habitat-specialization and seed dispersal-limitation that constitute the rest of the thesis.

To examine the question of habitat-specialization, I analyze the degree to which tree and shrub species are associated with topographically/hydrologically defined habitats on the 50-ha FDP plot of BCI (Chapter 2). I develop a torus-randomization method, as a novel statistical technique that avoids false assumptions made by the widely used Chi-square tests of habitat-associations. This analysis supports the hypothesis that most species in the BCI forest are habitat-generalists.

I then demonstrate that differences in growth and mortality rates on slope versus plateau sites of the 50-ha FDP plot generally cannot be predicted from apparent habitat-affinities, further supporting the generalist hypothesis (Chapter 3). These results fail to explain, however, why some species show strong habitat associations with respect to slope and plateau sites.

Through common-garden experiments on the 50-ha FDP plot, I show that growth and mortality, for three slope-associated species and for one generalist species, are not differentially influenced by habitat (slope versus plateau sites) at the seedling stage (Chapter 4).

I conclude by analyzing the evidence for limited seed-dispersal, using data from an 8-yr seed-trap study on the 50-ha FDP plot on BCI. Most species disperse their seeds short distances. Short distance dispersal and large inter-individual distances for adult trees result in locally species-poor seed-inputs relative to the species-richness of the local tree community. Limited dispersal itself is sufficient to alter local recruitment patterns substantially, but whether it results in a decline of tree diversity, from the level maintained by unlimited seed-dispersal, will depend on the balance of competition, dispersal, and attack by enemies of seeds and seedlings.

ACKNOWLEDGMENTS

I came to Princeton because of its graduate students, post-docs, and faculty members. I will leave Princeton with many fond memories of you and your families. You have been a constant source of information and inspiration. I thank you *all* with deep appreciation. Among those Princeton students, post-docs, and faculty members, and members of their families, who have contributed the most to my graduate experience are: Hiroshi Akashi, Kristin Ardlie, Cindy Bennington, Andrew Berry, Ben Bolker, John & Ruth Bonner, Marty Burd, Tormod Burkey, Kate Clark, Jon Cline, Scott Cromar, Lisa Curran, Andy Dobson & Annarie Lyles & Allegra, Giulio De Leo, Doug Deutschman & Elizabeth Perlin & Katherine, Jonathan Dushoff, Alexander Ellis, Doug Emlen & Kerri Bright, Simon Emms, Jeff Feder, Lila Fishman, Charles Foley, Scott Freeman, Lenny Gannes, Netzin Gerald & Dieter Steklis, Binney Girdler, Jim Gould, Liz Graham & Peter Velikonja, Peter & Rosemary Grant, Ted & Ruth Gullison, Leila Hadj-Chikh, Tom Hahn, Gregg Hartvigsen, Graham Head, Hope Hollacher & Ben Heller, Henry & Betty Horn & family, Steve Hubbell & Leslie Johnson, Martha Hurley, George Hurtt, Noriko Inoue, Alison Jolly, Paula Kahumbu & Joshua, Tim Kailing, Laura Katz & Dan Berger, Ann Kinzig, Jens Krause, Marty Kreitman, David Kutzler, Laura Landweber, Phil & Judith & Martha Lee, Simon & Carole Levin, Cynthia Lord, Liz Losos & David Schanzer, Bruce Lyon & Linda Hamilton, Carlos & Martha & Aurora Raven Martínez del Río, John McDonald, Adina Merenlender, Alan & Karen & Adrian & Cameron Masters, Jane Molofsky, Paul Moorcroft & Julie Burkley, Helene Muller-Landau, Philip & Gladys & Brian Muruthi, Cassandra Nuñez, Diane O'Brien, Seán & Anne O'Brien, Tim O'Brien & Margaret Kinnard, Enrique Ortiz & Monica, Jake Overton, Steve & Lisa Pacala & family, Eirikur Palsson, Mercedes Pascual & Ilina, Chris Peterson, Ken Petren, Naomi Pierce, Nigel Pitman, Mark Roberts, Jon Paul Rodríguez, Dan & Nancy Rubenstein & family, David Saltz, John & Sue Saponara, Don Stratton & Helen Young & family, David Smith &

Amy Worlton, Luís & Laura & Lucas Solórzano, David Stern, Kristina Stinson & Jim Robinson, Ted Sullivan, I-fang & Rei-Ying Sun, Martin Taylor, Sean Thomas, Anne Torjussen, Philippe Tortell, Thomas Valqui, Steve Vail, Carlos Valle, Todd Vision, Diane Wagner, Marta Wayne, Jim Wetterer, Miguel Zavala, and Wolfgang. I especially thank Jorge Ahumada for many years of unflagging friendship.

Upon arriving in Princeton, I soon realized that several other members of the community would play significant roles in my life as a graduate student. In particular, I wish to thank Mary Arnesen, Kimberley Black, Amy Bordvik, Linda Cholewiak, Gianina Cifelli, Mary Cupples, Pat Denton, David Goodman, Fred Herndon, John Little, Beth Nichols, Anju Sahni, Louise Schaeffer, Kathy Sullivan, Hannah Suthers, Nancy Van Doren, and especially Mona Fazio, MaryRose Guimond, Ranveig Jakobson, Kim Kelly, Carolanne Lowrie, and Evelyn Wolfe for helping me on numerous occasions.

My field work was conducted on Barro Colorado Island (BCI), operated as a research station by the Smithsonian Tropical Research Institute (STRI) in Panamá. For help, advice, and friendship in Panamá, I thank Oris Acevedo, Salomon Aguilar, George Angehr, Pilar Angulo, Nigel Asquith, John Barone, Patricia Bermejo, Osvaldo Calderón, Walt Carson, Tom & Lissy Coley, Fernando Cornejo, Catherine Craig, Diane DeSteven, Patricia Escobar, Milton García, Nelida Gomez, Savi & Nimal Gunatilleke, Charles Handley, Andrés Hernandez, Elisabeth Kalko, Kaoru Kitajima, Damond Kyllo, Lizzy Leigh & family, Suzanne Loo de Lao (who deserves an extra thank you for many hours of programming), Omar Lopez, Jenny Maas, José Luís Machado, Mamoru Matsuki, Deedra McClearn, Troy Mielke, Marcela Moscol, John Nason, Sandra Patiño, Steve Paton (who deserves an extra thank you for several hours of programming and several pepperoni pizzas) & María Joséfa, Rolando Pérez, Jim Roper, Rosa, Lars Rosengreen, Milagro Ruiz, Mirna Samaniego, Mary Schultz &

family, Eduardo Sierra, Lazlo Veigh, Jorge Ventocilla, Rainer Wirth, Mirjam Wurth, and Nicole Zangen. I especially thank Astrid Ferrer, José Luís Andrade, Herve Cochard, Jim Dalling, Doug Emlen, Greg Gilbert, Manuel Guariguata, Beth King, and Gerhard Zotz for the times we've shared.

For help in the field I thank Rafael Aizprúa, Robert Woolsey, Enith Rojas, Ricardo Racines, Alexander Ellis, and Tobin Hahn. Elizabeth Stacy deserves a special thank you for supplying me with seeds of *Tocoyena pittieri*.

Quiero también darles agradecimientos a Zeida y a los miembros de la oficina del CTFS, a todos los guardabosques y empleados de la Isla de Barro Colorado, a toda la gente de la biblioteca del STRI, Tupper, y Tivoli, y, especialmente a Vielka Rodríguez y Daniel Millán en la isla, y Gloria Maggiori, María Leone, Georgina de Alba, Isis, Marcela, Mirna y Roberto en Tupper.

STRI Scientists who have been either directly or indirectly influential in the completion of this thesis are: Annette Aiello, Tony Coates, Paul Colinvaux, Richard Condit, Mireya Correa, Bill & Mary Jane Eberhard (who deserve a special thank you for a much needed vacation just before this dissertation was completed), Robin Foster, Allen Herre, Egbert Leigh, Jr., Dolores Piperno, Stan Rand, Ira Rubinoff, Alan Smith (who will always be remembered for several enlightened conversations), Nick Smythe, Don Windsor, Klaus Winter, and Joe Wright (who deserves a special thank you for frequent advice and for sharing the seed-trap data presented in Chapter 5). Thank you for your advice, encouragement, and criticism.

I thank my committee - Steve Hubbell, Henry Horn, Don Stratton, Steve Pacala and Andy Dobson - who asked me to think more critically about solving problems than I ever had. I hope this thesis reflects the results of some of those thought processes.

I thank Sigma Xi, Princeton University, and STRI for providing financial and logistical support to complete the investigations presented in this dissertation. I also thank STRI's Terrestrial Research Committee for approving my proposal and granting me permission to conduct investigations within the 50-ha Forest Dynamics Project (FDP) plot of BCI.

Many people have been involved in producing the vast database that now exists for the 50-ha FDP plot on BCI. I wish to thank Steve Hubbell and Robin Foster for initiating and continuing their active involvement in the project, Richard Condit for joining the project to contribute his expertise, Suzanne Loo de Lao for helping to manage the database, and Rolando Pérez for knowing the forest. I wish to thank all of those who have contributed to this project, but who have remained anonymous. Thank you also for your contributions to long-term tropical forest research!

Many more friends and family members have played significant roles in my life during the past 6 years. Since my professional life during these years has been dominated by thesis-related concerns, I wish to thank those who have remained anonymous. I cherish and appreciate your companionship even though I have chosen to restrict these lists to those who have helped me in more-or-less direct measure to produce a finished dissertation.

Mom, Dad, and Chad have been a constant source of support of the most important kind. I love you back.

Finally, my most heartfelt thanks and admiration I extend to Jessica Eberhard, who has unconsciously yet continually reminded me during the past few years that a full life is so much more than this.

I dedicate this dissertation to Grandma Florence Brinkert,
and to the memories of Grandpa Henry Harms,
Grandma Lillian Harms, and Grandpa Edward Brinkert,
for their dedication to education in its broadest sense.

Table of Contents

CHAPTER 1

Habitat-Specialization and Seed Dispersal-Limitation in a Neotropcial Tree Community

Species-diversity can be measured in a variety of ways (Whittaker 1970; Magurran 1988). If one uses Whittaker's (1970) "alpha diversity" - the number of species found within local communities - tree species-diversity increases, on average, as one follows a temperate to tropical latitudinal gradient (Pianka 1966; Currie and Paquin 1987; Huston 1994; Rosenzweig 1995). Furthermore, tropical lowland, non-swamp tree communities often harbor several times the number of species in temperate-zone forests of comparable sample area and elevation (Black *et al.* 1950; Gentry 1988a, 1988b; Phillips *et al.* 1994). The existence of extremely species-rich tree communities within tropical latitudes is undisputed, but the origin and maintenance of tropical levels of biological diversity remain among the most important unresolved puzzles in ecology and evolutionary biology (Richards 1969; Whitmore 1975; Schluter and Ricklefs 1993; Leigh 1996).

Hutchinson's (1961) "Paradox of the Plankton" - more species coexisting than there are limiting resources - appears especially pertinent when applied to tropical trees, since the many species of extant angiosperms share requirements for a small number of resources (Harper 1977; Tilman 1982). Furthermore, all free-standing tropical trees, for which photosynthetic pathways are known, utilize the same biochemical process to capture radiant energy - C_3 photosynthesis (Osmond *et al.* 1982) - and most of these species share the same generalized vesicular-arbuscular mycorrhizae that aid in the capture of soil nutrients (Janos 1980). Articulation of Hutchinson's Paradox helped spur the search for coexistence mechanisms for such apparently similar organisms (Tilman and Pacala 1993).

Not only are tropical trees competing for the same resources, but competition among individuals must be intense through ontogeny, since many fewer adult trees can be packed into the same area occupied by a given number of saplings or seedlings. Consideration of the "Competitive Exclusion Principle" (Hardin 1960), by which dominant competitors are expected to exclude (cause the local extinction of) those species less well-endowed for given climatic and biotic regimes (Gause 1934; MacArthur 1972; Silvertown and Law 1987) raises the question: How is high local diversity maintained in the face of strong competitive interactions that should lead to the competitive exclusion of most species? Hypotheses to explain the maintenance of diversity in species-rich forests posit a wide range of mechanisms to reduce or eliminate the chance that any given species will suffer extinction through competitive exclusion.

Several hypotheses for the maintenance of high levels of species-richness postulate a dominant role for specialization and niche-differentiation within a heterogeneous abiotic environment (Ashton 1969; Ricklefs 1977; Huston 1979; Denslow 1980; Orians 1982; Tilman 1982, 1988). Many of these hypotheses focus on the light environment and its variability among sites, especially *vis-à-vis* gap dynamics (Ricklefs 1977; Denslow 1980; Orians 1982). Tilman's early Resource-Based Competition Theory (1982, 1988) demonstrated that species could theoretically partition soil resources based on ratios of resource-use efficiency. Other hypotheses propose that niche-differentiation and disturbance frequency interact to produce diversity differences among sites. Diversity differences result from differences in disturbance frequency (Horn 1975; Strong 1977; Connell 1978) or growth rates following disturbance (Huston 1979, 1994) which dictate the range of viable life-history strategies along a competition-colonization axis (Tilman 1994), which in turn determines membership in the pool of species capable of surviving in the community.

Other hypotheses for the maintenance of high levels of species-richness propose that density-dependent or frequency-dependent attack by predators, pests, or pathogens maintain populations through demographic disadvantages when the populations are at high density or are common, coupled with demographic advantages when those same populations are at low density or are rare (Gillett 1962; Janzen 1970; Connell 1971;

Augspurger 1983a, 1984c). The specific mechanism behind the hypothesis proposed independently by Janzen (1970) and Connell (1971) is that seeds or seedlings rarely survive beneath or near conspecific adults due to the impact of enemies that attack in a negative density-dependent or distance-to-adult-dependent manner.

Hubbell and Foster (1986a) proposed, developing further an argument made by Connell (1980), that competitively equivalent species result from convergence due to evolutionary histories of selection in biotically unpredictable neighborhoods. Consequently, although competition among individuals may be intense, deterministic competitive exclusion among pairwise species rarely occurs. Population dynamics are then governed by non-equilibrial random walks that result in long times to extinction relative to speciation rates (Hubbell 1979; Hubbell and Foster 1986a). Although there is a continual temporal turn-over of species under such circumstances, species-richness is maintained at an equilibrial level determined by the opposing processes of speciation and extinction (Hubbell 1995).

Recently, Hurtt and Pacala (1995) showed, through modeling, that seed dispersal-limitation slows community dynamics, even if there are strong competitive asymmetries among species. If most sites do not receive seeds from dominant competitors for those sites, then many sites are captured by lower ranking species in the competitive hierarchy. This “winning by forfeit” is the mechanism that slows competitive exclusion and helps to maintain diversity over long periods of time in the model (Hurtt and Pacala 1995).

Since each of the above mechanisms was proposed to account for the maintenance of diversity in communities, tests of these various mechanisms require datasets that encompass the community-level of biological organization.

The 50-ha Forest Dynamics Project plot of Barro Colorado Island

The Forest Dynamics Project (FDP) of Barro Colorado Island (BCI), Panamá provides one of the few available databases with which to test hypotheses for the maintenance of high levels of species-richness in tropical forests (Condit 1995). S. Hubbell and R. Foster initiated the project in 1980. Hubbell, Foster, and their team of assistants established a reference grid of 1250 quadrats of 20 x 20-m within a 50-ha plot of forest (Hubbell and Foster 1983, 1990a; Condit 1995). Topography of the plot was mapped by surveying the elevation at the corners of each 20 x 20-m quadrat, and then linearly interpolating at 5-m intervals along the sides of each 20 x 20-m quadrat.

The site for the 50-ha FDP plot was originally chosen for its uniformity of relief and forest age (S. Hubbell and R. Foster, pers. comm.). Nevertheless, topographic variation exists across the plot

(Hubbell and Foster 1983, 1986c). Furthermore, hydrological differences are related to the existing topographic relief (Becker *et al.* 1988; Condit *et al.*, in press). A low-lying, seasonally inundated swamp and seasonal streams are found on the plot. Shallow slopes are found near the eastern and southern edges of the plot. Due to the underlying geology of the island, slopes are kept more moist during the dry season compared with the main plateau of the plot (see Chapter 2; Becker *et al.* 1988).

Once trees on the plot were mapped, highly non-random distribution patterns became evident. Not only were most species' distribution patterns clumped at a variety of spatial scales (Hubbell and Foster 1986a), but several species showed strong patterns of association, through Chi-square tests, with distinct topographic features of the plot (Hubbell and Foster 1983, 1986c). Furthermore, several species showed congruent distributions with respect to topographic features, especially with the swamp and shallow slopes (Hubbell and Foster 1983, 1986c). Together these patterns suggested that many species may be habitat-specialists on the 50-ha FDP plot, which could help to explain some of the diversity found there.

Distribution patterns have often been used to infer habitat-specialization (*e.g.*, Whittaker 1956, 1970). The implicit assumption of this inference is that the realized distributions of plants are reflections of their fundamental niches (*sensu*

Hutchinson 1957). Chi-square tests, however, cannot rule out several other mechanisms that could lead to clumped distribution patterns related to habitat features. For example, restriction to certain habitats may be imposed by interactions with other species, *e.g.*, competitors, predators, or pathogens (Tansley 1917; Connell 1961; Paine 1966; Thomson *et al.* 1996). Source-sink population dynamics may also obscure habitat-relationships when "source" sub-populations supplement the recruitment of "sink" sub-populations that would otherwise, on their own, become extirpated (Pulliam 1988; Pulliam and Danielson 1991; Thomson *et al.* 1996). Furthermore, limited distribution patterns may be the ephemeral or transient result of a history of recent immigration and limited seed-dispersal (Ricklefs 1987; Primack & Miao 1992; Ricklefs & Latham 1993; Losos 1993, 1995). The extent to which the non-random distribution patterns of tropical tree species reflects habitat-specialization, a history of limited dispersal from initial colonization sites, or other causes of clumping is very little known and understudied on BCI and elsewhere.

It was recently discovered that not only do several species show non-random patterns with respect to the 50-ha FDP plot's topography, but so does species-diversity (Condit *et al.* in press). Two measures of diversity, species-richness measured on a per stem basis and species-diversity measured as Fisher's alpha, are both significantly higher on slopes than on the main plateau of the 50-ha FDP plot (Condit *et al.* in press). This pattern sparked renewed interest in the habitat-specialization question, since understanding the factors that cause diversity gradients contributes to our understanding of the maintenance of diversity.

Chi-square tests of habitat-associations, although often employed (Brandani *et al.* 1988; Hubbell and Foster 1983, 1986c; Basnet 1992), assume independence among conspecific stems. In an attempt to partially correct for the failure of the independence assumption, I develop a new statistical technique for determining association patterns between species and habitat types. I use the technique to estimate the prevalence of habitat-specialization among BCI tree species, using the tree distribution data. I show in Chapter 2 that many fewer species have strong positive or negative habitat associations than suggested by the earlier analyses based on Chi-square tests.

Dynamic Data from the 50-ha FDP Plot

Since the 50-ha FDP plot was established, 4 complete censuses have been made of the plot's non-liana, woody stems with diameters $\geq$ 1 cm at 1.3 m above the ground (diameter at breast height - DBH); the most recent census was completed in 1995 (Hubbell and Foster 1983, 1990a). During each census, each tree and shrub $\geq$ 1-cm DBH is measured and identified and each new stem is tagged and its map coordinates are recorded to the nearest 0.1 m.

The dynamic information made available for the 50-ha FDP plot allowed tests of several hypotheses for the maintenance of diversity. The principle tests thus far have been of niche-differentiation with respect to the light environment, and of the generalized Janzen-Connell Hypothesis.

Specialization with respect to the light environment has been tested in several ways. First, analyses of growth and mortality with respect to canopy height has shown that the BCI species fall along a life-history trade-off axis between maximal growth rate in high light conditions versus survival in understory shade conditions (Hubbell and Foster 1992). However, three-quarters of the BCI species cluster relatively tightly at the shade-tolerant end of the spectrum (Hubbell and Foster 1992). In a second analysis, the recruitment of non-pioneer species does not depend on light environment (Hubbell *et al.* in press). Taken together, the implication from these studies is that adaptation to the available light environment results in a distinct difference between shade-tolerant and shade-intolerant species, with a few scattered in between, but that the majority of species are found at the shade-tolerant end of the spectrum and are indistinguishable by growth and mortality rates with respect to differences in gap-structure (Hubbell and Foster 1992).

The Janzen-Connell Hypothesis was initially tested on a community-wide basis for the BCI 50-ha plot using quadrat-based, static data from the first census (Hubbell and Foster 1986a). Little evidence for Janzen-Connell effects were found, since for most tree species a positive, linear relationship was found between the number of adult trees per ha and the number of 1-2 cm DBH saplings per ha (Hubbell and Foster 1986a). More appropriate tests of the Janzen-Connell Hypothesis involve dynamic data (Clark and Clark 1984). Such tests have been made on data for species of the 50-ha FDP plot (Hubbell *et al.* 1990b; Condit *et al.* 1992ab; Wills *et al.* in press). Using focal adult analyses, several species showed recruitment patterns consistent with Janzen-Connell effects, but many more species did not (Hubbell *et al.* 1990b; Condit *et al.* 1992ab). However, as Schupp (1988, 1992) pointed out, analyses based on focal adults may focus on an inappropriate scale to detect density-effects. The most recent quadrat-based analysis suggests that many more species show density effects on sapling growth, survival, and recruitment than had previously been detected (Wills *et al.* in press). Janzen-Connell effects appear to be pervasive among many species of the BCI forest, yet it remains to determine whether the magnitude of these effects is sufficient to regulate species' abundances and to prevent competitive exclusion in this forest.

The analyses presented above are "mean-field" analyses, which assume that the processes they are considering do not vary throughout the 50-ha FDP plot. Consideration of the habitat-association patterns would suggest that such an approach ignores potentially important spatial heterogeneity. The dynamic information coupled with habitat information allowed me to ask whether growth, mortality, and recruitment differ across habitat types. I present these analyses in Chapter 3.

Growth, mortality, and recruitment are generally highly variable within populations of tropical trees (Hartshorn 1990; Condit *et al.* 1995). The extent to which this variation is related to environmental factors other than light has been little studied *in situ*. Those species associated with slope and plateau sites identified as such in Chapter 2 may be habitat-specialists, and, if so, would be expected to perform differently within and outside of their preferred habitats. Regardless of how well realized habitat affinity reflects fundamental niche requirements, differences in growth, mortality, and/or recruitment with respect to topography is of interest since such differences might constitute source-sink meta-population dynamics that could help maintain diversity. In Chapter 3 I estimate and compare the growth, mortality, and recruitment rates of species on slope versus plateau sites. I find that habitat location is not a good predictor of growth or mortality. However, many species that are significantly associated with slope or plateau sites, either positively or negatively, have higher than expected recruitment rates on the slope.

Many spatial patterns may arise from events early in the life-cycles of plants, especially when those plants are long-lived trees. Performance differences at size-classes smaller than 1-cm DBH may determine distribution patterns. In Chapter 4 I compare the seedling performance on slope and plateau sites for selected species: three slope-associated species, one widespread species, and one very rare species. No differences in growth or survival on slope versus plateau sites appeared within species. Taken together with the results from Chapter 3 there is no current basis on which to conclude that differences in growth or mortality have resulted in the distributional differences observed among the species on the 50-ha FDP plot. Periodic, but severe droughts may be important to determining spatial patterns of recruitment into the seedling/sapling layer. It is also possible that the small, yet statistically insignificant differences in mortality compound over the lifetimes of trees and result in differential patterns of distribution. I discuss this issue in Chapters 3 and 4. However, a definitive answer to this question will require modeling forest dynamics once seed production and seed dispersal parameters are known.

Together with earlier analyses of growth, mortality, and recruitment with respect to heterogeneity in light availability, my results suggest that regeneration-niche differences and habitat-specialization play more limited roles in maintaining diversity in the BCI forest than previously thought.

Seed-Dispersal on the 50-ha FDP plot

Seed-production and seed-dispersal provide the raw material on which all subsequent processes act to sculpt spatial patterns of recruitment; where no seed of a given species lands, no seedling of that species will arise, and, only where seeds land does a species have a non-zero probability of recruiting an individual into the population (Schupp *et al.* 1989; Schupp 1995; Clark and Ji 1995). Despite its potential importance, the relationship between spatial patterns of adult trees relative to spatial patterns of the seed-rain has received little empirical attention in studies of tropical forest dynamics (Schupp 1995; Clark and Ji 1995).

In 1986, S. Joseph Wright of the Smithsonian Tropical Research Institute established a series of seed-traps along the trail system of the 50-ha FDP plot of BCI. From 1 January 1987 until the end of December in 1994, all seeds and fruits or fruit fragments ≥ 1 mm diameter have been identified and counted on a weekly basis. The seed-traps were initially erected to examine phenological patterns in the BCI forest. However, the 8-year dataset is also amenable to answering questions about spatial patterns of the community-wide seed-rain.

The final chapter of this thesis is a description of the community-wide seed-rain onto the 50-ha FDP plot of BCI based primarily on data from the seed-trapping project. I weigh the evidence for limited seed-dispersal, a necessary requirement for dispersal-limitation. Most species appear to be strongly dispersal-limited in this forest. Out of 108 canopy tree species, each trap received at least one seed from an average of only 16 species over the 8-year period, 1987-1994, inclusive. Only 31 out of 182 (17%) of the midstory and canopy tree species dispersed seeds to $\geq$ 50 ($\geq$ 25%) of the 200 seed-traps and the probability that any trap received seeds of a given species fell, for most species, as the distance from the nearest conspecific adult of the focal species increased.

Pioneer and non-pioneer species show marked differences in dispersal distances and in seed-to-recruit ratios. For example, on average, a pioneer recruit into the 1-2 cm DBH size-class requires 359,000 seeds, whereas a non-pioneer requires nearly an order of magnitude fewer, or 52,000 seeds.

Implications of the Current Research

The habitat analyses lend very little support to the hypothesis that habitat-specialization plays a substantial role in maintaining diversity in the BCI forest. However, habitat-specialization may be related to diversity differences among sites. It is particularly intriguing that soil moisture levels during the dry season may produce a one-way filter for species on the 50-ha BCI plot, which allows only those species capable of surviving dry periods to be found in abundance on the plateau sites.

Dispersal appears to be limited for the majority of species on BCI. Pervasive, limited dispersal among species results in few species arriving as seeds to any particular colonization site on the forest floor. The contribution that limited dispersal makes to the maintenance of diversity in the BCI forest depends on the other processes that act to determine recruitment probabilities. If strong competitive asymmetries exist among the species of this forest, limited dispersal reduces the chances that competitive dominants reach all sites to which they are best suited, allowing many individuals to establish through winning-by-forfeit (Hurtt and Pacala 1995). If strong competitive asymmetries do not exist and species can be considered competitive equals, then limited dispersal may promote a reduction in local, community-level diversity while helping to maintain meta-community diversity (Hubbell in press), unless dispersal is so limited that seeds are never dispersed beyond the crowns of parent trees, in which case current diversity levels would be maintained indefinitely. If strong Janzen-Connell effects prevail throughout the BCI tree community, then not only is the pool of species arriving at any given site small due to limited dispersal, but those seeds represented in the highest density or most near to conspecific adults may have very little opportunity to make the transition into the seedling pool of that site. The consquences of different levels of seed dispersal-limitation coupled with Janzen-Connell effects have yet to be explored theoretically, but should be explored now that it has been demonstrated that few species arrive as seeds to any given site.

The universe of recruitment possibilities spans a range of outcomes that encompass both rapidly eroding diversity relative to the adult tree community and the long-term maintenance of existing levels of diversity. The demonstration of limited seed-dispersal may narrow the universe of possibilities since it has been shown that limited seed-dispersal dramatically effects the outcome of other recruitment processes, at least in modeling contexts (Hurtt and Pacala 1995; Hubbell in press). However, the boundaries of this subset of possibilities are unknown without knowing the magnitude and pervasiveness of competitive asymmetries and the strength and pervasiveness of density- or frequency-dependent demographics.

CHAPTER 2

Habitat-Associations of Tree and Shrub Species in a Neotropical Forest

INTRODUCTION

Foresters and field biologists assert that many, if not most, species of tropical trees are found restricted to particular climatic or edaphic conditions, both across regional spatial scales of many km^2 (Ashton 1964, 1977; Gentry 1992; Tuomisto and Ruokolainen 1994; Clinebell *et al.* 1995; Veenendaal *et al.* 1996) and at more restricted, local scales of less than several hectares (Gartlan *et al.* 1986; Basnet 1992; Lieberman *et al.* 1995). The concordant distribution of tree species with environmental factors may result from habitat-specialization, but our mechanistic understanding of these patterns is minimal (Tuomisto and Ruokolainen 1994; Condit 1996; Veenendaal *et al.* 1996). Without understanding the relationships between species' distributions and abiotic factors, we are also ignorant of the relative contribution that habitat specialization makes to the maintenance of diversity, at all scales, in tropical forests (Bazzaz 1991).

In practice, three methodological and conceptual difficulties must be considered in measuring and interpreting specialization and generalization using static data from sample plots in tree communities. First, the degree to which species are specialized or generalized is only meaningful in a comparative context and with reference to particular environmental axes (Colwell and Futuyma 1971; Futuyma and Moreno 1988). In other words, the extent to which species specialize in terms of resource requirements or stress tolerance is an inherently relative question.

Second, an observed match between the distribution of a sessile organism and a particular habitat may have arisen by any of several mechanisms (Pickett and Bazzaz 1978; Goldberg 1982, 1985; Austin *et al.* 1990; Bazzaz 1991; Wesser and Armbruster 1991; Thomson *et al.* 1996). For example, the pattern of distribution itself cannot be used to distinguish between specialization to the abiotic environment and restriction imposed by interactions with other species, *e.g.*, competitors, predators, or pathogens (Tansley 1917; Connell 1961; Paine 1966; Thomson *et al.* 1996). In other words, the fundamental niche cannot be inferred from measuring the realized niche, which is in general reduced relative to the fundamental niche (Hutchinson 1957; Thomson *et al.* 1996). Source-sink population dynamics may also obscure habitat-relationships when "source" sub-populations supplement the recruitment of "sink" sub-populations that would otherwise, on their own, become extirpated (Pulliam 1988; Pulliam and Danielson 1991; Thomson *et al.* 1996). Furthermore, limited distribution patterns may be the ephemeral or transient result of a history of recent immigration and limited seed-dispersal (Ricklefs

1987; Primack & Miao 1992; Ricklefs & Latham 1993; Losos 1993, 1995).

A third difficulty with studies of habitat-specialization concerns identifying patterns of habitat-association and has been less broadly acknowledged than the two aforementioned difficulties. Studies that endeavor to identify statistical correlates of the distribution patterns of trees often make the implicit assumption that trees are independently distributed with respect to conspecifics (Greig-Smith 1952; Condit 1996). However, the independence assumption is violated by the reproductive and recruitment patterns of trees. Among tree species, most seeds are not dispersed far from the maternal parent (see Chapter 5) and give rise to recruits that are near to conspecific adults and conspecific recruits (Condit *et al.* 1992a). The clumped spatial dispersion patterns common to tropical trees (Hubbell 1979; Armesto *et al.* 1986) are likely due, in part, to their limited seed-dispersal abilities. Since recruitment is spatially contagious with adult trees and among recruits, limited seed dispersal means that individual trees do not appear on the landscape independently; their positions are spatially autocorrelated (Leduc *et al.* 1992; Legendre 1993; Thomson *et al.* 1996).

Hubbell and Foster (1983) described the striking degree to which the distribution patterns of several species matched particular topographic features of the 50-ha Forest Dynamics

Project (FDP) plot of Barro Colorado Island (BCI), Panamá. To quantify these patterns, Hubbell and Foster (1983) employed Chi-square Goodness-of-Fit Tests to determine patterns of association between trees $\geq$ 20 cm diameter at breast height (DBH) with coarse topographic features on the 50-ha FDP plot. Later, using all stems $\geq$ 1 cm DBH, Hubbell and Foster (1986c) again used Chi-square statistics to test for association patterns between species and topographic features of the 50-ha FDP plot. Although Chi-square Goodness-of-Fit tests are commonly used for determining patterns of association between tree species and habitat types (Hubbell and Foster 1983, 1986c; Basnet 1992), these tests rely on the implicit assumption that each stem may be treated as an independent sample unit (Snedecor and Cochran 1980).

My objective in this study is to reconsider the question of habitat-specialization of species within the 50-ha FDP plot on BCI. I ask whether the distributions of species with respect to habitat types are likely to have arisen by chance, given the short-distance dispersal patterns of trees. In order to improve upon previous studies, a procedure was required for generating null distributions of trees given that the location of a young tree is not independent of the locations of its maternal parent or siblings.

The method I developed is based on a Monte-Carlo simulation to generate null distributions for stems in mapped habitats. In this procedure, the habitat map is randomly moved about a torus while the map of tree locations for a given species remains unchanged. For each randomized, torus-translation of the habitat map, I determined the proportion of all stems represented by the focal species in each habitat. The resulting proportions formed a distribution to which I compared the proportion of all stems represented by the focal species on the true habitat map. I shall refer to this novel procedure as the torus-randomization method. The torus-randomization maintains the spatial structure of the tree populations of interest. Futhermore, physical spatial structure within and among habitats is maintained; although habitats do become divided as they are translated across boundaries of the 50-ha map, habitats maintain their shapes, contiguity, and spatial relationships.

METHODS

This study makes use of data collected from the 50-ha Forest Dynamics Project (FDP) plot of Barro Colorado Island (BCI), Panamá (see Hubbell & Foster 1983, pg. 28; or Hubbell & Foster 1986b, pg. 82 for topographic maps of the FDP plot). The elevation, temperature, and rainfall regime of BCI places the island in the Holdridge Life Zone category of “tropical moist forest” (Holdridge 1967). Detailed descriptions of the climate, geology, flora and fauna of BCI can be found in Croat (1978) and Leigh *et al.* (1982, 1990).

The FDP plot was established and gridded with a coordinate system, based on 20x20-m quadrats, of which there are 1250, in 1980. All stems of free-standing shrubs and trees ≥1 cm DBH on the 50-ha FDP plot have been mapped, identified, tagged, and measured on four separate occasions beginning with the initial census of 1980 - 1982. The first census, hereafter referred to as the 1982 census, took nearly 18 months to complete (S. P. Hubbell, pers. comm.). The second (1985), third (1990), and fourth (1995) censuses have each required about a year to complete (Hubbell and Foster 1983, 1992; Condit *et al.* 1992b, 1995). The names of the species included in these censuses are found in Appendix 1. Tallies of the number of species divided into growth form categories are provided in Appendix 2.

Defining the Habitats

The site for the 50-ha FDP plot on BCI was originally chosen for its relative uniformity of relief and forest age (S. P. Hubbell and R. B. Foster, pers. comm.). However, variation in topography, edaphic conditions, and forest age exists across the plot (Hubbell and Foster 1983, 1986c). In this paper I focus on small-scale topographic variation evident as plateau, slope, stream, and low-lying swamp sites within the 50-ha plot.

Specifically, I divided the 50-ha FDP plot into 6 habitats (details are given below), which I shall refer to as: Young Forest, High Plateau, Low Plateau, Slope, Stream, and Swamp (Table 2.1). Each of the 1250 20x20-m quadrats of the 50-ha FDP plot that could be unambiguously assigned to one of the habitat categories was included in the analyses. I excluded from the analyses all 20x20-m quadrats that included more than one of these habitats. Excluded quadrats are referred to as "mixed" in Figures 2.1 and 2.2, and in Table 2.1.

For these analyses, Young Forest is defined as second growth forest that is 70 - 100 yr old (Hubbell and Foster 1983). Young Forest borders the FDP plot along its northeastern edge and extends into the plot (Fig. 2.1). Young Forest 20x20-m quadrats were identified by R. B. Foster and account for about 2 of the 50 ha (Table 2.1; Fig. 2.1). The remaining 48 ha are considered old-growth forest (Hubbell and Foster 1986b). The forest on these 48 ha is > 500 years old. There may have been a few temporary precolumbian encampments in the old-growth forest prior to construction of the Panama Canal, but this forest has not suffered heavy impact from human activity (*e.g.*, swidden agriculture) in the past 1000 years (Hubbell and Foster 1986b; Piperno 1990; Condit *et al.* 1992b). Foster and Brokaw (1982) discuss differences in structure and composition attributable to differences in forest age at this site. I have chosen to concentrate on patterns evident within the old forest, so I exclude the Young Forest 20x20-m quadrats from these analyses.

BCI consists almost entirely of well-drained upland soils (Dietrich *et al.* 1982). However, a low-lying, seasonally inundated swamp is present on the 50-ha plot. The Swamp was defined by mapping standing water at the end of the wet season in 1992. The Swamp accounts for about 1.5 ha of the FDP plot (Table 2.1; Fig. 2.1). I consider the Swamp as a distinct habitat because swamps are often found to be floristically distinct from the surrounding vegetation due to the physiological requirements necessary for plants to tolerate water-logged soils (*e.g.*, Kwan and Whitmore 1970; Lieberman *et al.* 1985).

Quadrats designated as Stream are those that include distinct seasonal streams, usually surrounded by relatively steep ravines (see also Hubbell and Foster 1986c). Streams are found in the NE corner of the FDP plot and in the SW corner, draining the Swamp (Fig. 2.1). Although these streams often dry up late in the dry season, they usually contain water well into each dry season. Without direct moisture estimates in the Stream 20x20-m quadrats, I make the *a priori* assumption that the Stream 20x20-m quadrats are among the wettest areas (excluding the Swamp) in the FDP plot. This is based on the common observation, at other sites, that some forest species are often restricted to moist riparian habitats (Oliveira-Filho *et al.* 1990, 1994).

Due to the hydrology and geology of BCI, the slopes of the FDP plot are more moist than the plateau during the dry season (see also Hubbell and Foster 1986c; Becker *et al.* 1988; Condit *et al.* in press). An andesite cap underlies the highest elevation plateau portion of the plot (Johnsson and Stallard 1989; Leigh 1996). Water percolates through the soil onto this cap and drains to the edges (the slopes). With direct soil moisture estimates along two slope-plateau transects, Becker *et al.* (1988) demonstrated that soil water potentials are maintained at higher levels on the slope during the dry season, compared to the plateaus of the 50-ha plot.

Soil properties are also related to differences in topography on BCI. The soils on the steep slopes of BCI are shallower and more rapidly eroding than are the soils on the plateaus (Johnsson and Stallard 1989). Johnsson and Stallard (1989) asserted that physiographic influences are greater than lithological influences in determining chemical and structural properties of BCI soils. The apparent differences in soil structure and chemical composition related to topography (Johnsson and Stallard 1989) *may* further contribute to patterns of species association with respect to topography (especially in distinguishing between slope and plateau habitats). However, whether this generalization applies to plateau versus slope in the 50-ha plot is unknown, since Johnsson and Stallard (1989) studied steeper topographic gradients than those on the 50-ha FDP plot itself.

Yavitt and Wieder (1988) contend that soils from different sites on BCI are nearly indistinguishable in terms of N, P, and S mineralization. However, all of their samples came from plateau and swamp sites. Although there is some degree of heterogeneity among BCI soils, the magnitude of the differences or the spatial pattern of heterogeneity with respect to properties that are important to plants *within* the 50-ha FDP plot remain unknown.

Elevation was measured at the corners of every 20x20-m quadrat of the 50-ha plot before the first census began in 1980. The mean elevation of the four corners of each 20x20-m quadrat is used here as the designated elevation for each 20x20-m quadrat. The slope for each 20x20-m quadrat was estimated as the mean angular deviation from horizontal of each of the four triangular planes formed by connecting 3 of the 20x20-m quadrat's corners. Since elevations and slopes were averaged over each 20x20-m quadrat, the analysis "smoothes over" some micro-scale topographic variation. A 7° slope cut-off was used to define Slope and Plateau sites since this best included otherwise isolated sloping regions of the plot. A cut-off of 152 m above mean sea-level was used to separate High Plateau from Low Plateau sites since this was approximately the mid-elevation of the primary slopes on the 50-ha FDP plot.

Habitat Affinities According to Chi-square Analysis

Hubbell and Foster (1983) did not exclude the young forest region of the 50-ha FDP plot from their analysis. Hubbell and

Foster (1983, 1986c) chose to present summaries for the entire community rather than to supply information on individual species and they did not include details of how the plot was divided into habitat types. I therefore redid the Chi-square analysis in a manner that is directly comparable to results of the torus-randomizations.

I used the 303 species of trees and shrubs measured, mapped, and identified in the 1990 census of the 50-ha FDP plot. All stems $\geq$ 1-cm DBH were used to determine habitat regions in which species were over- and under-represented by testing the null hypothesis that stems were distributed among habitat regions at random.

The Chi-square test of Goodness-of-Fit is, by definition, a two-tailed test since a deviation of an observed value away from its corresponding expected value results in the same χ^2-value regardless of the direction of the deviation. I use $P<0.05$ to indicate statistical significance for these tests.

To account for differences in community-wide stem density among habitats (Table 2.1), expected values are stem-based, as opposed to area-based. In order to test as many species in as many of the 5 main habitats as possible, I adjust the test according to the number of stems each species has in the 5 habitats. For a given species, I first determine whether or not each habitat is usable. To do so, I first generate an initial expected value for a given species in a given habitat. This initial expected value is the total number of stems of the focal species in all 5 habitats multiplied by the proportion of stems of all species in all 5 habitats accounted for by the focal habitat. For each species, a habitat is considered unusable if an expected value is ≤ 1 (Snedecor and Cochran 1980, pg. 77). I then generate a final expected value for each species-habitat combination by multiplying the total number of stems of the focal species in all usable habitats by the proportion of stems of all species in those habitats accounted for by the focal habitat. I calculate χ^2-values using these final expected values. For each species-habitat combination, I compare the χ^2-value to a critical χ^2-value with degrees of freedom equal to one less than the number of habitats included for that species. For example, for common, widely distributed species, 5 habitats were available for comparisons and the critical value for significance was $\chi^2_{df=4} = 9.49$. For less common or less widely dispersed species, fewer habitats were included, reducing the available degrees of freedom and also reducing the magnitude of the critical χ^2-value.

Habitat Affinities According to Torus-Randomization

For each species in each habitat, I determined the proportion of all stems, summed over all species, that were of the focal species, *i.e.*, the stem-frequency of the focal species in the focal habitat. I then compared the true stem-frequency to a null distribution of stem-frequencies for the focal species in the focal habitat. The null distribution of stem-frequencies came from 1000 random translations of the habitat map about a torus. One can visualize the randomization procedure by imagining the habitat map being randomly moved about a torus lying beneath the stationary trees.

Since there are 50 quadrats of 20x20 m along the X-axis of the 50-ha FDP plot and 25 quadrats along the Y-axis, there are (50 x 25) = 1250 possible translations of the habitat map, assuming no rotations, based on 20x20-m quadrats on the torus. To obtain 1000 of these maps, I generated 1000 random X-coordinates between 0 and 49 and 1000 random Y-coordinates between 0 and 24, making certain that each pair of coordinates was unique. For each pair of non-overlapping random coordinates I shifted the intact map's 20x20-m quadrats eastward by the X-value and northward by the Y-value on the torus. This procedure is illustrated in Figure 2.2 which shows one of the 1000 torus-based translations of the habitat map.

For each species in each habitat of each map, the stem-frequency is the proportion of all stems in that habitat represented by the species being considered. Let $P_{true\ i\ j}$ be the true proportion of stems of species i in habitat j out of all stems in that habitat. Let $P_{torus\ k,\ i\ j}$ be the proportion of stems of species i in habitat j out of all stems in that habitat for the torus-based map k. Finally, let S be the number of stems.

$$P_{true\ i\ j} = S_{true,\ i\ j} / \sum_{i=1}^{303} S_{true,\ i\ j}$$

$$P_{torus\ k,\ i\ j} = S_{torus\ k,\ i\ j} / \sum_{i=1}^{303} S_{torus\ k,\ i\ j}$$

There are 303 species, so i ranges from 1 to 303; there are 5 habitats, so j ranges from 1 to 5; and there are 1000 torus-based maps, so k ranges from 1 to 1000.

I generated a distribution of stem-frequencies for each species in each habitat using the 1000 torus-based maps. That is, for k=1 to 1000, I have a distribution of $P_{torus\ k,\ i\ j}$. I then determined where the true stem-frequency ($P_{true\ i\ j}$) for that species in that habitat lay on the distribution, *i.e.*, for each k, is:

$$P_{true\ i\ j} > P_{torus\ k,\ i\ j}\ ,\ \text{or}$$

$$P_{true\ i\ j} < P_{torus\ k,\ i\ j}\ ,\ \text{or}$$

$$P_{true\ i\ j} = P_{torus\ k,\ i\ j}\ ?$$

This procedure is illustrated for *Beilschmiedia pendula*, a species that has a strong positive association with the slope and a strong negative association with the swamp, in Figure 2.3.

If the observed stem-frequency for a focal species in a particular habitat is greater than 97.5% of the torus-randomizations for that species-habitat combination, then that species is considered to be positively associated with the habitat under consideration. If the observed stem-frequency for a focal species in a particular habitat is less than that in 97.5% of the torus-randomizations for that species-habitat combination, then that species is considered to be negatively associated with the habitat under consideration. If the observed stem-frequency is greater than the torus-randomizations in fewer than 97.5% of them, and if the observed stem-frequency is less than the torus-randomizations in more than 2.5% of them, then the focal species is considered to be neutrally distributed with respect to the habitat under consideration.

RESULTS

The area accounted for by each habitat and the total number of stems found in each habitat are listed in Table 2.1. The total number of stems ≥ 1-cm DBH encountered for each species on the 50-ha FDP plot of BCI in 1990 and the densities of those stems by habitat are presented in Appendix 3.

Results from the Chi-square Analysis

The Chi-square results for all 303 species are presented in Appendix 4, and they are summarized in Table 2.2. Those species-habitat combinations resulting in expected values ≤ 1 are indicated in Appendix 4.

An expected value of 1 is obtained for the smallest of the 5 habitats included in this study, the swamp, when there are 65 stems. The tallies in Table 2.2 therefore include only those species for which there were > 65 stems in the 5 habitats. Some of the species that were excluded from the analysis are probably rare due to habitat-specialization to relatively uncommon habitat types such as the swamp and stream-sides. For example, *Eleais oleifera*, the Panamanian oil palm, has too few stems on the 50-ha FDP plot to test for swamp association, even though all 16 of its 50-ha FDP plot stems occur within the swamp (Hubbell and Foster 1986c, pg. 214).

Overall, the Chi-square results are congruent with the results from Hubbell and Foster (1983, 1986c); the majority of species showed some degree of habitat association.

Results from Torus-Randomization

Appendix 5 presents the results from the torus-randomization procedure for each species. To maintain the $P<0.05$ level of significance for the torus-randomization, I used a two-tailed test with $P<0.025$ in each tail. Positive associations are those in which the proportion of maps with ($P_{true\ i\ j} > P_{torus\ k,\ i\ j}$) is ≥ 0.975 and negative associations are those in which the proportion of maps with ($P_{true\ i\ j} < P_{torus\ k,\ i\ j}$) is ≥ 0.975. Using only those species for which there were > 65 stems in the 5 habitats, in every case, except for 1, in which a significant association appears according to the randomization procedure, that association is also significant according to the Chi-square analysis (*cf.* Appendix 4 and Appendix 5). *Inga sapindoides*, the exception, is significantly negatively associated with the swamp according to the randomization procedure, but not according to the Chi-square analysis.

For each habitat, fewer species show significant association patterns, positive or negative, with topography by the torus-randomization procedure than according to the Chi-square tests (Table 2.2 and Figure 2.4; see also Hubbell and Foster 1983, 1986c). For example, on Low Plateau sites the Chi-square analysis resulted in 53 sufficiently abundant species significantly positively associated compared to 8 species significantly positively associated in the torus-randomization procedure. Furthermore, in an earlier version of the Chi-square analysis, in which pairwise comparisons of habitats were made, even more species showed strong patterns of positive and negative association with each habitat.

DISCUSSION

Association Patterns by Chi-square versus Torus-Randomization

A primary assumption of Chi-square Goodness-of-Fit Tests is that the observations are independent (Snedecor and Cochran 1980). The independence assumption is in direct conflict with the processes that bring about the distribution patterns of trees in forests (Condit 1996). Most seeds are dispersed locally and give rise to recruits that are near to conspecific adults and to one-another, *i.e.*, the positions of trees are not independent of one-another. As a result, many habitat-association patterns apparent by Chi-square analyses may be the result of causes other than habitat-specialization.

Three examples illuminate some of the difficulties with interpretations of positive habitat-associations based on Chi-square analyses. First, *Chamguava shippii* appears to be strongly positively associated with the Low Plateau of the 50-ha FDP plot (Appendix 4). However, the population of *C. shippii* appears to have established relatively recently on the 50-ha FDP plot, and is spreading out from its initial point of colonization on the central portion of the Low Plateau (Hubbell and Foster 1986c, pg. 224). Second, *Inga pezizifera* is strongly positively associated with the Slope and Stream habitats that dominate the eastern 1/3 of the 50-ha FDP plot (Appendix 4). *I. pezizifera* is common to the east of the 50-ha plot, but only the western edge of its population distribution on BCI extends onto the 50-ha plot itself (Hubbell and Foster 1986c, pg. 222). Finally, *Anaxagorea panamensis* is strongly positively associated with the Slope (Appendix 4), yet *A. panamensis* is a shrub of small stature with balistically dispersed seeds and is currently known only from two sites: 2 adjacent hectares on the 50-ha plot of BCI and along the Gigantito River on Gigante Peninsula, a mainland site near BCI (R. B. Foster pers. comm.; pers. obs.). The 2 hectares in which *A. panamensis* is found on the 50-ha FDP plot are in the northwestern portion of the plot, distant from the principal Slope areas along the eastern and southern borders of the 50-ha FDP plot. In contrast to the Chi-square habitat-association patterns, none of the above species show significant positive habitat-associations according to the torus-randomizations.

Torus-randomization does not rely on the independence assumption which hampers the Chi-square analysis. The torus-randomization method results in many fewer significant positive and negative habitat-association patterns. However, the torus-randomization method is not a perfect correction for the limitations of the Chi-square analysis. For example, *Drypetes* *standleyi* seems to be invading the 50-ha plot from the southeast (S. Hubbell and R. Foster, pers. comm.) and shows a significant association with the slope by both the Chi-square and torus-randomization procedures. It is possible that the significant positive association is a transient pattern that will disappear as the population of *D. standleyi* continues to spread across the 50-ha FDP.

Source-sink dynamics are especially problematic for the torus-randomization procedure. A widespread distribution characterized by source-sink dynamics could, in theory, be indistinguishable from a widespread distribution due to habitat-generalization. However, this situation would only occur if the recruitment subsidies from the source populations were sufficient to maintain sink populations of the same relative stem-densities as the source populations. In practice, sink populations are likely to be characterized by lower stem-densities as a consequence of lowered demographic performance (growth, mortality, and recruitment).

Methods other than the torus-randomization method could have been used to produce distributions with which to compare true stem-densities. Two possibilities are: 1) random placement of the appropriate number of 20x20-m quadrats for each habitat, or 2) random placement of a sufficient number of contiguous 20x20-m quadrats for each habitat. However, a strength of the torus-randomization method is that the habitat maps maintain the approximate shapes and contiguity of the true habitat maps. The Stream 20x20-m quadrats in the true map are arranged in narrow "bands" as opposed to Plateau quadrats which are arranged in contiguous "blocks". These relative shapes are maintained in maps generated by torus-randomization. Some contiguity is lost as the torus is "wrapped" around the borders of the plot, but the majority of quadrats have consistent neighborhood habitat-composition. A difficulty that arises from the torus-randomizations is that separate maps are not strictly independent estimates of stem-densities per habitat since small shifts in both the x and y coordinates result in small changes in the overall distribution of habitats.

Habitat Specialization

Specialists and generalists must be defined in relative terms (Colwell and Futuyma 1971). If realized habitat-associations can be used as estimates for the degree to which species are "specialized" to particular habitats, the torus-randomization procedure clearly shows more "slope-specialists" than "plateau-specialists", despite the fact that slope sites represent a substantially smaller percentage of the 50-ha FDP plot than do plateau sites. Strong slope associates include: *Poulsenia armata* (Hubbell and Foster 1983, pg. 30), *Unonopsis pittieri* (Hubbell and Foster 1986c, pg. 213), *Guatteria dumetorum*. *Ocotea whitei* is a known stream specialist (R. B. Foster, pers. comm.) and shows slope affinity. It is striking that *Beilschmiedia pendula*, *O. whitei*, and *O. oblonga*, the first, second, and sixth most common species of Lauraceae found on the BCI 50-ha plot are positively associated with the slope. These species are among the largest-seeded non-palm, non-liana species on the 50-ha plot.

Fewer species are strongly associated with plateau sites according to the torus-randomization procedure, but they include: *Coussarea curvigemmia*, *Faramea occidentalis*, and *Laetia thamnia* (see Hubbell and Foster 1986c, pg. 213 for a map of *F. occidentalis*). There are apparently many generalists with respect to topography, of which *Alibertia edulis*, *Chrysophyllum argenteum*, and *Pterocarpus rohrii* are examples (Hubbell and Foster 1986c, pg. 214 for a map of *P. rohrii*).

Several species tend to avoid the swamp, but swamp associates include several fig and palm species. These are the most striking taxonomic patterns from the distribution analyses. *Prioria copaifera* is a surprise because it is considered a swamp specialist in Panamá, but avoids the swamp on the 50-ha FDP plot on BCI and is relatively common in upland areas (Condit *et al.* 1993b).

Topography and Species-Richness

Recent analyses demonstrated a species-richness gradient on the 50-ha FDP plot; Slope sites have more species, on a per stem basis, than do Plateau sites (Hubbell 1995; Condit *et al.*, in press). Rather than being due to a turn-over of species, this pattern seems due to an addition of species on the moister slopes (Hubbell 1995; Condit *et al.*, in press). In agreement with this interpretation of the pattern, fewer species show strong positive associations with plateau sites than species that show strong positive associations with slope sites, despite the difference of relative area represented by these two habitat types (Table 2.1, Table 2.2). It seems that species are added as one follows a moisture gradient from Plateau sites to Slope sites.

During a census of seedlings in a 1x1-m sub-quadrat of each 5x5-m sub-quadrat of each 20x20-m quadrat of a 5-ha portion of the 50-ha FDP plot, Wechsler (1995) found no difference in diversity in the seedling layer on Slope and Plateau sites. Wechsler (1995) speculated that diversity differences in the sapling to adult size-classes may be due to periodic droughts that cause differential mortality in the seedling layer, resulting in a one-way filter for seedlings - some cannot tolerate the drier conditions of the plateau in extreme years, but all or most can survive on the slopes. The extent to which this mechanism can account for the diversity gradient requires further testing.

The limited number of species strongly associated with the swamp is in accord with the lowest species-richness across the 50-ha FDP plot being in the swamp (Condit *et al.* in press).

The Coexistence of Habitat-Generalists with Habitat-Specialists

Several species of trees and shrubs show strong patterns of association with habitat sites of the 50-ha FDP plot of BCI, although the majority of species are habitat-generalists. Combined with evidence from Welden *et al.* (1991) and from Hubbell *et al.* (in press) that there are few species specialized to portions of the light regime, I conclude that there are relatively few realized habitat-niche specialists in the BCI forest. Those species that do appear to be specialized to habitat-types appear to be incapable of excluding generalists. Does this imply that there is no trade-off to being a generalist in this forest? Are habitat-specialists and habitat-generalists equally well-suited to the habitats in which they currently occur? To begin to answer these questions, it remains to determine the mechanistic basis, which may be species-specific, for the patterns of association and lack of association with habitat types on the 50-ha FDP plot. The first question in this direction that I shall pursue is: Do realized habitat-specialists show different patterns of growth, mortality, and recruitment on Slope versus Plateau sites as compared to realized-niche generalists? A step towards answering this question is the subject of Chapter 3.

Table 2.1. Habitat regions and the distribution of 244,102 stems ≥ 1-cm DBH from the 303 species found in 1990 on the 50-ha Forest Dynamics Project plot of Barro Colorado Island, Panamá.

Forest Type	Slope	Elevation	No. of 20 x 20-m quadrats	Total area (ha)	Percent of 50-ha FDP plot area	Total no. of stems	Percent of 50-ha FDP plot stems
Old Forest - Low Plateau	< 7°	< 152 m	620	24.80	49.60	126,461	51.81
Old Forest - High Plateau	< 7°	≥ 152 m	170	6.80	13.60	31,145	12.76
Old Forest - Slope	≥ 7°	All	284	11.36	22.72	55,449	22.72
Young Forest	All	All	48	1.92	3.84	9636	3.95
Swamp	All	All	30	1.20	2.40	3365	1.38
Stream	All	All	32	1.28	2.56	5683	2.33
Mixed	All	All	66	2.64	5.28	12,363	5.06

Table 2.2. Comparison of results from the Chi-square analysis and from the torus-randomization analysis of habitat affinities for all individuals ≥ 1-cm DBH of all 169 species for which there were > 65 stems in the 5 main habitats during the 1990 census of the 50-ha Forest Dynamics Project plot of BCI. For each habitat, "+" indicates significant positive association at $P<0.05$ for Chi-square and $P<0.025$ for torus-randomization; "-" indicates negative association at the same levels of significance.

Microhabitat	Chi-square	Randomization
High Plateau +	30	5
High Plateau -	82	15
Low Plateau +	53	8
Low Plateau -	61	18
Slope +	45	33
Slope -	51	16
Stream +	45	14
Stream -	26	2
Swamp +	45	31
Swamp -	42	17

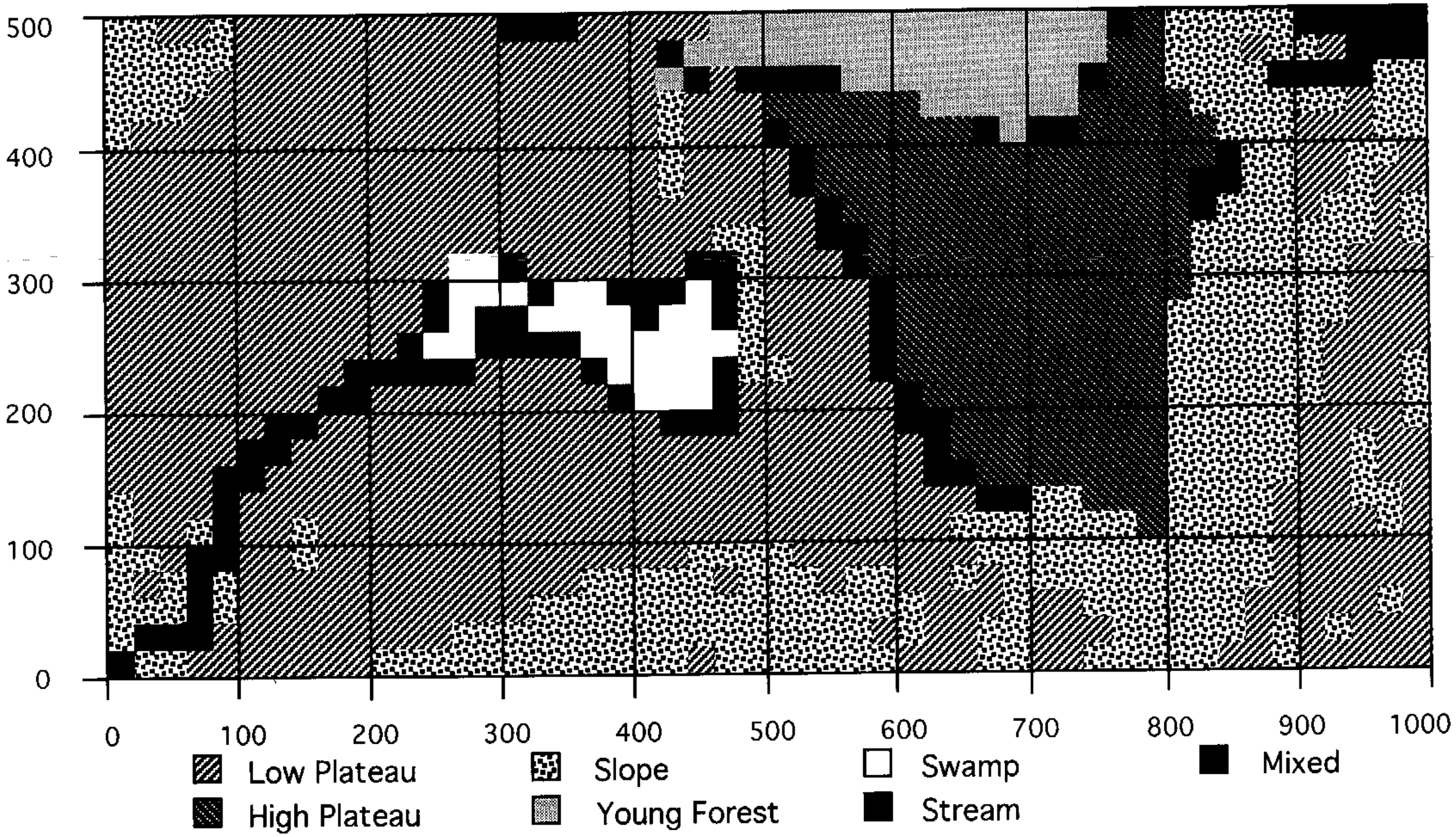


Figure 2.1. Habitat map of the 50-ha Forest Dynamics Project plot of Barro Colorado Island, Panamá, based on 20x20-m quadrats.

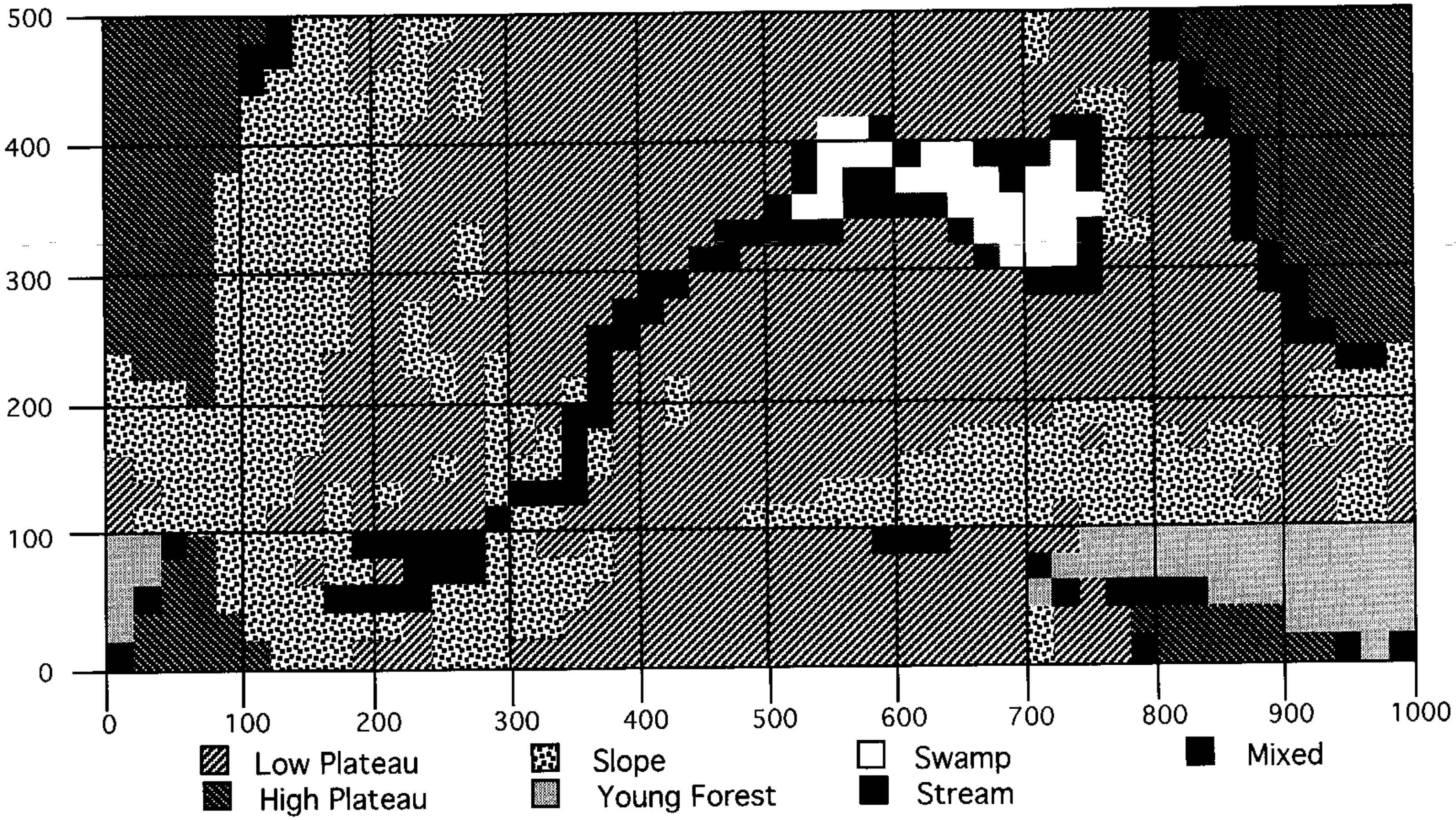
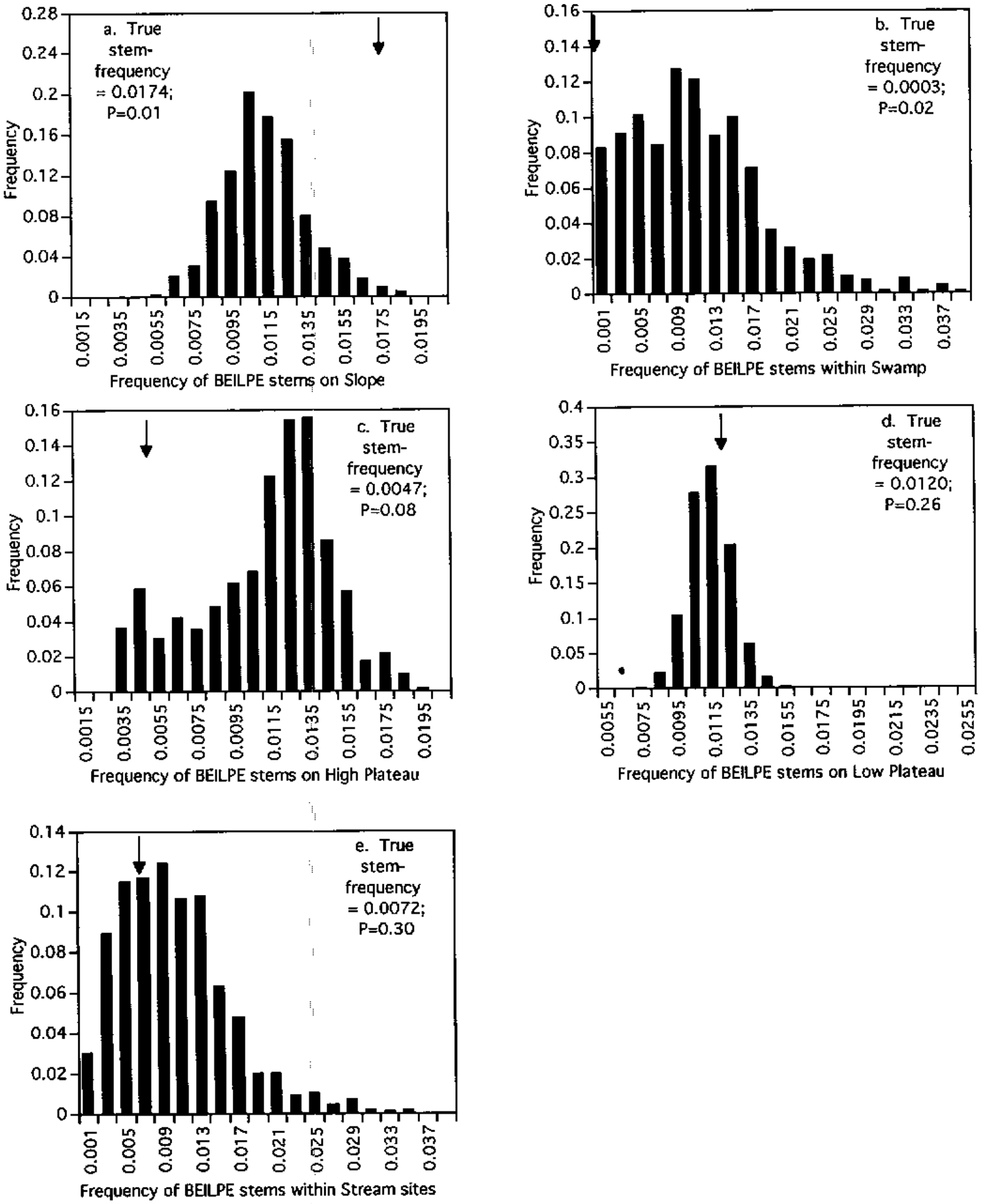


Figure 2.2. One of the 1000 torus-based translations of the habitat map of the 50-ha Forest Dynamics Project plot of Barro Colorado Island, Panamá.



Figures 2.3a-e. Stem-frequencies of *Beilschmiedia pendula* in each habitat for the 1000 torus-based map translations of the 50-ha FDP plot. The arrow in each figure indicates the stem-frequency for the true habitat map. *B. pendula* shows a strong positive association with the Slope (**a**; P<0.025) and a significantly negative association with the Swamp (**b**; P<0.025), but is neutrally distributed with respect to the Low Plateau (**c**; P>0.025), the High Plateau (**d**; P>0.025), and Stream sites (**e**; P>0.025).

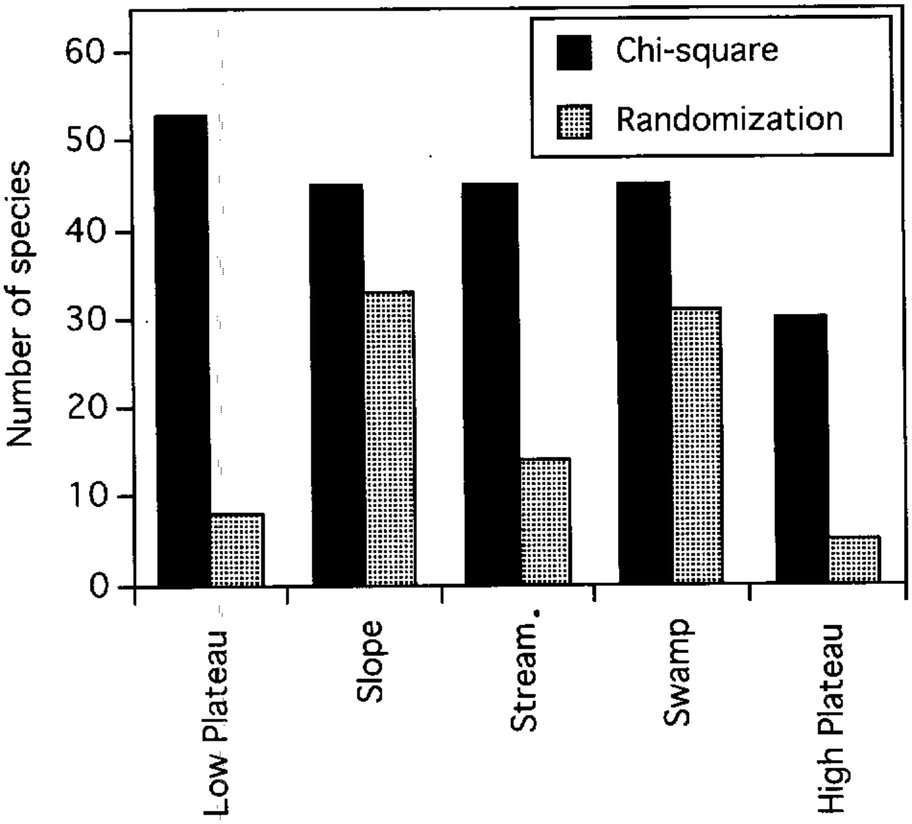


Figure 2.4. Comparison of results from the Chi-square tests and from the torus-randomization analysis. Bars represent the number of species showing positive habitat associations for all individuals ≥ 1-cm DBH out of all 169 species for which there were > 65 stems in the 5 main habitats during the 1990 census of the 50-ha Forest Dynamics Project plot of Barro Colorado Island, Panamá. $P<0.05$ for Chi-square tests and $P<0.025$ for torus-randomization tests.

CHAPTER 3

The Effect of Habitat on the Growth, Mortality, and Recruitment of Woody Species in a Neotropical Forest

INTRODUCTION

Intraspecific variation in growth and mortality rates of tropical trees is often quite high (Lieberman *et al.* 1985; Clark and Clark 1994; O'Brien 1994). One important correlate of variation in growth and mortality rates is heterogeneity in the availability of incident light. For example, Welden *et al.* (1991) found that many juvenile trees of the 50-ha Forest Dynamics Project (FDP) plot of Barro Colorado Island (BCI), Panamá showed differential growth, mortality, and recruitment with respect to canopy height, their surrogate for light availability. On a forest-wide basis, Clark and Clark (1994) found that growth rates of trees, including canopy individuals, were enhanced during years of low rainfall, which were years of high insolation due to low cloud cover, suggesting that even many canopy trees may be light-limited.

The influence of environmental factors other than light on growth and survival among tropical trees is much less well known. Existing field studies suggest that factors other than light do, under some circumstances, account for significant variation in growth and survival. In one field study, Bullock (1992) found effects of soil-type on the growth and mortality of 3 species of dioecious trees in La Selva and that sex and size were not consistently strong bases for predicting the growth or mortality of adult trees of those species. Condit *et al.* (1995) found that mortality rates differed between the two inter-census intervals, of approximately four years each, for many of the trees and shrubs of the 50-ha FDP plot. A severe drought occurred during the first inter-census interval. Condit *et al.* (1995) speculated that higher mortality during that period was due to the influence of lower water availability during that time.

The patterns of positive and negative association with habitat features of the 50-ha FDP plot found in Chapter 2 may be due to intraspecific differences in survival, growth, or reproduction within different habitats. Whether or not differences in relative stem densities exist, performance differences might suggest relative abilities to cope with local habitat conditions and, to the extent that differential growth and survival determine competitive ability, would also indicate competitive differences in different habitats.

Since performance under given conditions has been shown to vary through ontogeny for some tropical tree species (Clark and Clark 1992), differences in performance may be manifest in growth or survival rates at any or all stages of a tree's life-cycle.

It is important, therefore, to examine all stages of the life-cycle to determine whether or not performance differences appear.

The objective of this chapter is to determine the extent to which intraspecific differences in growth, mortality and recruitment are related to habitat, by comparing individuals on Plateau and Slope sites of the 50-ha Forest Dynamics Project (FDP) plot of Barro Colorado Island (BCI), Panamá. Specifically, I determined whether growth and mortality differed for stems ≥ 1-cm DBH and whether recruitment rates into the 1-2 cm DBH size-class differed with respect to the two habitats.

METHODS

The data for the following analyses come from the 50-ha FDP plot of BCI (see Chapter 2 for a full description of the study site and of the data available for trees and shrubs found there). In order to facilitate comparisons between this and other investigations of the 50-ha FDP plot database, the protocols I used for including stems in the analyses are similar to those previously employed (Condit *et al.* 1993ab, 1995; O'Brien 1994). Below I describe the similarities and differences between my methods and those of previous investigators for including and excluding stems and for calculating growth and mortality rates using the 50-ha FDP plot database.

Growth Rates

For individual stems, I estimated growth rate as the increment in DBH between the 1982 and 1990 censuses, converted to an annual value for the inter-census interval:

$$(DBH_2\text{-}DBH_1)/t$$

where DBH_2 is the DBH in mm during the 1990 census, where DBH_1 is the DBH during the 1982 census, and where t is the number of years that have elapsed between the two DBH measurements for the focal stem. This estimate of growth rate was also used by Condit *et al.* (1993ab).

During the 1982 and 1985 censuses, trees with DBH > 55 mm were measured to the nearest 5 mm, but during the 1990 census all diameters were measured to the nearest 1 mm (Condit 1993ab). Therefore, following Condit *et al.* (1993ab) and O'Brien (1994), I rounded tree diameters down to the next smallest 5 mm increment for trees with diameters > 55 mm in the 1990 census. Rounding DBH values down may bias growth estimates, but Condit *et al.* (1993b) showed through simulations that the bias had relatively little impact on estimates of growth.

Also following Condit *et al.* (1993ab), I eliminated trees whose DBH appeared to shrink by > 5%/yr and trees whose DBH appeared to increase > 75 mm/yr. Some of the large trees appeared to shrink > 5%/yr because during the 1982 census large trees were measured around their buttresses, while during the following two censuses large trees were measured at a marked point above their buttresses. I assume, as did Condit *et al.* (1993a), that trees that appeared to shrink or grow more than the above rates represent errors of the kind just mentioned or other imperfections in the data. Condit *et al.* (1993b) found that these criteria successfully eliminated trees with erroneous measurements and provided growth rate estimates near the median in an intensive study of the demography of *Prioria copaifera*.

For these growth analyses, I did not include live trees which broke off and subsequently resprouted, irrespective of their apparent growth rates. Finally, I did not include trees with multiple stems in the growth analyses.

I conducted separate Analyses of Covariance (ANCOVAs) for each species for the inter-census interval 1982-1990 using SYSTAT statistical software (SYSTAT 1992). Annual growth rate was the response variable and a habitat-term was the main effect variable. Size (DBH in 1982) and conspecific density (number of conspecifics $\geq$ 1-cm DBH within the same 20x20-m quadrat) were included as covariates in the model.

For the ANCOVA analyses I used the following full model:

$$\begin{aligned}\text{DBH increment} = {} & \text{C} + \text{Habitat} + \text{DBH}_1 + \text{Density} + \\ & \text{Habitat}^*\text{DBH}_1 + \text{Habitat}^*\text{Density} + \\ & \text{DBH}_1{}^*\text{Dens} + \text{Habitat}^*\text{DBH}_1{}^*\text{Density}\end{aligned}$$

For each species I compared the fit of the full model ANCOVA to the following reduced model ANCOVA that does not include habitat terms:

$$\text{DBH increment} = \text{C} + \text{DBH}_1 + \text{Density} + \text{DBH}_1{}^*\text{Density}$$

In these models, C is a constant, *Habitat* is either Slope or Plateau (combined Low Plateau and High Plateau), DBH_1 is the DBH during the 1982 census, and *Density* is the density of all stems $\geq$ 1-cm DBH in 1982 in the 20x20-m quadrat within which the focal stem was found.

Other estimates of growth rates have been advocated and used in other studies of trees from the 50-ha FDP plot (Condit *et al.* 1993a). However, the instantaneous growth rate used by Condit *et al.* (1993a) is strongly size-dependent. I chose to use annualized DBH increments because they are not strongly size-dependent, they are nearly always normally distributed, and they result in normally or nearly normally distributed residuals for most species in the ANCOVA models.

Each ANCOVA produced an R^2 value, which is the proportion of the variance in growth accounted for by the model. By subtracting the R^2 value of the reduced model from the R^2 for the full model, I obtained a measure of the amount of variance in growth accounted for by habitat terms. I use this derived measure to determine the degree to which habitat can be considered a predictor of growth rates.

Mortality Rates

Size-dependent mortality has been documented in some tropical trees (Clark and Clark 1987; Hartshorn 1990; DeSteven 1994), especially shade-intolerant species (Hubbell and Foster 1990a). For this reason, and to facilitate comparisons with an analysis of mortality by Condit *et al.* (1995), in which stems were divided into two separate size-classes, mortality was estimated in this study for two size-classes: 1) individuals $\geq$ 1-cm DBH yet < 10-cm DBH, and 2) individuals $\geq$ 10-cm DBH.

For each species, I determined the number of stems alive on Plateau sites (combined Low Plateau and High Plateau sites) and the number alive on Slope sites in the 1982 census and the number that died or disappeared by the 1990 census. I applied these data to the most frequently used formula for calculating mortality for tropical trees (Condit *et al.* 1995; Sheil *et al.* 1995). The mortality rate m was calculated as:

$$m = \frac{\ln(N_0) - \ln(N_t)}{t} \qquad (1)$$

where N_o is the number of initial stems and N_t is the number of those N_o stems alive after t years have passed. This measure of mortality is best described as an instantaneous measure of decline per unit of population (Sheil *et al.* 1995). The inter-census time interval, t, varies among individuals, from 7.23 - 9.89 years for stems 10-99 mm DBH and from 7.35 - •11.57 years for stems > 10-cm DBH. Therefore, for each mortality rate, I used the arithmetic mean inter-census interval of the stems included in N_o. Condit *et al.* (1995) justify the use of mean inter-census intervals for these data by showing that the introduced bias in mortality rate is in all cases very small relative to the mortality rate estimate.

Condit *et al.* (1995) advocate using non-overlapping 95% confidence intervals around m to test for significant differences between the estimates of m for two sets of stems. However, it can be shown that this test uses a very conservative α-level, on the order of $\alpha=0.005$, for statistical significance. By randomly sampling from two standard Normal distributions and by taking the absolute value of the difference between each pair of draws, I found that approximately 0.5% of the cases were greater than or equal to four standard deviations apart - four standard deviations being the magnitude of the difference between two populations with non-overlapping 95% confidence intervals. In order to determine the appropriate confidence intervals required to produce an overall test for differences between mortality rates at the $\alpha=0.05$ level, I found that 5% of the absolute values of the differences from the above simulation were greater than or equal to 2.8 standard deviations apart. The tails of a standard Normal distribution that are 2.8 standard deviations apart contain 16% of the distribution, with 8% in each tail. Therefore, in order to compare mortality rates between Slope and Plateau habitats at the $\alpha=0.05$ level, one needs to determine whether or not the 84% confidence limits for the two estimates of mortality rates overlap.

I calculate 84% confidence limits for each mortality rate estimate through a procedure analogous to that used by Condit *et al.* (1995). I use the normal approximation to the binomial variance to estimate the variance around the number of dead stems, D, as long as $D > 5$. This is the recommendation given by Dixon and Massey (1969; Condit *et al.* 1995). I use the variance around D to determine the 84% confidence limits around D. I convert these limits into mortality rate confidence limits using Eq. 1 (Condit *et al.* 1995). When $D \leq 5$, the normal approximation for a binomial distribution is unstable. I therefore determine lower 84% confidence limits when $D \leq 5$ by searching for the value of D for which the exact cumulative probability from a binomial distribution of obtaining the observed value for D or less is 8%

(Condit *et al.* 1995). Upper confidence limits were found by determining the value of D for which the cumulative probability of obtaining the observed value for D or less is 92%.

Recruitment

For these analyses, recruits were defined as stems that first reached DBH $\geq$ 1-cm, but were < 2-cm, in a given census. I compared recruitment on Plateau versus Slope sites using Chi-square deviations from random recruitment. I calculated expected values for the Chi-square tests by multiplying the total number of recruits on Slope and Plateau (combined Low Plateau and High Plateau) sites for a focal species by the proportion of adults of that species in the focal habitat out of all adults on Slope and Plateau sites. By calculating expected values in this way, I am testing for differences in recruitment rates on a per capita basis of adult trees.

RESULTS

Growth Rates

R^2 values are extremely low for the full ANCOVA models, and lower still are the values for the variance explained by the habitat terms in those models (Appendix 6). In all cases, habitat terms account for < 20% of the variance in growth rates, and habitat terms account for > 10% in only two species for which at least one habitat term is significant (Appendix 6; Figure 3.1). It is, therefore, evident that a combination of size (measured as DBH) in 1982, conspecific density at the 20-m scale, and habitat-location cannot be used to predict, with accuracy, the growth of an individual from 1982 to 1990.

Mortality Rates

Sign-tests demonstrate that the number of species showing higher absolute mortality rates on Slope sites is no different than the number showing higher absolute mortality rates on Plateau sites (Table 3.1). Even by grouping species according to their habitat affinities (according to the results of Chapter 2), I found that those species that show strong Slope-affinity are no more likely to have lower mortality on the Slope than are those species that show strong Plateau affinity (Sign-tests, $P>0.05$ for both Slope-associated and for Plateau-associated species; Figure 3.2). In fact, for the 1-10 cm DBH size-class, among those species that were strongly Plateau-associated and had $\geq$ 50 stems on the 50-ha FDP plot in 1990, six species had higher absolute mortality on Slope sites and seven species had higher absolute mortality on Plateau sites. Again for species with $\geq$ 50 stems in 1990, of those species that were strongly Slope-associated, 18 species had higher absolute mortality on Slope sites and 16 had higher absolute mortality on Plateau sites.

Mortality rates for Slope and Plateau sites were significantly different for at least one size-class for only 23 species (Appendix 7). In each case, these significant differences appear only in the 1-10 cm DBH size-class, except in *Poulsenia armata* in which both size-classes show a significant difference between Slope and Plateau sites. In five of these 23 species, higher mortality is found on Slope sites and in the remaining 18 species, higher mortality is found on Plateau sites.

Recruitment

Recruitment rates were more strongly influenced by habitat than were growth or mortality (Appendices 8, 9). In 1985, 43 out of 156 species included in the analyses had significantly more recruits per adult than expected on one of the two habitats. In 1990, 38 out of 153 species had significantly more recruits per adult than expected on one of the two habitats.

In the 1985 census, more species had higher recruitment than expected on the Slope compared to the Plateau (χ^2 Goodness-of-Fit, $P<0.05$), while in the 1990 census there were approximately equal numbers of species with recruitment rates higher than expected in each of the two habitats ($P>0.05$). In 1985, out of 43 species with a significant difference in recruitment between habitats, only eight species (19%) had higher recruitment on

Plateau sites. In 1990, out of 38 species with a significant difference in recruitment between habitats, only 12 species (32%) had higher recruitment on Plateau sites. Although a significant difference in one census was not always accompanied by a significant difference in the other census, for almost all species that showed a significant difference in one census, the direction of the recruitment excess in the other census was the same (Appendices 8, 9).

There were 151 species with ≥ 50 stems on the five habitat types identified in Chapter 2 and for which recruitment differences between Slope and Plateau sites could be examined in either 1985 or 1990. Of those 151 species, 31 were found positively associated with the Slope and 13 species were found positively associated with either the High Plateau or the Low Plateau (Chapter 2). Twelve species were found negatively associated with the Slope and 27 species were found negatively associated with either elevation-class of the Plateau. Only one species was found positively associated with one elevation-class of the Plateau and negatively associated with the other elevation-class of the Plateau, *Triplaris cumingiana*, and it was excluded from these tallies. No species that was positively associated with the Slope was also positively associated with either of the elevation-classes of the Plateau.

Of the 31 Slope-associated species, most had higher recruitment rates on Slope sites (Figure 3.3a), ten had significantly higher recruitment on Slope sites ($P<0.05$), while one, *Poulsenia armata*, had significantly higher recruitment on Plateau sites ($P<0.05$) in 1985. In 1990, eight of the Slope-associated species had significantly higher recruitment on Slope sites and one, *Inga marginata*, had significantly higher recruitment on Plateau sites. Of the 12 Slope-avoiding species, 4 had significantly higher recruitment on Slope sites and one, *Mouriri myrtilloides*, had significantly higher recruitment on Plateau sites in 1985. In 1990, 3 of the Slope-avoiding species had significantly higher recruitment on Slope sites and two had significantly higher recruitment on Plateau sites.

Of the 13 Plateau-associated species, most had higher recruitment rates on Slope sites (Figure 3.3b), six had significantly higher recruitment on Slope sites ($P<0.05$), while one, *Mouriri myrtilloides*, had significantly higher recruitment on Plateau sites ($P<0.05$) in 1985. In 1990, five of the Plateau-associated species had significantly higher recruitment on Slope sites and two had significantly higher recruitment on Plateau sites. Of the 27 Plateau-avoiding species, two had significantly higher recruitment on Slope sites and two had significantly higher recruitment on Plateau sites in 1985. In 1990, 6 of the Plateau-avoiding species had significantly higher recruitment on Slope sites and one had significantly higher recruitment on Plateau sites.

In summary, for most of the species showing strong patterns of either positive or negative association with either Slope or Plateau sites of the 50-ha FDP plot of BCI, there was a significant excess in recruitment on the Slope sites in either 1985 or 1990.

DISCUSSION

Recruitment varied significantly with habitat in about 1/3 of the > 150 species tested, suggesting that reproduction or events early in the life-cycles of these species may contribute to differences in habitat-related performance. It is interesting to note that in the majority of cases of significant difference in recruitment between Slope and Plateau sites, the Slope sites had higher recruitment, regardless of habitat affinity. This is a curious result. Slope-associated species might be expected to have higher recruitment than expected on the Slope, but why Slope-avoiding, Plateau-associated, and Plateau-avoiding species should show higher than expected recruitment on the Slope is puzzling. Perhaps Slope is the most conducive habitat to seedling establishment, regardless of apparent habitat affinity.

Only nine of the 23 species with significant differences in mortality between Slope and Plateau sites are significantly associated either positively or negatively with Slope or Plateau sites according to the torus-randomization method of Chapter 2.

For five of these nine species, the interpretation of the mortality differences is in accord with their habitat-association patterns. *Beilschmiedia pendula*, *Poulsenia armata*, and *Protium costaricense* are Slope-associated species, with higher mortality on Plateau sites as compared with Slope sites for 10-99 mm DBH stems, and with higher mortality on Plateau sites for ≥100 mm DBH stems of *P. armata*. *Trichilia tuberculata* is a Low Plateau-avoiding species with higher mortality on Plateau sites than on Slope sites for the 10-99 mm DBH size-class. *Platymiscium pinnatum* is a Low Plateau-associated species with higher mortality on Slope sites.

However, four of the nine species with significant differences in mortality between Slope and Plateau sites and that are significantly associated either positively or negatively with Slope or Plateau sites had mortality differences opposite to the predicted direction. *M. myrtilloides* is a Low Plateau-associate and a Slope-avoiding species with higher mortality in the 10-99 mm DBH size-class on Plateau than on Slope sites. *Faramea occidentalis* and *Palicourea guianensis* are negatively associated with the Slope, yet show higher mortality on Plateau than on Slope sites. Finally, *Inga umbellifera* shows a positive association with Low Plateau sites, yet has higher mortality on Plateau sites.

The majority of species showed no significant difference in mortality on Slope versus Plateau sites. The possibility exists that the mortality analyses are of insufficient power to detect differences in mortality that, when compounded over the lives of canopy trees, could result in density differences of the magnitude observed for Slope-associated species of the 50-ha FDP plot. The results presented in Table 3.1 and Figure 3.2, however, do not suggest that a pattern of differential mortality among species has been masked by small sample size or short inter-census duration, since in all cases the number of species with higher absolute mortality rates on Slope sites is not statistically different from the number of species with higher absolute morality rates on Plateau sites. Power to detect morality differences may have been relatively low, but the observed mortality patterns do not suggest that increasing the power of these tests would significantly alter the conclusions regarding the comparison of mortality rates for Slope-associated and Plateau-associated species in the two habitats.

The results of this study suggest that once individuals become established as $\geq$ 1 cm DBH stems on the 50-ha FDP plot, the habitat conditions in which they are found plays little role in determining subsequent performance. It is, however, possible that Slope microsites vary in character from near the Plateau-end of a dryness spectrum to much wetter and that Plateau-associated species are found on the Slope only in these drier microsites. To test this idea will require detailed information regarding tree-to-tree variation in soil water availability. The conclusions in this chapter also do not preclude the possibility that events that take place earlier during the life-cycles of these plants are the primary determinants of patterns of habitat affinity found on the 50-ha FDP plot of BCI.

Variation in tree seedling and small sapling growth and mortality among conditions that represent different habitat types has been shown to influence the relative performance of trees in pot experiments (Latham 1992) and the outcome of community composition in a model of temperate-zone forest communities calibrated from field data (Kobe 1996). In Chapter 4 I therefore describe the common garden experiments that I conducted in order to determine the extent to which growth and survival vary with habitat at the seedling stage for selected Slope-associated species and an apparent “habitat-generalist”.

Table 3.1. Comparisons of mortality rates on Slope sites versus on Plateau sites from 1982 to 1990 for species found on the 50-ha Forest Dynamics Project Plot of Barro Colorado Island, Panamá. Mortality rates for each species and habitat are provided in Appendix 7. For each size-class, the sign-test determines whether or not more species had higher mortality in one habitat compared with the other.

	Number of	Number of species for which mortality is greater on			
Size class	species	Plateau	Slope	Neither	Sign-test
10-99 mm	146	77	66	3	P>0.05
≥ 100 mm	52	22	29	1	P>0.05

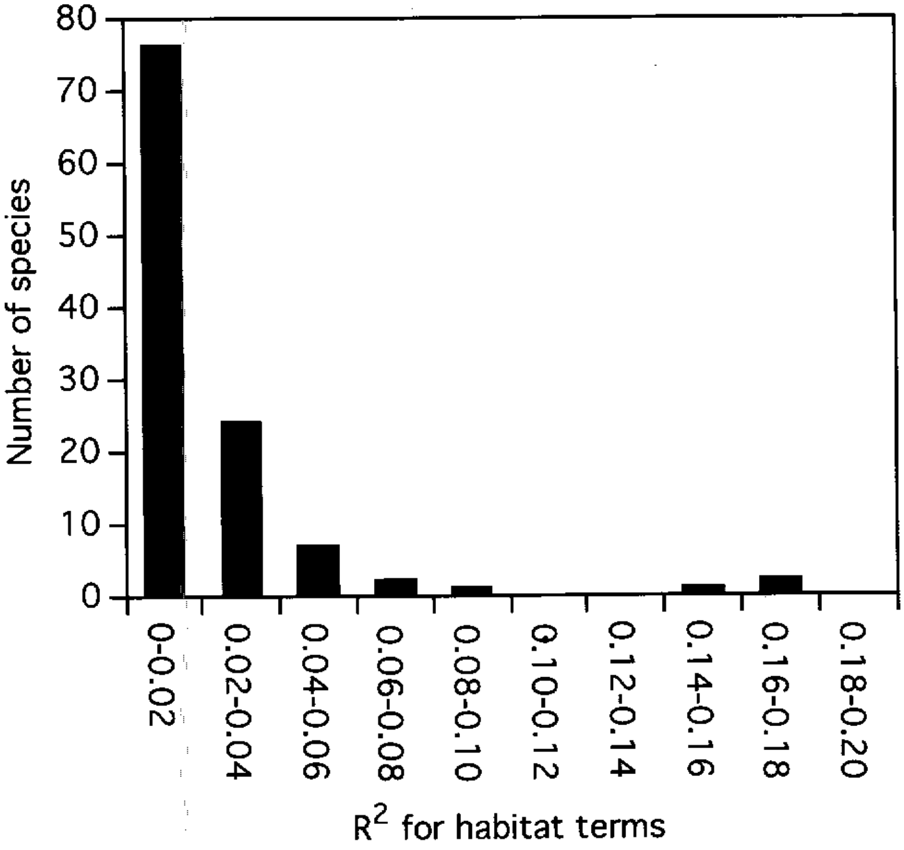


Figure 3.1. Frequency distribution of R^2 values for habitat terms in the ANCOVA analyses of growth for species found on the 50-ha Forest Dynamics Project plot of Barro Colorado Island, Panamá. See Appendix 6 for a list of R^2 values by species.

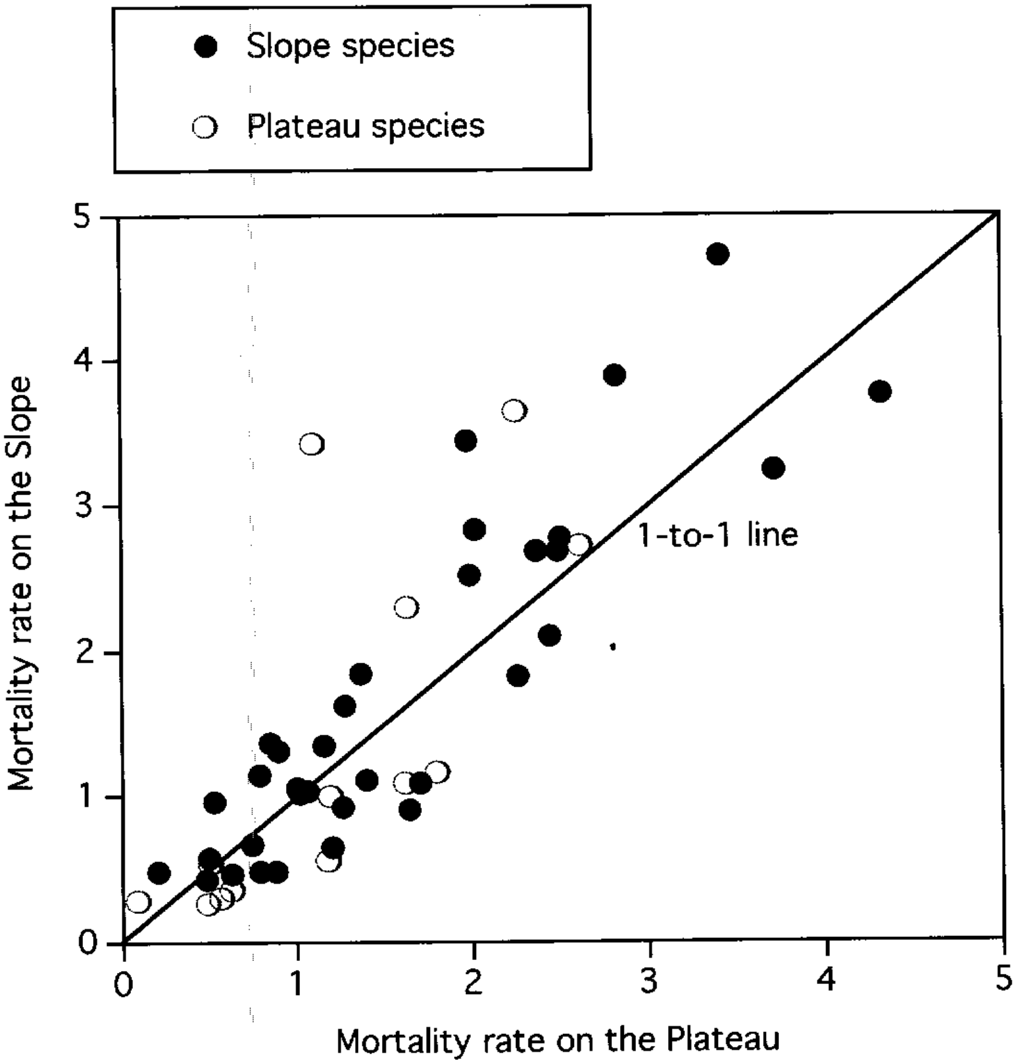


Figure 3.2. Mortality rate on the Slope versus mortality rate on the Plateau from 1982 to 1990 for species positively associated with the Slope (solid circles) and species positively associated with the Plateau (open circles) of the 50-ha Forest Dynamics Project plot of Barro Colorado Island, Panamá.

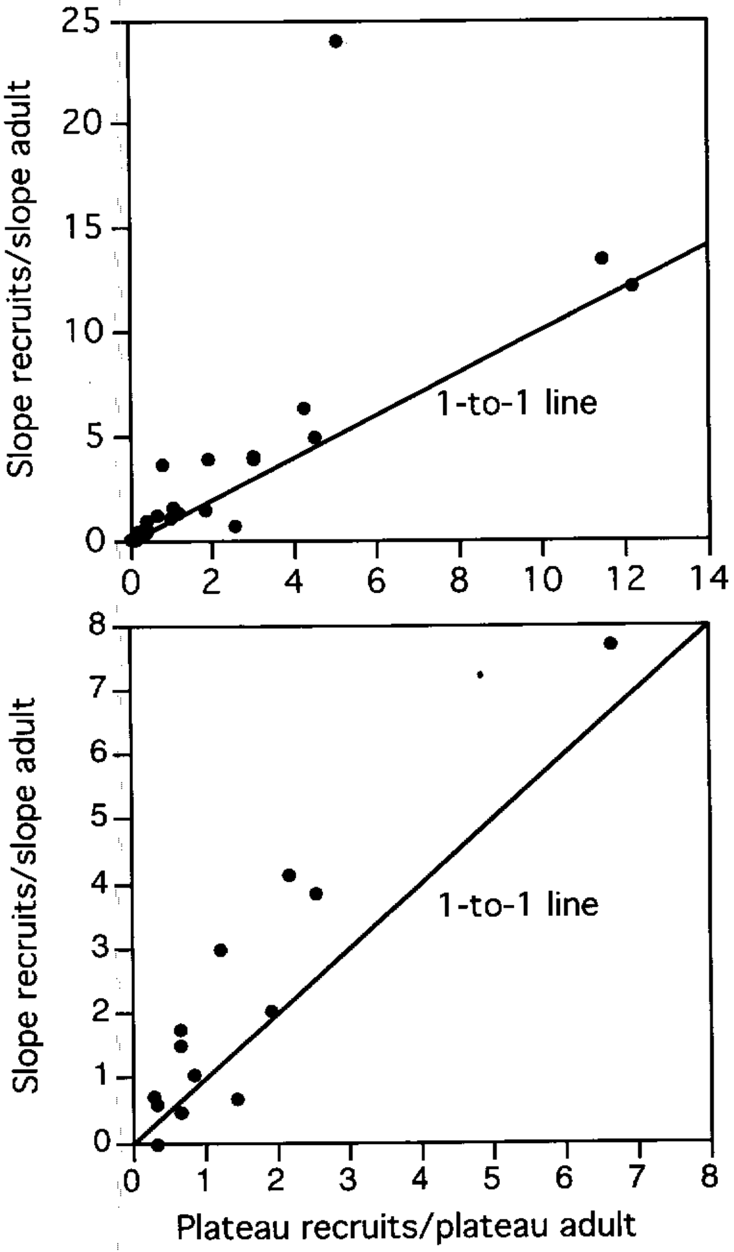


Figure 3.3 ab. Recruits per adult in 1985 on the Slope plotted against recruits per adult in 1985 on the Plateau for species of the 50-ha Forest Dynamics Project plot of Barro Colorado Island, Panamá. To be included, a species must have sufficient stems on the plot to be included in the recruitment analysis. **a.** Species positively associated with the Slope. **b.** Species positively associated with the Plateau. Note the change in scale on both axes between the figures.

CHAPTER 4

Seedling Performance of Five Tree Species on Two Habitats of a Neotropical Forest

INTRODUCTION

Plant species distributions are generally geographically restricted and locally clumped or patchy (Watt 1947; MacArthur 1972; Silvertown 1982), and each species usually has a distribution unlike that of other species (Gleason 1926; Whittaker 1967). Determining the causes of these patterns of distribution is one of the primary pursuits of plant ecologists (Crawley 1986).

Explanations for the varied distributions among species within communities of plants take a variety of forms. For example, a restricted and patchy distribution may be the result of adaptations to specific environmental conditions (Goldberg 1985; Wesser and Armbruster 1991; Mustart and Cowling 1993). Alternatively, interactions with competitors (Goldberg 1985; Wesser and Armbruster 1991; Latham 1992), consumers (Meehan *et al.* 1977; Louda 1982a, 1982b; Webb and Willson 1985; Whelan *et al.* 1991), or pathogens (Burger 1992) may restrict the distribution of a species. Finally, historical processes may have lead to the current, and perhaps ephemeral, distribution (Ricklefs

1987; Primack & Miao 1992; Ricklefs & Latham 1993; Losos 1993, 1995).

Environmental correlates of plant distributions may suggest causes for restricted distributions, but to understand the mechanism(s) that caused a given, restricted distribution, experimental manipulations are often necessary (Cavers and Harper 1967; Greig-Smith 1983, pg. 130; Goldberg 1985; Veenendaal *et al.* 1996). Experiments are especially helpful to separate biological effects from accidents of spatial history. Common-garden and seedling-transplant experiments are frequently used to determine the extent to which individuals of species with restricted distributions are capable of germinating, surviving, growing, and/or reproducing under conditions similar to and different from those under which they are naturally found (Neilson and Wullstein 1983; Prince and Carter 1985; Wesser and Armbruster 1991; Veenendaal *et al.* 1996).

Patterns of association with habitat features for tree and shrub species of the 50-ha Forest Dynamics Project (FDP) plot of Barro Colorado Island (BCI), Panamá were described in Chapter 2. A few species showed striking patterns of association with the shallow slopes of the 50-ha FDP plot (Appendix 5). Species strongly associated with slopes may be unable to tolerate the lower dry season soil-water potentials found on plateau sites (Becker *et al.* 1988). If this is the mechanism driving slope-association, individuals of slope-associated species should show reduced growth or survival on plateau relative to slope sites, especially during the dry season.

In Chapter 3 I showed that few differences in growth and survival in the size-classes ≥ 1-cm DBH exist between Slope and Plateau habitats of the 50-ha FDP plot. However, since mortality rates are often highest in the seed and seedling stages of plants, differential mortality in those stages may form persistent patterns (Harper and White 1974; Cook 1979; Clark and Clark 1985).

In this chapter I describe the first experimental test of the hypothesis that species associated with the slopes of the 50-ha plot of BCI are restricted to the slopes through differential growth and/or survival on slopes relative to plateau sites at the seedling stage and that species not restricted to the slopes or plateaus of the 50-ha plot are capable of surviving and growing on either type of habitat equally well.

METHODS

For each of five species of trees, indigenous to BCI and demonstrating a range of habitat affinities, I collected 300 - 500 seeds from the forest floor of the old forest during the early rainy season (May-June) of 1993 (see Chapt. 2 for a description of the study site). To avoid the high mortality of the post-germination phase common to tropical tree seedlings (DeSteven 1994), I cleaned seeds of fruit pulp and planted them in individual pots, filled with sieved, native soil, in a screened growing-house on BCI. Since the growing-house is in a large clearing on BCI, and is therefore unprotected from the sun, the seed-pots were placed on benches that were covered by shade-cloth to provide shade similar to understory conditions of the forest.

In order to provide seeds with conditions most like those found in the field, no fertilizer or fungicide treatments were applied to the seeds. Seeds germinated and were allowed to grow for one year in the growing-house. Substantial mortality resulted prior to transplanting to common gardens in the field. Fungal infections were common, and herbivorous insects and squirrels gained entry into the growing-house on several occasions, inflicting heavy damage. The resulting initial sample sizes of healthy seedlings primarily reflect these mishaps.

A list of the five species used in this study, along with characteristics of those species, is found in Table 4.1. All five species are either midstory or canopy trees as adults, and they represent five different taxonomic families. All but *Tocoyena pittieri* are common species on the 50-ha FDP plot. For three of the five species, recruitment rates into low-canopy and high-canopy sites were estimated by Welden *et al.* (1991) and suggested that *Beilschmiedia pendula*, *Calophyllum longifolium*, and *Tetragastris panamensis* are shade-tolerant. *V. surinamensis* has also been shown to be shade-tolerant through field experiments (Howe 1986, 1990a; Fisher *et al.* 1991). The response of *Tocoyena pittieri* to shade was not known prior to this investigation.

According to the torus-randomization procedure of Chapter 2, *B. pendula*, *C. longifolium*, and *V. surinamensis* are strongly positively associated with the slopes of the 50-ha FDP plot. *T. panamensis* is not positively or negatively associated with any topographic features of the 50-ha FDP plot. Too few stems of *Tocoyena pittieri* are found on the 50-ha FDP plot to determine habitat affinities by the torus-randomization. However, little is known of the habitat affinities or of the regeneration-niche of *T. pittieri* and seeds were available. The main comparison I was interested in, therefore, was between the realized habitat-generalist *T. panamensis* and the realized slope-specialists, *B. pendula*, *C. longifolium*, and *V. surinamensis*. The initial expectation was that individuals of *B. pendula*, *C. longifolium*, and *V. surinamensis* on Slope sites would out-perform, in terms of growth and/or survival, individuals growing on Plateau sites, but that individuals of *T. panamensis* would show no differences in growth or survival between Slope and Plateau sites.

I transplanted seedlings to the 50-ha FDP plot on BCI during the week of 1 June 1994. Different numbers of healthy seedlings were available per species at the time of transplantation due to differential mortality in the growing-house (see Table 4.2 for the numbers of seedlings transplanted). Since nearby conspecific adults have been shown to affect the growth and survival of seedlings for some species in this forest (Augspurger 1983a; Hamill 1986; Gilbert *et al.* 1994), seedlings were transplanted to common-garden sites at least 20 m from any adult trees of the species in the common-garden. I used 46 separate common-garden plots spread across the eastern half of the 50-ha FDP plot of BCI. Seedlings were planted in pairs in the plots, half on Slope sites and half on Plateau sites. All five species were represented in 19 plots on the Slope and 19 on the Plateau. Too few seedlings of *C. longifolium*, *T. panamensis*, and *T. pittieri* were available for all 46 plots. *C. longifolium* and *T. pittieri* were transplanted to 34 of the plots and *T. panamensis* was transplanted to 40 of the plots. All common-gardens were located in the shade beneath intact canopy, *i.e.*, non-gap sites.

I visited all 400 of the transplanted seedlings approximately two weeks following transplanting. One individual had disappeared by that time, three others had been broken off at their bases (one by a falling branch), and three had been completely defoliated by herbivores. There appeared to be no transplanting-shock to any of the remaining seedlings of *B. pendula*, *C. longifolium*, *T. panamensis*, or *V. surinamensis*, which appeared healthy and intact. The leaves on seedlings of *T. pittieri*, however, drooped and this may have been a sign of water-stress.

All seedlings were censused once during the week of 4 February, 1995 and once during the week of 10 June 1995, eight months and 12 months, respectively, after transplanting. During each census the status (alive or dead) and the size of each plant was recorded. Size was measured as basal stem diameter, number of leaves, and height to apical meristem.

In order to test the hypothesis that intraspecific variation in survival at the seedling stage is related to habitat, mortality between slope and plateau sites was compared using a Chi-square Test for Independence on each species. I avoided using the mortality rate equation from Chapter 3 (Equation 1) since at high mortality rates m takes on values greater than one and its use at high mortality rates has been criticized (Sheil *et al.* 1995). In order to test the hypothesis that intraspecific variation in growth at the seedling stage is related to habitat, changes in height and changes in number of leaves for each species on Slope versus Plateau sites was tested using Mann-Whitney U-tests. Interspecific differences in performance were also tested by separate ANOVAs for height growth and leaf number increase on Slope versus Plateau sites.

Although the primary focus of this experiment was on differences in performance on Slope versus Plateau sites, the data were amenable to testing for growth and/or survival differences as a function of initial size. In order to test the hypothesis that larger seedlings out-perform smaller seedlings in the understory, the initial size of survivors was compared to the initial size of those that died using 1-tailed, unpaired t-tests for each species.

RESULTS

Mortality rates were high and no significant differences in mortality were detected in comparisons of Slope versus Plateau sites, either within species or combining all species (Table 4.2). It was impossible to determine the cause of mortality for the majority of the seedlings that died, since no physical evidence of their deaths could be found, *i.e.*, most seedlings that died disappeared completely from the common-garden sites. It is unlikely that transplanting *per se* adversely affected the seedlings of all species except for *T. pittieri*. The leaves on seedlings of *T. pittieri* drooped and some developed necrotic patches soon after transplanting. *T. pittieri* faired poorly throughout the transplanting experiment in the shaded common-garden sites.

Including all plots, the seedlings that survived the 1-yr interval in four of the five species showed significant height increases over that interval (Table 4.3). *T. pittieri*, however, lost height (Table 4.3). The apparent shrinkage among seedlings of *T. pittieri* is difficult to explain. It is possible that these seedlings were drooping or slightly bent over when measured on the post-transplanting censuses, leading to apparent shrikage.

Only *T. panamensis* showed significant increases in the total number of leaves over the 1-yr interval (Table 4.4). *B. pendula* and *T. pittieri* showed significant net decreases in leaf number over the 1-yr interval (Table 4.4). Leaves were not marked, so I do not know the extent to which leaves were lost and replaced.

There were no significant differences in either height growth or changes in leaf number on Slope versus Plateau sites (Tables 4.5 and 4.6, Figure 4.1). According to the ANOVA analyses, there were strong species effects, but no significant habitat effects or habitat-by-species interactions on either height change or leaf number change over the 1-yr interval (Tables 4.7 and 4.8, respectively).

Size affected the probability that seedlings survived to the end of the 1-year interval. Smaller seedlings had a higher probability of mortality than did larger seedlings (Table 4.9). In table 4.9, only 3 of 15 comparisons show that those that died were larger initially than those that survived, but in none of those 3 cases is the comparison significant at the $\alpha=0.05$ level. Even though the 3 measures of size change are correlated, every significant t-test in Table 4.9 is for survivors starting out larger than those seedlings that died.

DISCUSSION

Most studies of tropical tree seedlings have focused either on growth and survival with respect to light conditions (Augspurger 1984a) or on the performance of individuals in relation to their proximity to conspecific adult trees (Augspurger 1983a; Hamill 1986). Many fewer studies have been concerned with the growth and survival of tropical forest seedlings with respect to differences in edaphic conditions, soil moisture availability, or topographic features (Ashton *et al.* 1995; Veenendaal *et al.* 1996).

The observed mortality patterns with respect to topography found in this study were unexpected. Location within Slope versus Plateau habitat had no significant impact on growth or survival of seedlings of each of the five species considered. The results of this study therefore provide little support for the hypothesis that differential growth or survival at the seedling stage on Slope versus Plateau sites can account for differences in abundance in those two habitat types.

The observed mortality patterns with respect to initial seedling size were as expected. Several studies have shown that larger seedlings of tropical species have significantly higher survival and growth rates than smaller seedlings (Schupp 1988; Clark and Clark 1985).

The two rarest species on the 50-ha FDP plot, *V. surinamensis* and *T. pittieri*, had the highest mortality rates as seedlings (Table 4.2). *V. surinamensis* has been shown to survive poorly as seedlings on BCI (Howe 1990a, 1990b; Fisher *et al.* 1991; Molofsky and Fisher 1993). De Steven (1994) collected survival data over several years for later-stage saplings of *Tetragastris panamensis*. In her study, *T. panamensis* had high survivorship compared to other, less common 50-ha FDP plot species (De Steven 1994). It is possible that differential overall mortality levels at the seedling and small sapling stage contribute to the overall relative abundance differences among species on the 50-ha FDP plot (Table 4.1). However, no published data exist for growth and survival of seedlings of *B. pendula*, *C. longifolium*, or *T. pittieri* over longer periods of time or including other size-classes than those considered in the present study, so this should be considered a tentative possibility.

Ashton *et al.* (1995) conducted experiments with four species of *Shorea* in Sri Lanka. No statistics were used for mortality analyses, but, similar to the results from the present study, changes in height for seedlings in the understory were nearly identical for all species in all sites (Ashton *et al.* 1995).

In an experiment with tree species from the temperate zone, Latham (1992) found that seedlings of selected tree species changed rank in growth performance across resource gradients, leading Latham (1992) to suggest that interspecific trade-offs in competitive abilities may promote coexistence in temperate forests composed of those species used in his study. Where seedlings do not differ in performance from site-to-site, coexistence by this mechanism is untenable.

Despite the negative results of these experiments, *i.e.*, the fact that neither growth nor mortality was related to topography for the five species considered, these results do not preclude the possibility that differential growth and/or mortality at the seedling stage is a primary cause of differential patterns of distribution with respect to topography evident in the database for larger size-classes (stems ≥ 1 cm DBH). These experiments were conducted over the short-term (1 year), were hampered by small sample sizes, and only considered the responses of five species.

It is prudent to ask whether the sample sizes available for these experiments were sufficient to detect mortality differences of sufficient magnitude to result in the density differences that the three Slope-associated species in this analysis display as ≥ 1-cm stems. I conducted a power analysis on the Chi-square tests for differences in mortality between Slope and Plateau sites for the four species that did not have exactly the same number of individuals die in the two sites. By this analysis, I determined that the observed mortality difference on Slope and Plateau sites would have been significant with a sample size of 114 and of 124 for *C. longifolium* and *V. surinamensis*, respectively, but would have required sample sizes of 680 and 967 for *T. panamensis* and *T. pittieri*, respectively. However, *C. longifolium* and *T. pittieri* had higher absolute mortality on the Slope while *T. panamensis* and *V. surinamensis* had higher mortality on the Plateau. Through a simple population model I found that the observed mortality differences, although small, are sufficient to produce dramatic differences in adult densities if they are assumed to be constant and their effects compound over the many years that it takes these species to reach adulthood - estimated to be between 180 and 250 years for *B. pendula*, *C. longifolium*, *T. panamensis*, and *V. surinamensis* (Hubbell *et al.* unpubl. ms.). However, the absolute differences in mortality rates for the Slope-associated species are in the predicted direction for only one species (more seedlings of *V. surinamensis* died on the Plateau), are in the opposite direction for another (more seedlings of *C. calophyllum* died on the Slope), and are equivalent for the third species (*B. pendula*). To fully explore the possibility that small, statistically insignificant mortality differences could give rise to statistically detectable differences in adult densities, however, would require parameterizing a simulation model of the forest, a requirement that is not possible until we have accurate seed production and seed-dispersal parameters for each of these species.

It is critical to note that this experiment was conducted over a time period during which no severe drought occurred of the intensity or duration of those that periodically strike central Panamá, especially in conjunction with El Niño-Southern Oscillation events (Leigh *et al.* 1990). These severe droughts, that strike every few years, may be especially important to determining the sites in which species of the BCI forest are capable of establishing as saplings.

Three future directions of research could further our understanding of the distribution patterns of the selected species and the rest of the BCI 50-ha FDP plot community. First, growing-house experiments should be conducted to determine the response of seedlings to the full range of conditions experienced in the understory and to determine the physical factors responsible for any differential growth and survival. Second, seed germination experiments are needed to determine whether strong differences exist during the seed-seedling transition on Slope versus Plateau sites. Finally, a wider range of species in longer-term experiments are necessary to understand the generality of these results. Longer-term experiments would not only include a larger portion of the juvenile life-stage of long-lived tree species, but would also increase the chances of encompassing the extremes of year-to-year variation in climatic conditions.

Table 4.1. Characteristics of species used in the common garden seedling experiment on the 50-ha Forest Dynamics Project plot of Barro Colorado Island, Panamá. The habitat-designation refers to the apparent habitat-affinity, of each species, with respect to Slope and Plateau sites, based on the torus-randomization tests of Chapter 2 (see the Methods section of Chapter 4 for further details of habitat-designations). The Colonizing Index is the percentage recruitment of new saplings (1-4 cm DBH) in 1985 into low canopy sites as determined by Welden *et al.* (1991) and used as an index of gap colonization by Condit *et al.* (1995).

Species (Family) - habitat	Growth form	Colonizing Index from Welden *et al.* (1991)	Total number of stems on FDP 50-ha plot		
			1982	1985	1990
Beilschmiedia pendula (Lauraceae) - Slope	T	20.64	2376	2671	2750
Calophyllum longifolium (Guttiferae) - Slope	T	20.74	649	722	893
Tetragastris panamensis (Burseraceae) - Neutral	T	13.63	3253	3699	4085
Tocoyena pittieri (Rubiaceae) - Rare	M	?	6	8	7
Virola surinamensis (Myristicaceae) - Slope	T	?	300	259	239

Table 4.2. Seedling common-garden experiment on the 50-ha Forest Dynamics Project plot of Barro Colorado Island, Panamá.

Species	Total number of seedlings planted in June 1994 (1/2 on the Slope and 1/2 on the Pleateau)	Total number of survivors to February 1995 (%)	Total number of survivors to June 1995 (%)	Survivors to June 1995 on the Slope (%)	Survivors to June 1995 on the Plateau (%)	Chi-square comparison of survivors and deaths between Slope and Plateau sites
Beilschmiedia pendula	92	65 (71)	52 (56)	26 (57)	26 (57)	0.00 NS
Calophyllum longifolium	68	54 (79)	44 (65)	19 (56)	25 (74)	2.32 NS
Tetragastris panamensis	80	54 (68)	43 (54)	23 (58)	20 (50)	0.45 NS
Tocoyena pittieri	68	39 (57)	22 (32)	10 (29)	12 (35)	0.27 NS
Virola surinamensis	92	14 (15)	6 (7)	5 (11)	1 (2)	2.85 NS
All Seedlings	400	226 (57)	167 (42)	83 (42)	84 (42)	0.01 NS

Table 4.3. Comparison of initial height and height at one year for survivors, both plateau and slope, of the seedling common-garden experiment.

Species	n	Initial height (cm) ± S.E.	End height (cm) ± S.E.	Wilcoxon Signed-Rank test
Beilschmiedia pendula	52	20.6 ± 0.9	22.0 ± 0.9	p<<0.01
Calophyllum longifolium	44	15.9 ± 0.6	18.5 ± 0.7	p<<0.01
Tetragastris panamensis	43	15.4 ± 0.4	18.2 ± 0.5	p<<0.01
Tocoyena pittieri	22	23.5 ± 1.1	20.8 ± 1.1	p=0.04
Virola surinamensis	6	21.0 ± 1.8	23.8 ± 1.7	p=0.03

Table 4.4. Comparison of initial initial number of leaves and number of leaves at one year for survivors, both plateau and slope, of the seedling common-garden experiment.

Species	n	Initial number of leaves ± S.E.	End number of leaves ± S.E.	Wilcoxon Signed-Rank test
Beilschmiedia pendula	52	5.7 ± 0.3	4.4 ± 0.3	p<<0.01
Calophyllum longifolium	44	6.5 ± 0.2	6.8 ± 0.4	p=0.35
Tetragastris panamensis	43	5.5 ± 0.3	6.9 ± 0.4	p<<0.01
Tocoyena pittieri	22	8.2 ± 0.3	2.9 ± 0.4	p<<0.01
Virola surinamensis	6	3.7 ± 0.4	2.7 ± 0.8	p=0.24

Table 4.5. Comparison of change in height over the 1-year interval in Slope versus Plateau common-garden plots.

Species	Change in height on Plateau ± S.E. (n)	Change in height on Slope ± S.E. (n)	Mann-Whitney U-test
Beilschmiedia pendula	1.2 ± 0.4 (26)	1.8 ± 0.3 (26)	p=0.43
Calophyllum longifolium	2.7 ± 0.3 (25)	2.5 ± 0.6 (19)	p=0.90
Tetragastris panamensis	2.8 ± 0.3 (20)	2.8 ± 0.3 (22)	p=0.94
Tocoyena pittieri	-3.9 ± 1.5 (12)	-1.1 ± 1.9 (10)	p=0.32
Virola surinamensis	Insufficient	Insufficient	Insufficient

Table 4.6. Comparison of change in leaf number over the 1-year interval in Slope versus Plateau common-garden plots.

Species	Change in leaf number on Plateau ± S.E. (n)	Change in leaf number on Slope ± S.E. (n)	Mann-Whitney U-test
Beilschmiedia pendula	-1.4 ± 0.5 (26)	-1.2 ± 0.4 (26)	p=0.79
Calophyllum longifolium	0.3 ± 0.6 (25)	0.4 ± 0.6 (19)	p=0.87
Tetragastris panamensis	1.3 ± 0.6 (20)	1.6 ± 0.5 (22)	p=0.49
Tocoyena pittieri	-5.5 ± 0.6 (12)	-5.2 ± 0.7 (10)	p=0.79
Virola surinamensis	Insufficient	Insufficient	Insufficient

Table 4.7. ANOVA table for the change in height of 1-yr survivors from the seedling common garden experiment comparing Slope and Plateau sites. Only *Beilschmiedia pendula*, *Calophyllum longifolium*, *Tetragastris panamensis*, and *Tocoyena pittieri* are included in the Species term.

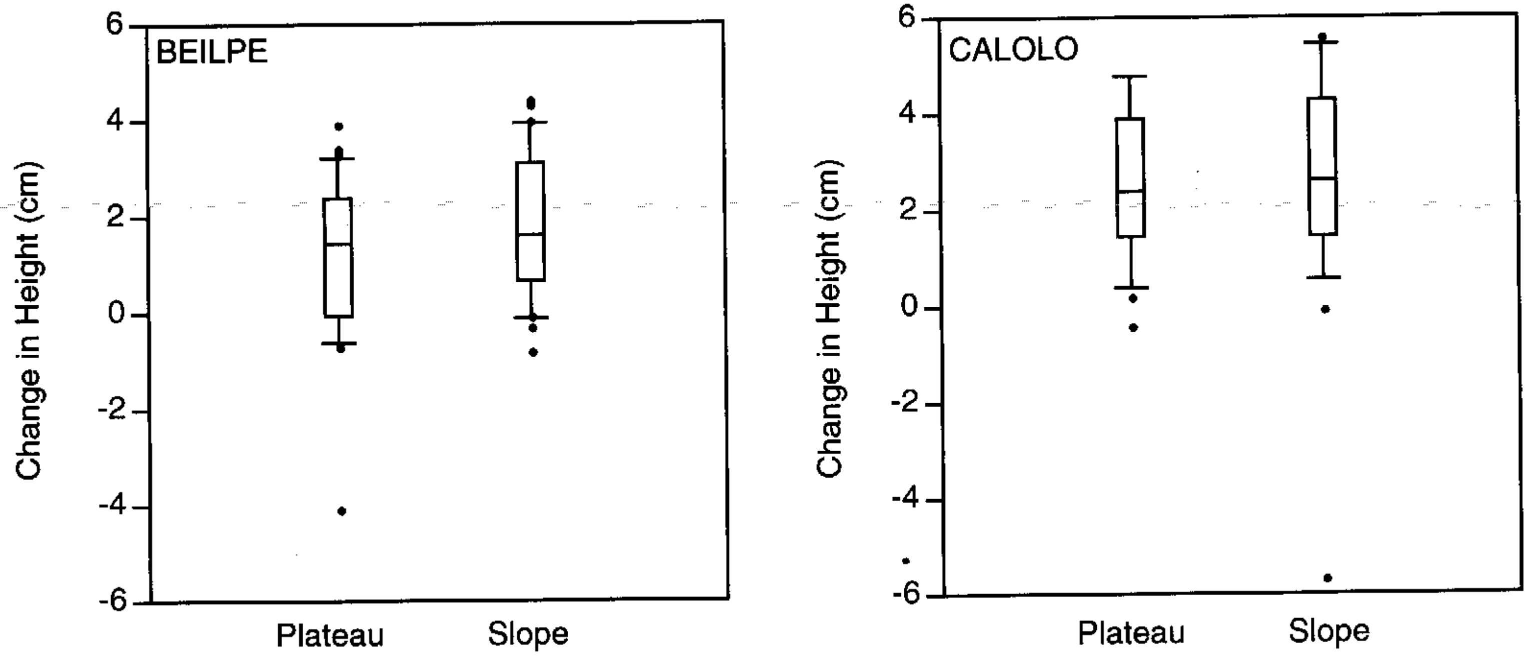
Factor	DF	Sum of Squares	Mean Sum of Squares	F-value	P-value
Species	3	475.5	158.5	24.2	<<0.01
Habitat	1	20.8	20.8	3.2	0.08
Species * Habitat	3	36.7	12.2	1.9	0.14
Residual	152	993.7	6.5		

Table 4.8. ANOVA table for the change in number of leaves of 1-yr survivors from the seedling common garden experiment comparing Slope and Plateau sites. Only *Beilschmiedia pendula*, *Calophyllum longifolium*, *Tetragastris panamensis*, and *Tocoyena pittieri* are included in the Species term.

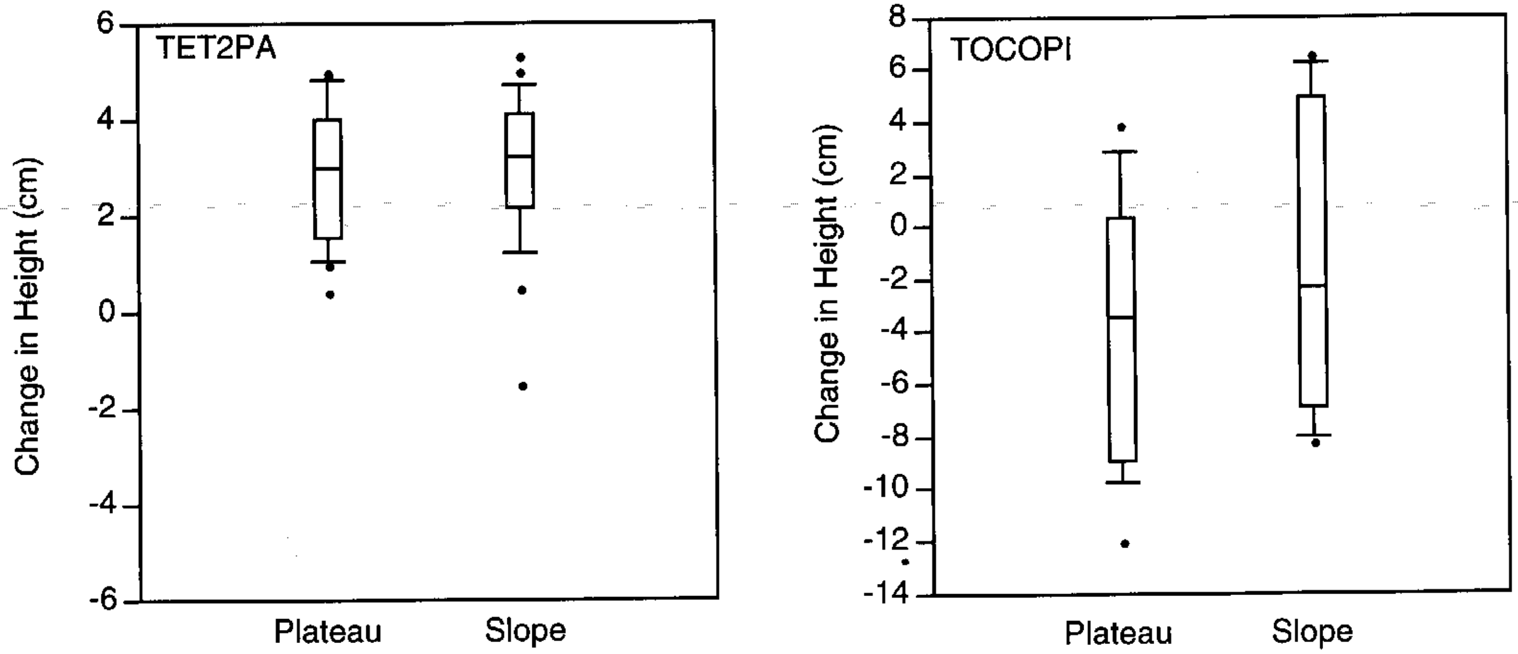
Factor	DF	Sum of Squares	Mean Sum of Squares	F-value	P-value
Species	3	719.5	239.8	42.8	<<0.01
Habitat	1	1.9	1.9	0.3	0.56
Species * Habitat	3	0.2	0.1	0.0	0.99
Residual	152	850.7	5.6		

Table 4.9. Comparison of seedling sizes for seedlings that suvived and those that died during the first year of the common-garden experiment on BCI, using 1-tailed unpaired t-tests.

Species & size measurement	Initial size survivors	n	> or <	Initial size those that died	n	P-values
Beilschmiedia pendula Diameter (mm)	3.8 ± 0.8	52	>	3.6 ± 0.9	40	0.09
Beilschmiedia pendula Height (cm)	20.6 ± 6.3	52	>	18.7 ± 5.3	40	0.07
Beilschmiedia pendula Number of leaves	5.7 ± 1.8	52	>	4.7 ± 1.8	40	0.01
Calophyllum longifolium Diameter (mm)	3.0 ± 0.5	44	<	3.1 ± 0.5	24	0.47
Calophyllum longifolium Height (cm)	15.9 ± 3.9	44	>	15.3 ± 5.5	23	0.32
Calophyllum longifolium Number of leaves	6.5 ± 1.6	44	>	5.5 ± 1.7	24	0.01
Tetragastris panamensis Diameter (mm)	3.0 ± 0.6	43	>	2.8 ± 0.5	37	0.01
Tetragastris panamensis Height (cm)	15.4 ± 2.5	43	<	15.8 ± 2.1	37	0.22
Tetragastris panamensis Number of leaves	5.5 ± 1.7	43	>	5.2 ± 1.4	37	0.25
Tocoyena pittieri Diameter (mm)	5.7 ± 1.2	22	>	5.6 ± 1.0	46	0.35
Tocoyena pittieri Height (cm)	23.5 ± 5.0	22	<	23.6 ± 6.0	46	0.47
Tocoyena pittieri Number of leaves	8.2 ± 1.5	22	>	7.6 ± 1.4	46	0.05
Virola surinamensis Diameter (mm)	6.2 ± 0.7	6	>	5.8 ± 0.8	86	0.15
Virola surinamensis Height (cm)	21.0 ± 4.3	6	>	18.9 ± 3.2	86	0.07
Virola surinamensis Number of leaves	3.7 ± 1.0	6	>	3.2 ± 1.0	86	0.14



Figures 4.1 ab. The change in height (cm) over one year for seedlings of *Beilschmiedia pendula* and *Calophyllum longifolium* in the common-garden experiements to compare performance on Plateau versus Slope sites.



Figures 4.1 cd. The change in height (cm) over one year for seedlings of *Tetragastris panamensis* and *Tocoyena pittieri* in the common-garden experiments to compare performance on Plateau versus Slope sites. Note the change in scale on the y-axis for *Tocoyena pittieri*.

CHAPTER 5

Supply-Side Ecology of a Neotropical Forest: Evidence for Dispersal-Limitation

INTRODUCTION

Supply-side ecology is concerned with the production, dispersal, and establishment of recruits (Lewin 1986; Roughgarden *et al.* 1987). These processes play critical roles in the population and community dynamics of trees, since where no seed of a given species arrives, no recruit of that species can become established (Harper 1977; Schupp *et al.* 1989; Schupp and Fuentes 1995).

When the size of a population of organisms is limited by the number of recruits entering that population, the population is said to be recruitment-limited (Lewin 1986; Roughgarden *et al.* 1987). Recruitment-limitation in sessile organisms with dispersive propagules has two components, as discussed by Pielou (1960), Roughgarden *et al.* (1985), Eriksson and Ehrlén (1992), Hurtt and Pacala (1995), and Schupp and Fuentes (1995). The first component of recruitment-limitation is dispersal-limitation (Ribbens *et al.* 1994; seed-limitation in Hurtt and Pacala [1995] and in Schupp and Fuentes [1995]). We have very little understanding of the degree to which natural plant populations are limited by the number of seeds produced and the distances they are dispersed, leading Crawley (1990) to remark that, "It is curious that the simple experiment of sowing extra seeds and recording the number of recruits has been carried out so seldom."

Once dispersed, the conditions that some seeds encounter may hinder germination and/or seedling establishment. The second component of recruitment-limitation is therefore safe-site or microsite-limitation (Harper 1977; Horn 1981; Eriksson and Ehrlén 1992; Ribbens *et al.* 1994; Hurtt and Pacala 1995).

High rates of random mortality are characteristic of seeds, seedlings, and young saplings (Sarukhán 1978, 1980; Wyatt-Smith 1987). However, the degree of microsite-limitation experienced by a population of trees depends on the extent to which deterministic processes govern the probability that a dispersed seed could become established at each site in the forest. Ontogenetic shifts in resource-requirements may occur during the early stages of a tree's life-cycle, so the probability of establishment in a site must integrate over those developmental stages leading up to the stage at which a plant is considered to have become established in the population (Bazzaz 1991; Clark and Clark 1992; Schupp 1995; Schupp and Fuentes 1995). In a strictly microsite-limited population, the probability of establishing in sites other than "safe-sites" for germination and establishment (*sensu* Harper 1977) or outside of "enemy-free space" (*sensu* Jeffries and Lawton 1984) is zero, so that simply adding seeds would not serve to increase the size of the population (Ribbens *et al.* 1994). Only by improving the conditions of sites, thereby increasing the probabilities of establishment in some sites, would the population size increase, regardless of whether or not extra seeds were added.

Of course, dispersal-limitation and microsite-limitation can operate simultaneously (Eriksson and Ehrlén 1992). The relative magnitudes of dispersal-limitation and microsite-limitation can make the difference between orderly, predictable successional patterns and "preemptive crazy quilts" in which the secondary forest is a patchwork, with each patch dominated by the species that happened to be nearby and producing seeds to colonize the disturbance that initiated the succession (Horn 1981). To construct an example for mature forest, consider a forest in which the probability of establishment is greater than zero, yet less than one in all sites. However, the current level of seed input is insufficient for plants to establish in all sites, since the probability of having an established plant in any given site is the product of the number of seeds that arrive and the probability that a seed will become established. In this hypothetical example, adding seeds would increase the size of the established population, but so would improving the conditions of some sites.

A variety of studies have demonstrated the importance of differential dispersal-limitation in models of coexistence between two plant species. Foremost among these are the studies in which one species is a "fugitive species" (*e.g.*, Skellam 1951; Hutchinson 1951; Horn and MacArthur 1972). In these models, trade-offs exist between devoting resources to reduce dispersal-limitation (*i.e.*, increased reproductive output and dispersal ability) versus devoting resources to reduce microsite-limitation (*i.e.*, increased competitive ability). The usual result is that a poorer competitor or fugitive species is capable of coexisting together with a better competitor as a result of the poorer competitor's colonization advantage.

Tilman (1994) claimed to be the first to extend the two-species fugitive species models to many species, by showing that the stable coexistence of an unlimited number of competitors and fugitives can occur with the appropriate trade-offs between competitive ability and dispersal ability. However, this had been assumed to be possible by earlier authors (*e.g.*, Skellam 1951; Horn and MacArthur 1972), had been stated explicitly by Hastings (1980), and is the basis for the shifting mosaic conceptual model as applied to forests (Watt 1947; Bormann and Likens 1979). According to the shifting mosaic model, poor competitors are good dispersers that gain a temporary advantage over good competitors in canopy gaps by arriving earlier to those gaps (Watt 1947; Bormann and Likens 1979; Clark and Ji 1995).

Hurtt and Pacala (1995) showed that dispersal-limitation may play a substantial role in community dynamics even when no competition-colonization trade-off exists among species. In their model, each species is the best competitor somewhere on the landscape, and all species are at least somewhat dispersal-limited. Since individuals of each species are frequently absent from sites in which they would be the dominant competitor, individuals of other species capture those sites. Hurtt and Pacala (1995) referred to this phenomenon as "winning-by-forfeit". Winning-by-forfeit is the mechanism that slows community dynamics in their model, so that communities behave as though their member species were in ecological drift as opposed to being structured by highly deterministic competitive interactions.

Dispersal also plays a critical role in the population and community dynamics of species in a model that assumes competitive equivalence among members of its community of sessile organisms (Hubbell, in press). In this model, several local communities are connected by dispersal and are therefore part of a single meta-community. Differences in dispersal rate are modeled as different rates of replacement of deaths in local communities by immigrants from the meta-community. Dispersal rates have strong effects on the levels of local relative abundance and diversity, as well as on levels of meta-community diversity. Under high dispersal rates, individual species are represented in local communities at or near their meta-community relative abundance levels and local species diversity is relatively high. However, species that are rare in the meta-community are driven extinct by competition for representation in the seed-pool by the common species. Conversely, with low dispersal rates, local diversity drops as local communities become islands of monodominant stands. Local monodominance maintains more rare species, and higher regional diversity, in the meta-community. The influence of dispersal on the diversity of this model system is therefore strong but scale-dependent.

A thought experiment demonstrates that extreme dispersal-limitation could maintain any given level of diversity indefinitely, regardless of the type and magnitude of competitive interactions possible in the community. Imagine that every adult tree produces seeds, but the seeds of each adult only fall beneath each tree's own crown. If crowns do not overlap, then each tree would replace itself with a single reproductive offspring that takes its place in the forest. Conspecifics replace conspecifics with a perfect one-to-one match and so neither competitive exclusion nor drift to extinction can occur.

To take an empirical perspective, a variety of studies suggest that dispersal-limitation may be of great importance in communities of herbaceous plants and shrubs. For example, Matlack (1994) used indirect evidence to suggest that herbaceous plants and shrubs in the understory of successional forest stands in the Delaware/Pennsylvania Piedmont zone are often dispersal-limited. In stands of regrowth disjunct from intact forest, understory species-richness of herbaceous and shrub species was greater in older stands and in stands closer to potential seed-sources than in younger and more isolated stands.

Primack and Miao (1992) found evidence for dispersal-limitation by experimentally dispersing seeds of four annual species into sites in which individuals of those species were absent. Thirty-four sites were seeded and populations of two species became established and grew in three of the new locations, within 200 m of natural populations, indicating that lack of dispersal to those sites had previously limited the range of those species.

Eriksson and Ehrlén (1992) used a combination of seed-addition and disturbance in the form of vegetation removal to show that both dispersal-limitation and microsite-limitation were important in the herbaceous species and shrubs of their study. Of 14 species used in their experiments, nine species showed evidence of dispersal-limitation by increasing in abundance either: 1) in undisturbed sites with seeds added relative to undisturbed control sites, or 2) in disturbed sites with seeds added relative to disturbed control sites.

Despite these community-level theoretical advances and empirical demonstrations of dispersal-limitation for populations of herbaceous plants and shrubs, Clark and Ji (1995) remarked that, "recruitment represents a potentially important, yet poorly described, aspect of tree population dynamics". Seed dispersal imposes constraints on recruitment, since recruits can only appear in sites to which seeds dispersed. Spatially limited seed dispersal is therefore a necessary requirement of dispersal-limitation.

My objective in this chapter is to assess the evidence for dispersal-limitation in a species-rich community of tropical trees by determining the degree to which dispersal is limited in that community. Specifically, I ask:

1) Integrating over several years, how many species disperse seeds to any particular site?
2) How broad is the coverage of dispersed seeds by each species?
3) Is the seed-rain more species-rich in more species-rich sites?
4) How often do species disperse seeds more broadly than the rain of their flowers would predict?
5) Does the similarity of seed-trap contents show negative spatial autocorrelation?

6) Does the probability of a species dispersing seeds to a particular site diminish with the distance of that site from the nearest adult tree of the focal species?
7) How do species classified as pioneer versus non-pioneer according to their tolerance of low-light conditions compare with respect to seed-to-recruit ratios and seed-dispersal abilities?

METHODS

A majority of the data used in this chapter comes from the largest dataset of its kind, generated from the extensive seed- and fruit-trapping project initiated by S. J. Wright of the Smithsonian Tropical Research Institute on the 50-ha Forest Dynamics Project (FDP) plot of Barro Colorado Island (BCI, the study site described in Chapter 2). I supplemented the seed-trap data with direct measurements of seed-dispersal away from selected individual adult trees.

Seed-trap Data

In order to monitor the community-wide rain of seeds, fruits, and flowers onto the 50-ha FDP plot, S. J. Wright placed 200 seed-traps, approximately evenly spaced, along the trail system of the plot (Figures 5.4 - 5.8). Each trap is a 0.5-m x 0.5-m square PVC frame supporting a shallow, open-topped, 1-mm nylon-mesh bag, suspended 0.8 m above the ground on four PVC stakes. The mean nearest neighbor distance between traps is 18.9 ± 3.6 m (standard deviation) and the range is 4.1 to 28.0 m.

From 1 January 1987 to 31 December 1994, every seed, fruit, and seed-bearing fruit fragment ≥ 1 mm that fell into the traps was counted and identified to species on a weekly basis. Seeds smaller than 1 mm were identified, but not counted. Flowers were identified and their presence in traps was recorded, but flowers were not individually counted.

The data from these traps are appropriate for analyzing the community-wide seed-rain resulting from primary dispersal (Phase I dispersal in the terminology of Chambers and MacMahon [1994]). Since these traps have openings 0.8 m above the ground, they miss the re-distribution of seeds that occurs due to secondary dispersal once seeds have reached the ground (Phase II dispersal in Chambers and MacMahon [1994]). With the exception of a few species (*e.g.*, *Dipteryx panamensis* - Forget 1993; *Gustavia superba* - Forget 1992), the importance of secondary dispersal to most tropical forest tree species is unknown (Schupp and Fuentes 1995). Regardless, secondary dispersal is a function of the pattern created by primary dispersal (Schupp and Fuentes 1995). Since little is known about the manner in which secondary dispersal changes patterns set by primary dispersal, I consider the focus on primary dispersal, imposed on this study by the sampling design, a profitable step towards better understanding recruitment in this forest.

For most analyses I used the full 8-year trapping period from 1987 through 1994, inclusive. For several analyses I used only the midstory (M) and canopy (T) trees of the 50-ha FDP plot, since many of the shrubs (S) of small stature and understory trees (U) bear some of their seeds at heights below the level of the openings of the seed traps. The growth form of each species included in the database of the 50-ha FDP plot is given in Appendix 1 and the number of species in each growth form category is given in Appendix 2.

To quantify the species-richness of the local seed-rain, I first tallied the number of species, by growth form, that dispersed seeds to each seed-trap during each trapping period of an integer number of years from one through eight. A species is included in the tally for a given trap if $\geq$ 1 seed and/or $\geq$ 1 fruit containing a mature seed appeared in the trap during the given period.

The rate of addition of species to the list of those that have fallen into each trap is likely to dimish with time, *i.e.*, the cumulative number of species having fallen into a trap is an asymptotic function of the elapsed time. To estimate the amount of time it would take for all species on the 50-ha FDP plot to disperse at least one seed to a given, average trap, I found the slope of the regression of the log of the average number of species not yet dispersed to each trap versus the length of the trapping period. The point at which the regression crosses zero on the y-axis gives the length of time it would take for all but one species to have seeds dispersed to an average trap. This calculation provides a lower-bound estimate for the time it would take for all species to reach a given trap, on average. I found this length of time for three growth form categories: canopy trees, midstory plus canopy trees, and all woody, free-standing 50-ha FDP plot species.

A species-richness gradient characterizes the 50-ha FDP plot of BCI, with more species per stem on Slope sites compared with Low Plateau sites (Hubbell 1995; Condit *et al.*, in press; see Chapter 2 for details on dividing the plot into habitat types). To determine whether seed-traps on the more species-rich Slope sites collected more species as seeds compared to seed-traps on Low Plateau sites I used a Mann-Whitney U-test to test for differences in the mean number of species per trap, over the 8-year trapping period, within three growth form categories: 1) canopy trees, 2) midstory plus canopy trees, and 3) all woody, free-standing 50-ha FDP plot species.

For each species, I tallied the number of traps into which seeds fell during the full 8-year trapping period. Since flowers do not produce structures to promote their own dispersal, the spatial distribution of flowers provides one estimate of the traps found beneath the crowns of adults of each species. I therefore also tallied the number of traps to which flowers arrived over the same period and compared these with the numbers of seed-bearing traps.

To determine whether seeds were more likely to fall into traps near to conspecific adult trees, for each species that was common in the seed-rain, I found the proportion of traps receiving seeds when found in different distance classes from the nearest conspecific adult tree. The size at which trees become reproductive is used to define adult trees. The best estimates for these sizes are from R. Foster and are derived from extensive experience with these species. Reproductive sizes are given in Appendix 1. For this analysis, all traps were excluded that were nearer a border of the 50-ha FDP plot than an adult of the focal tree species.

I estimated the decay of similarity of trap contents with distance by calculating both Jaccard's Index of Similarity and Pearson's Product-Moment Correlation Coefficient and determining the extent to which these measures of similarity change with distance between traps for all pairwise combinations of traps and for the sub-set of trap pairs $\leq$ 100 m apart.

I made several comparisons of seed-trap contents for pioneer versus non-pioneer species. Pioneer and non-pioneer trees were defined as such by their relative abilities to tolerate shade and survive under conditions of low light availability. For the following analyses, species are considered to be pioneers if they were given pioneer designation in Condit *et al.* (1995) because of low survivorship in locations with low canopy-heights, or if they were classified as pioneer species in the 50-ha FDP database as a result of being common in secondary forests near the 50-ha FDP plot (Hubbell and Foster, unpubl. list). I first determined the number of seeds per recruit for both pioneer and non-pioneer species, in order to compare the seed-to-recruit ratios of species divided into these two life-history categories. These ratios are rough calculations based on the total number of seeds that fell during an average year per ha divided by the total number of saplings that recruited per average ha during an average year. This ratio was calculated once using only pioneer species and once using only non-pioneer species.

I also examined the species-richness and similarity of seeds within traps compared to trees in each trap's neighborhood for both pioneer and non-pioneer species. For each tree-neighborhood I used trees within a square quadrat, of 20-m per side, centered on the focal trap. I compared the species-richness of seed-trap contents to the species-richness of the tree-neighborhoods of the seed-traps, but species-richness does not take into consideration the species overlap or similarity between trap-content and tree-neighborhood species lists. Jaccard Similarity Indices were therefore calculated as a measure of the cross-correlation between trap-contents and tree-neighborhoods, for comparing the strength of these correlations between pioneer and non-pioneer species. To determine whether or not an observed Jaccard's Index for a given trap with its own tree-neighborhood was higher than expected by chance, I calculated Jaccard's Index for the focal trap's seed-contents with each of the other 199 traps' tree-neighborhoods. The probability of observing a Jaccard's Index equal to or larger than the observed is given by the proportion of Jaccard's Indices calculated from tree-neighborhoods other than the focal trap's that are equal to or larger than that for the given trap's tree-neighborhood.

Direct Measurements of Dispersal Curves

In 1994, I counted the seeds in four wedge-shaped, 10° transects out from the bases of relatively isolated individual trees of three species near the end of their fruiting seasons in 1994. Trees were chosen on the basis of reproductive status. Trees were also chosen on the basis of relative isolation from other conspecific fruiting adults in order to avoid overlapping seed shadows.

RESULTS

The Number of Species per Trap

Within each growth form, the number of species that each trap captured as seeds increased as the length of the trapping period increased (Tables 5.1, 5.2, 5.3; Figure 5.1). Out of 305 species of shrubs, understory trees, midstory trees, and canopy trees present on the 50-ha FDP plot, each seed-trap captured the seeds of 29.0 ± 7.0 species (mean ± 1 SD) as seeds over the full 8-yr trapping period (Table 5.1; Figure 5.2a). Of those species 22.4 ± 6.1 were midstory plus canopy tree species (Table 5.2; Figure 5.2b), and 16.4 ± 4.3 were canopy tree species only (Table 5.3; Figure 5.2c).

On average, 619 years would be required for a given trap to receive seeds from each of the 305 species of shrubs, understory trees, midstory trees, and canopy trees of the 50-ha FDP plot (Table 5.4, *Ficus* species were not included). Each trap requires 375 years to receive all midstory plus canopy trees as seeds and 288 years to receive ≥ 1 seed of all canopy trees (Table 5.4). After 100 years, each trap, on average, would receive 119 species of shrubs, understory trees, midstory trees, and canopy trees as seeds, 39% of the 305 species in those growth forms on the 50-ha FDP plot (Table 5.4).

There were more species of seeds per trap in each of the growth form categories on Slope compared to Plateau sites (Figure 5.3). However, in each of the three growth form categories, the difference was not significant.

The Number of Traps Reached by Each Species

The number of traps that each species reached during the full 8-yr interval was low (Appendix 10). Only two species (*Jacaranda copaia* and *Terminalia amazonica*), out of 313 species monitored (including *Ficus* species), dispersed seeds to all 200 seed traps from 1987 to 1994, inclusive. One species, *Luehea seemannii*, dispersed seeds to all but one of the 200 seed-traps. Just over 1/3 of the species, 113 out of 313, dispersed no seeds to traps during the full 8-year trapping period. Only 40 species in total dispersed seeds to ≥ 50 traps (≥ 25% of traps), 15 species dispersed seeds to ≥ 100 traps (≥ 50%), and 8 species dispersed seeds to ≥ 150 traps (≥ 75%). Two of these 8 species, *Trichilia tuberculata* and *Alseis blackiana*, are the most abundant and the second most abundant species, respectively, on the 50-ha FDP plot out of the 182 midstory and canopy trees.

Of the 217 species with at least 1 trap containing either a seed or flower, 55 (25%) species had more traps with flowers than seeds, 15 (7%) species had an equal number of traps with flowers and seeds, and 147 (68%) species had more traps with seeds than flowers (Appendix 10).

Incidence as a Function of Distance to the Nearest Adult

For most species, the probability of having seeds reach a trap drops as the distance from the nearest conspecific adult tree increases (Table 5.5). For those species included in Table 5.5, the probability that a trap received ≥ 1 seed of the focal species drops, on average, from 0.46, to 0.21, to 0.16 as the distance from the nearest conspecific adult tree increases from 0-10 m, to 20-30 m, to 40-50 m, respectively (Table 5.6).

The reduced probability of seed-dispersal to traps distant from conspecific adults is evident by inspecting maps that simultaneously display: 1) seed-traps with seeds, 2) seed-traps without seeds, and 3) adult trees of the focal species (Figures 5.4 - 5.8). Of the species presented in these figures, *Jacaranda copaia* is exceptional in having seeds dispersed to all 200 seed-traps during the 8-year trapping period.

Decay of Similarity with Distance

The similarity of trap contents for the full 8-year trapping period, measured both as Jaccard's Index of Similarity and as Pearson's Product-Moment Correlation Coefficient, was significantly negatively related to distance, using all 19,900 pairs of traps and using the subset of pairs of traps within 100 m of one-another (Linear Regressions, $P<0.001$ in both cases). However, the R^2 values, whether using linear or quadratic fits, in each case were extremely low, between 0.006 and 0.048 for the linear fits, indicating that distance between traps is a very poor predictor of the similarity of the seeds they captured.

Pioneer versus Non-Pioneer Species

It requires, on average, 359,000 seeds per pioneer recruit into the 1-2 cm DBH size-class, whereas a non-pioneer recruit requires nearly seven times fewer, or 52,000 seeds. These calculations are rough estimates that assume that within the pioneer and non-pioneer categories each species has nearly the same seeds-per-recruit ratio, but must suffice until more thorough seed-trapping is conducted to determine the variance around the seeds-per-recruit ratio within each category, pioneer and non-pioneer.

On average, there are more species of pioneer seeds per trap than there are species of pioneer tree within 10 m of each seed-trap (Figure 5.9 a). On average, there are fewer species of non-pioneer seeds per seed-trap than there are species of non-pioneer tree within 10 m of each trap (Figure 5.9 b). However, when only adult trees are considered, for both pioneer and non-pioneer life-history categories, there are more species as seeds within traps than there are species as adults within 10 m of most traps (Figures 5.10 ab).

About 70 out of 200 traps have significantly higher Jaccard Similarity Indices than expected from a random draw of traps' tree-neighborhoods ($P<0.05$; Figure 5.11). However, pioneer species and non-pioneer species have substantially different P-value distributions (Figures 5.12 ab). For pioneers, many traps have non-overlapping species lists compared with their tree-neighborhoods, resulting in a large fraction of P-values equal to 1.

Direct Measurement of Dispersal Curves

In keeping with other direct measurements of dispersal curves, the data from the current study show a sharp drop in seed numbers with distance from the crown-edge of the reproductive tree (Figures 5.13 - 5.15). The degree of asymmetry in these seed-shadows is also striking and similar to previous studies (*e.g.*, Kitajima and Augspurger 1989).

DISCUSSION

Those who have used seed-trap data to examine the input of seeds into the forest understory have been surprised by how few species are found per trap, relative to the total species-richness of the communities within which those traps were located (Jackson 1981; Curran 1994; Loiselle *et al.* 1996). However, these studies have all been short-term or have considered only a sub-set of species. The current study also found few species per trap relative to the total number of species in the community within which the seed-traps are set.

One might criticize these estimates of the species-richness of the local seed-rain by pointing out that the seed-traps miss secondary dispersal - dispersal by rodents, ants, and other agents - which should further homogenize the seed-rain. However, there are also reasons to argue that this method may provide an *over*-estimate of the species-richness of the local seed-rain. Since seeds were only scored for maturity, but not for viability (despite the prevalence of pests, parasites, and predators that damage seeds prior to primary dispersal, *e.g.*, Gillett [1962]; Janzen [1971b]; DeSteven [1981]), and since many of the species found in a given trap represent a single seed during the 8-yr interval, the study may have *over*-estimated the mean number of species dispersing viable seeds to each trap location.

Even though the similarity of trap contents showed a significant decay with distance, the extremely low R^2 values of the regression models demonstrate the high degree of variability from one pair of traps to the next, even at approximately the same distance apart. However, with traps spaced about as far apart as the diameters of large trees, these traps do not allow an estimate of the variation that would be found beneath the canopy of a single adult canopy tree. If contents of traps spaced more closely than the traps used in this study were to vary as much as contents vary at the current distances, the current estimates of species-richness per trap might be considered high. However, if trap contents for traps within 4 m of one another are nearly identical, then one would conclude that few species reach any given site large enough for the recruitment of a sapling. Further trapping at smaller spatial scales than currently employed would help to resolve this issue. My own observations suggest that similarity values which incorporate relative abundance information as well as presence/absence information across species are likely to show similarity values that are high at short distances (< 5 m), and then taper off at longer distances (> 10 m). In contrast, the similarity indices which only consider presence/absence information may not be substantially larger at short distances (< 5 m) than those observed in the current study. The reason for this is that most of BCI's woody species show years of good and poor fruit-production. During good years, the seed-rain is heavy beneath adult crowns, but rapidly diminishes with distance from maternal trees. This pattern results in very steep dominance-diversity curves for the contents of individual seed-traps. As one observes seeds on the forest floor, dominant species remain dominant for several meters - on the order of one canopy tree's crown width - whereas singleton seeds are found haphazardly scattered within the matrix of one or two dominant species of seeds.

Most species showed evidence of limited dispersal. Few species dispersed seeds to more than a few traps over the entire 8-year trapping period. Furthermore, the probability that traps received seeds of a given species fell as the distance to the nearest adult tree of that species increased. These patterns suggest that traps nearer one-another than those in this study would likely contain similar contents, leading one to conclude that local seed-rain is relatively species-poor.

Leptokurtic Seed-Shadows

The measured seed-shadows of temperate-zone trees are generally leptokurtic with few seeds falling outside of a few canopy diameters of the maternal parent plant (Levin 1984; Hoppes 1988; Willson 1992). Leptokurtic seed-shadows of temperate-zone trees have been shown to impose constraints on colonization of old-fields and gaps found distant from seed-sources (Egler 1954; Greene and Johnson 1996). There are a few examples of seed dispersal curves or seed shadows for species of tropical trees (Howe and Westley 1986). Those that exist are for individual, usually isolated, adult trees (*e.g.*, Janzen *et al.* 1976; Janzen 1978 abc; Fleming and Heithaus 1981; Thomas *et al.* 1988; Kitajima and Augspurger 1989). Whitmore (1984, pg. 75) described the seed-shadow of an individual of *Shorea curtisii* in which no viable seeds were dispersed beyond 25 m, yet the rain of seeds infested with insects extended to 80 m from the base of the tree. All of those seeds beyond 25 m had been killed by seed-predatory weevils, rendering them lighter and more readily dispersed by wind. Each of these studies demonstrated a rapid decline in seed density with distance away from the focal trees, but the extent to which dispersal from isolated trees is representative of population-wide dispersal patterns cannot be gauged from these studies.

Estimating Dispersal Curves

Actual seed dispersal-curves are very difficult to measure, let alone to compare (Clark and Ji 1995). For example, long, shallow tails are difficult to detect and, when adult trees are near one-another, the tails of seed shadows overlap (Houle 1992; Ribbens *et al.* 1994). For trees within intact temperate-zone forests, Ribbens *et al.* (1994; Pacala *et al.* [1996]) used a maximum likelihood estimator to determine the parameters for dispersal curves for several species of trees in a forest of the eastern United States. All species except yellow birch, a gap-colonizing species, had estimated dispersal curves that fell off rapidly with distance from adult trees. Mean dispersal distances (MDD) for all species except yellow birch were < 20 m, while yellow birch had a MDD of > 60 m.

The estimator of Ribbens *et al.* (1994) relies on smooth, symmetric dispersal curves. In reality, seed-shadows are highly asymmetric. Whether seeds are dispersed by the wind (Kitajima and Augspurger 1989) or by animals (Figures 5.13, 5.14, 5.15) seed-shadows are generally not circular. Furthermore, concentric circles centered on the base of the trunk are not good representations for leaning trees whose center of mass of the seed-rain is not at the base of the trunk of the adult tree.

Although, the estimator designed by Ribbens *et al.* (1994) takes overlapping seed-shadows into account, and averages over asymmetries in seed-shadows, even more serious difficulties require further information before estimating dispersal parameters will be possible for the trees of the 50-ha FDP plot. Dioecy can be common in tropical tree communities (63 [20%] of the 313 woody species recorded from the 50-ha FDP plot of BCI), so basing dispersal on all adult individuals would tend to underestimate dispersal. Defining adults on the basis of DBH is likely to include many inappropriate individuals, since not all reproductive sized individuals fruit every year. Together, these characteristics of tropical trees contribute to the error in estimating dispersal curves. The more error that accumulates, the less confident one can be about making comparisons of dispersal parameters among species. Seed-trap data combined with information on the individuals that actually fruited during given time periods would serve to remedy many of the current problems associated with estimating dispersal curves for tropical trees.

Spatially Patchy and Temporally Variable Seed-Shadows

Not only are seed-shadows generally leptokurtic, assigning the same smooth curves to individuals of the same size (DBH) masks a great deal of underlying variability in the seed-shadows produced by individual adult trees (Hoppes 1988). For example, DeSteven (1994) found that unequal seed production among adult trees on BCI had dramatic consequences for the seedling layer. In each of three species of canopy tree studied, a few trees accounted for the majority of recruitment, with nearby seedling densities far greater than the sample averages. In 1994 I visited all adult-sized trees of four species on the 50-ha FDP plot of BCI and determined whether or not they fruited during the wet season that year. I was unable to determine the sex of all individuals, so the following are percentages out of all adult-sized trees. The percentage of all adult trees that actually produced fruits ranged from 34% to 54% of adult-sized individuals for dioecious species and 94% for a single bisexual species (Table 5.7).

Seed-production is also temporally variable. For example, Thomas and LaFrankie (1993) found that 19% and 71% of all adult-sized individuals of five dioecious species from a Malyasian rain forest flowered during a given year. On the 50-ha FDP plot, Murawski and Hamrick (1992) found that 74% of adult trees of *Cavanillesia platanifolia* flowered in 1987 and that only 49% flowered in 1988.

Clumped Dispersion Patterns and Rarity of Reproductive Trees

Clumped dispersion patterns and rarity are common characteristics of tropical tree species (Hubbell 1979; Hartshorn 1980; Hubbell and Foster 1986c; Armesto *et al.* 1986). Lieberman and Lieberman (1994) report a lower degree of clumping than other studies; however, they used nearest-neighbor distances for all trees within study plots, failing to remove those individuals found closer to an edge of the plot, inadvertently increasing mean nearest neighbor distances.

Pielou (1960) argued that an aggregated distribution can be caused by microsite-limitation or dispersal-limitation or both. Despite the cause of clumped dispersion patterns of adult trees, limited dispersal is one likely consequence (Pielou 1960), especially when combined with leptokurtic seed shadows and spatial and temporal heterogeneity in adult fecundity.

Lieberman *et al.* (1985) assert that the species-pool of colonists to any gap is large, but they concede that propagules of many species are not dispersed ubiquitously. Prior to the current study there were few data with which to evaluate the assertion of

Lieberman *et al.* (1985), since few large-scale, long-term studies have monitored the community-wide seed-rain in mega-diverse tropical plant communities (Jackson 1981; Curran 1994 - chapter 3; Loiselle *et al.* 1996). However, conclusions from some of these studies must be tempered by their short duration, limited spatial extent, or narrow focus on a sub-set of the tree community. For example, the studies by Jackson (1981) and by Loiselle *et al.* (1996) were of ≤ 1-yr duration. Curran's (1994) extensive seed-trap data for the Dipterocarpaceae of Bornean forests provides an exception and an important Old World comparison for the BCI seed-dispersal data. Curran (1994) found that during her 7-yr investigation of the 26 members of the Dipterocarpaceae, each seed-trap received, on average, 5.5 species of these wind-dispersed seeds. By comparison, on BCI there were seeds of 7.1 of the 29 species of wind-dispersed canopy trees, on average, in each trap during the 8-yr trapping period. Curran's (1994) seed-traps were larger than those used in the current study (2.5-m^2 versus 0.25-m^2), but it is unlikely that a difference in seed-capture area at that spatial scale biased the estimates relative to one another, and the results of the two studies are surprisingly similar.

Species with essentially unlimited dispersal

A few species seem to have unlimited seed-dispersal abilities. These species can be divided into two categories:

pioneer species with copious production of tiny seeds and extremely common species.

Two pioneer species, *Jacaranda copaia* and *Terminalia amazonica*, dispersed seeds to all 200 traps during the 8-year trapping period. Another pioneer species, *Luehea seemannii*, dispersed seeds to 199 of the seed-traps. These species are relatively rare canopy trees on the 50-ha FDP plot with small, wind-dispersed seeds.

T. tuberculata is the most common canopy tree of the 50-ha FDP plot and has medium-sized, animal-dispersed seeds, while *A. blackiana* is the second most common canopy tree on the plot and has very small, wind-dispersed seeds. *T. tuberculata* dispersed seeds to 193 traps during the 8-year trapping-period, while *A. blackiana* dispersed seeds to 169 traps during that interval. *Faramea occidentalis*, the most common understory tree on the 50-ha FDP plot, dispersed seeds to 190 traps, while *Hybanthus prunifolius*, the most common understory shrub on the 50-ha FDP plot, dispersed seeds to 178 traps.

Why are none of these species taking over the 50-ha FDP plot? From 1982 to 1990, the population size of *A. blackiana* did steadily increase from 7595 stems $\geq$ 1-cm DBH in 1982, to 8049 stems in 1985, to 8410 stems in 1990, an 11% increase over 1982. However, in 1995, there were 8171 stems of *A. blackiana*, a decrease in population size back toward the 1982 level. *T. tuberculata* followed a similar pattern, with an initial increase from 12,928 stems in 1982 to 13,292 stems in 1990, followed by a drop to 12,820 stems in 1995. Among the pioneers, *L. seemannii* has shown a net increase in population size of only 20 individuals. The population sizes of *J. copaia* and *T. amazonica* have been steadily decreasing, with fewer stems in each subsequent census after the initial census in 1982 of 342 and 62 stems, respectively, to the 1995 population sizes of 277 and 54, respectively.

It is likely that *A. blackiana*, *J. copaia*, *L. seemannii*, and *T. amazonica* are microsite-limited. *J. copaia*, *L. seemannii*, and *T. amazonica* are well-known large-gap colonizers (Welden *et al.* 1991) and gap area, defined as the area in which no vegetation is found above 5 m, varies from only 2.50% to 22.75% of each hectare of old-growth forest on the 50-ha FDP plot (Hubbell and Foster 1986b). Even though juvenile saplings of *A. blackiana* survive relatively well in shade (Welden *et al.* 1991), the tiny seeds produce very small seedlings. Tiny seeds are often unable to germinate through heavy leaf-litter (Molofsky and Augspurger 1992) and their seedlings are often unable to survive the low light levels of the understory (Foster and Janson 1985). It is likely that density-dependent attack by pathogens keeps *T. tuberculata* in check, since this is the species for which Janzen-Connell effects consistently appear in tests of both static and dynamic data (Condit *et al.* 1992a; Hubbell and Foster 1990b).

Limited Dispersal and Dispersal-limitation

A seed must not only arrive, but must also germinate and survive as a seedling in order to occupy a given site in the forest. For recruitment to be limited by seed production and dispersal, therefore, some sites must go without seeds that would have been suited for germination, survival, and growth. Results from this chapter suggest that the dispersal of seeds from reproductive adult trees is, in most cases, limited, and that the local rain of seeds in a species-rich tropical forest is of relatively low diversity. Several other studies suggest that by removing dispersal-limitation, seedlings could become established and grow in sites currently not occupied by individuals of those species.

For example, results from Chapter 4 suggest that seeds dispersed beyond their current locations can survive and grow. Dispersal-limitation is suggested by the fact that common garden sites were located away from conspecifics, yet seedlings survived and grew. If this is a common pattern and if seeds are not ubiquitously distributed throughout the 50-ha FDP plot, then dispersal-limitation is likely to play a strong role in the community dynamics of this forest.

Results from studies conducted by Hamill (1986) on BCI also suggest that many species are capable of surviving and growing as seedlings in sites distant from conspecific adults. Indeed many of the seedling transplants survived better when placed beneath heterospecific adult trees compared to those placed beneath conspecific adults.

Future directions

In order to better understand the recruitment process, we need to better understand the consequences of the patterns that result from the seed-rain to subsequent population and community dynamics. Monitoring the seed-rain inputs relative to the seedling layer outputs are a step in this direction.

The main question now is: Given the current level of dispersal-limitation, would diversity be augmented or would it diminish if the average level of dispersal-limitation were to be increased or decreased? The answer to this question depends on the other processes acting in the BCI forest. Manipulative experiments are needed to determine the extent to which altering seed-rain patterns alters population and community patterns.

Table 5.1. The number of shrub (S), understory (U), midstory (M), and canopy tree (T) species that fell as seeds into each of the 200 seed-traps on the 50-ha FDP plot of BCI, Panamá (see Appendix 1 for the species included in each growth form category and Appendix 2 for the number of species in each growth form category). A species is included in the tally for a given trap only if ≥ 1 mature seed and/or ≥ 1 fruit containing a mature seed fell into the trap during the given census period. For each mean and variance value, n=200.

Growth forms	Inclusive dates	Mean no. of species	Variance	Min. no. of species	Max. no. of species
S, U, M & T	1987 - 1994	29.0	48.4	14	55
S, U, M & T	1987 - 1993	27.1	43.7	13	49
S, U, M & T	1987 - 1992	24.7	40.4	11	47
S, U, M & T	1987 - 1991	21.8	33.0	10	41
S, U, M & T	1987 - 1990	18.6	30.1	6	36
S, U, M & T	1987 - 1989	15.8	23.6	2	33
S, U, M & T	1987 - 1988	13.2	16.6	2	28
S, U, M & T	1987 Only	8.4	9.1	1	16

Table 5.2. The number of midstory (M) and canopy tree (T) species that fell as seeds into each of the 200 seed-traps on the 50-ha FDP plot of BCI, Panamá (see Appendix 1 for the species included in each growth form category and Appendix 2 for the number of species in each growth form category). A given trap is included in the tally only if ≥ 1 mature seed and/or ≥ 1 fruit containing a mature seed fell into the trap during the given census period. For each mean and variance value, n=200.

Growth forms	Inclusive dates	Mean no. of species	Variance	Min. no. of species	Max. no. of species
M & T	1987 - 1994	22.4	37.5	9	42
M & T	1987 - 1993	20.9	33.2	9	39
M & T	1987 - 1992	19.0	30.9	9	37
M & T	1987 - 1991	16.7	24.5	7	34
M & T	1987 - 1990	14.3	22.3	4	30
M & T	1987 - 1989	12.5	18.2	1	28
M & T	1987 - 1988	10.5	13.3	1	23
M & T	1987 Only	6.4	7.2	1	14

Table 5.3. The number of canopy tree (T) species that fell as seeds into each of the 200 seed-traps on the 50-ha FDP plot of BCI, Panamá (see Appendix 1 for the species included in this growth form category). A given trap is included in the tally only if ≥ 1 mature seed and/or ≥ 1 fruit containing a mature seed fell into the trap during the given census period. For each mean and variance value, n=200.

Growth form	Inclusive dates	Mean no. of species	Variance	Min. no. of species	Max. no. of species
T	1987 - 1994	16.4	18.4	7	29
T	1987 - 1993	15.4	16.3	6	27
T	1987 - 1992	14.0	15.7	5	25
T	1987 - 1991	12.5	12.8	5	24
T	1987 - 1990	10.8	12.1	2	22
T	1987 - 1989	9.5	10.1	1	21
T	1987 - 1988	8.1	7.9	1	18
T	1987 Only	5.1	4.9	0	12
T	1988 Only	5.9	4.3	1	13
T	1989 Only	4.7	4.3	0	12
T	1990 Only	5.4	4.0	2	11
T	1991 Only	5.7	4.3	1	14
T	1992 Only	7.0	5.0	3	16
T	1993 Only	4.7	4.8	0	13
T	1994 Only	6.1	4.3	2	12

Table 5.4. Estimates of the average time it would take for all species to arrive to a given trap based on regressions of [log(number of species that have not yet arrived)] on (the number of years elapsed). Estimates of the average number of species to have arrived at a given trap after 100 years have elapsed are also provided and are calculated from the regression equations. See Appendix 1 for the species included in each growth form category.

Growth forms	Total number of species on the 50-ha FDP plot	Regression equation	R^2	Years for all but one species to have fallen into an average trap	Number of species to have fallen into an average trap after 100 years
S, U, M, & T	305	$y=-0.004x + 2.475$	0.99	619	119 (39%)
M & T	182	$y=-0.006x + 2.248$	0.99	375	44 (24%)
T	108	$y=-0.007x + 2.016$	0.99	288	20 (19%)

Table 5.5. The numbers of seed-traps with and without seeds (≥ 1 mature fruit and/or ≥ 1 mature seed) of the focal species over the 8-year interval 1987-1994, inclusive, and the proportion of traps receiving seeds over that interval for 5 distance classes from the nearest reproductive-sized individual on the 50-ha FDP plot in 1990. Included are the 56 species for which there were ≥ 5 total traps in each distance class. Traps that were nearer a plot border than to the nearest reproductive-sized individual of the focal species are not included. See Appendix 1 for reproductive sizes of each species.

	Number of traps with seeds of the focal species					Number of traps without seeds of the focal species					Proportion of traps with seeds of the focal species				
Species	0-10 m	10-20 m	20-30 m	30-40 m	40-50 m	0-10 m	10-20 m	20-30 m	30-40 m	40-50 m	0-10 m	10-20 m	20-30 m	30-40 m	40-50 m
ALCHCO	3	9	8	6	7	2	14	11	23	22	0.60	0.39	0.42	0.21	0.24
ALLOPS	1	1	2	2	2	7	18	28	29	33	0.13	0.05	0.07	0.06	0.06
ANACEX	4	5	3	2	1	1	2	10	8	15	0.80	0.71	0.23	0.20	0.06
APEIME	10	9	5	3	2	4	25	35	27	17	0.71	0.26	0.13	0.10	0.11
APEITI	1	0	2	2	0	6	12	18	14	17	0.14	0.00	0.10	0.13	0.00
AST1ST	2	1	0	0	0	15	40	48	37	18	0.12	0.02	0.00	0.00	0.00
BEILPE	16	16	5	5	3	1	13	17	14	12	0.94	0.55	0.23	0.26	0.20
CASEAR	8	0	0	2	0	4	15	23	27	20	0.67	0.00	0.00	0.07	0.00
CASESY	2	0	1	0	0	5	17	22	24	34	0.29	0.00	0.04	0.00	0.00
CASSEL	4	1	2	1	2	5	22	43	39	17	0.44	0.04	0.04	0.03	0.11
CECRIN	5	5	4	4	2	2	13	15	12	17	0.71	0.28	0.21	0.25	0.11
CEIBPE	0	1	3	2	0	5	8	13	14	10	0.00	0.11	0.19	0.13	0.00
COCCCO	0	0	1	0	1	5	9	19	13	20	0.00	0.00	0.05	0.00	0.05
CORDBI	12	17	9	8	4	4	29	23	21	17	0.75	0.37	0.28	0.28	0.19
DENDST	7	8	10	8	5	3	8	14	16	11	0.70	0.50	0.42	0.33	0.31
ERY2MA	0	0	0	0	0	7	24	21	48	26	0.00	0.00	0.00	0.00	0.00
EUGENE	1	0	0	0	2	5	20	26	23	30	0.17	0.00	0.00	0.00	0.06
GAR2IN	3	2	2	2	1	9	23	31	28	28	0.25	0.08	0.06	0.07	0.03
GUAPST	7	10	8	6	8	1	9	13	16	13	0.88	0.53	0.38	0.27	0.38
GUARSP	4	1	2	0	0	14	26	30	28	18	0.22	0.04	0.06	0.00	0.00
GUATDU	5	21	10	14	7	2	9	11	14	7	0.71	0.70	0.48	0.50	0.50
GUSTSU	16	4	0	0	0	26	42	49	35	11	0.38	0.09	0.00	0.00	0.00
HASSFL	21	17	10	8	1	12	43	29	26	12	0.64	0.28	0.26	0.24	0.08
HEISCO	13	17	13	12	8	9	26	32	20	11	0.59	0.40	0.29	0.38	0.42
HURACR	4	1	0	0	0	10	19	25	22	17	0.29	0.05	0.00	0.00	0.00
INGAQU	0	0	0	2	0	9	25	23	29	24	0.00	0.00	0.00	0.06	0.00
JAC1CO	20	29	42	28	21	0	0	0	0	0	1.00	1.00	1.00	1.00	1.00
LICAHY	0	0	0	0	0	5	19	13	21	9	0.00	0.00	0.00	0.00	0.00
LINDLA	2	7	3	2	4	5	14	29	28	25	0.29	0.33	0.09	0.07	0.14
LUEHSE	5	16	19	17	20	0	0	0	0	0	1.00	1.00	1.00	1.00	1.00

Table 5.5 continued.

	Number of traps with seeds of the focal species					Number of traps without seeds of the focal species					Proportion of traps with seeds of the focal species				
Species	0-10 m	10-20 m	20-30 m	30-40 m	40-50 m	0-10 m	10-20 m	20-30 m	30-40 m	40-50 m	0-10 m	10-20 m	20-30 m	30-40 m	40-50 m
MALMSP	0	3	1	1	0	16	33	35	24	20	0.00	0.08	0.03	0.04	0.00
MAQUCO	0	0	0	0	0	21	44	46	29	21	0.00	0.00	0.00	0.00	0.00
COOTCE	3	1	1	1	1	9	22	24	18	20	0.25	0.04	0.04	0.05	0.05
COOTWH	2	3	1	2	0	3	10	9	12	9	0.40	0.23	0.10	0.14	0.00
PLA1PI	6	6	7	0	0	0	7	13	22	27	1.00	0.46	0.35	0.00	0.00
PLA2EL	4	8	7	5	3	1	3	9	10	12	0.80	0.73	0.44	0.33	0.20
POULAR	3	6	1	0	0	5	14	15	17	7	0.38	0.30	0.06	0.00	0.00
POUTRE	1	6	5	8	8	4	13	14	14	16	0.20	0.32	0.26	0.36	0.33
POUTST	1	0	2	0	1	4	9	18	14	12	0.20	0.00	0.10	0.00	0.08
PRI2CO	7	1	0	0	0	2	15	13	11	7	0.78	0.06	0.00	0.00	0.00
PROTPA	0	2	1	2	0	15	34	43	33	18	0.00	0.06	0.02	0.06	0.00
PROTTE	8	17	11	6	4	7	17	28	22	25	0.53	0.50	0.28	0.21	0.14
QUARAS	32	45	30	20	10	2	8	8	5	4	0.94	0.85	0.79	0.80	0.71
SIMAAM	5	12	7	8	3	3	8	15	14	20	0.63	0.60	0.32	0.36	0.13
SOCREX	1	0	0	0	0	27	41	22	16	6	0.04	0.00	0.00	0.00	0.00
SPONRA	3	3	4	2	3	4	10	18	14	20	0.43	0.23	0.18	0.13	0.13
TAB1GU	4	6	7	4	5	2	5	8	9	8	0.67	0.55	0.47	0.31	0.38
TAB2AR	13	5	3	4	4	2	27	32	28	13	0.87	0.16	0.09	0.13	0.24
TET2PA	15	17	11	9	5	2	15	25	15	7	0.88	0.53	0.31	0.38	0.42
TRI2PA	3	6	3	1	0	10	12	37	25	16	0.23	0.33	0.08	0.04	0.00
TRIPCU	9	9	4	4	1	0	2	7	12	15	1.00	0.82	0.36	0.25	0.06
TROPRA	0	0	0	0	0	8	10	21	19	23	0.00	0.00	0.00	0.00	0.00
UNONPI	3	2	2	0	0	14	26	32	24	17	0.18	0.07	0.06	0.00	0.00
VIROSE	16	17	17	9	8	15	29	22	10	10	0.52	0.37	0.44	0.47	0.44
VIROSU	6	8	11	5	11	0	5	12	8	12	1.00	0.62	0.48	0.38	0.48
ZANTBE	1	6	5	5	2	6	16	13	23	18	0.14	0.27	0.28	0.18	0.10

Table 5.6. The mean and standard deviation of the proportion of traps with seeds in each of five distance classes from the nearest reproductive-sized individual for each of the 56 species listed in Table 5.5. Traps that were nearer the border of the 50-ha FDP plot than to the nearest reproductive-sized indivdual of the focal species are not included.

	Distance class in m				
Statistic	0-10	10-20	20-30	30-40	40-50
Mean	0.46	0.29	0.21	0.18	0.16
SD	0.34	0.29	0.23	0.23	0.23

Table 5.7. Fruiting in 1994 of all reproductive-sized trees of four species found on the 50-ha FDP plot of BCI in 1994. See Appendix 1 for species names and reproductive sizes. I was unable to determine the sex of all individuals of the dioecious species, so these numbers are counts of all individuals.

Species	Mating system	Number of individuals checked	Number of individuals with fruits	Percentage of individuals with fruits
BEILPE	Bisexual	118	111	94
BROSAL	Dioecious	60	22	37
OCOTWH	Dioecious	69	37	54
VIROSU	Dioecious	83	28	34

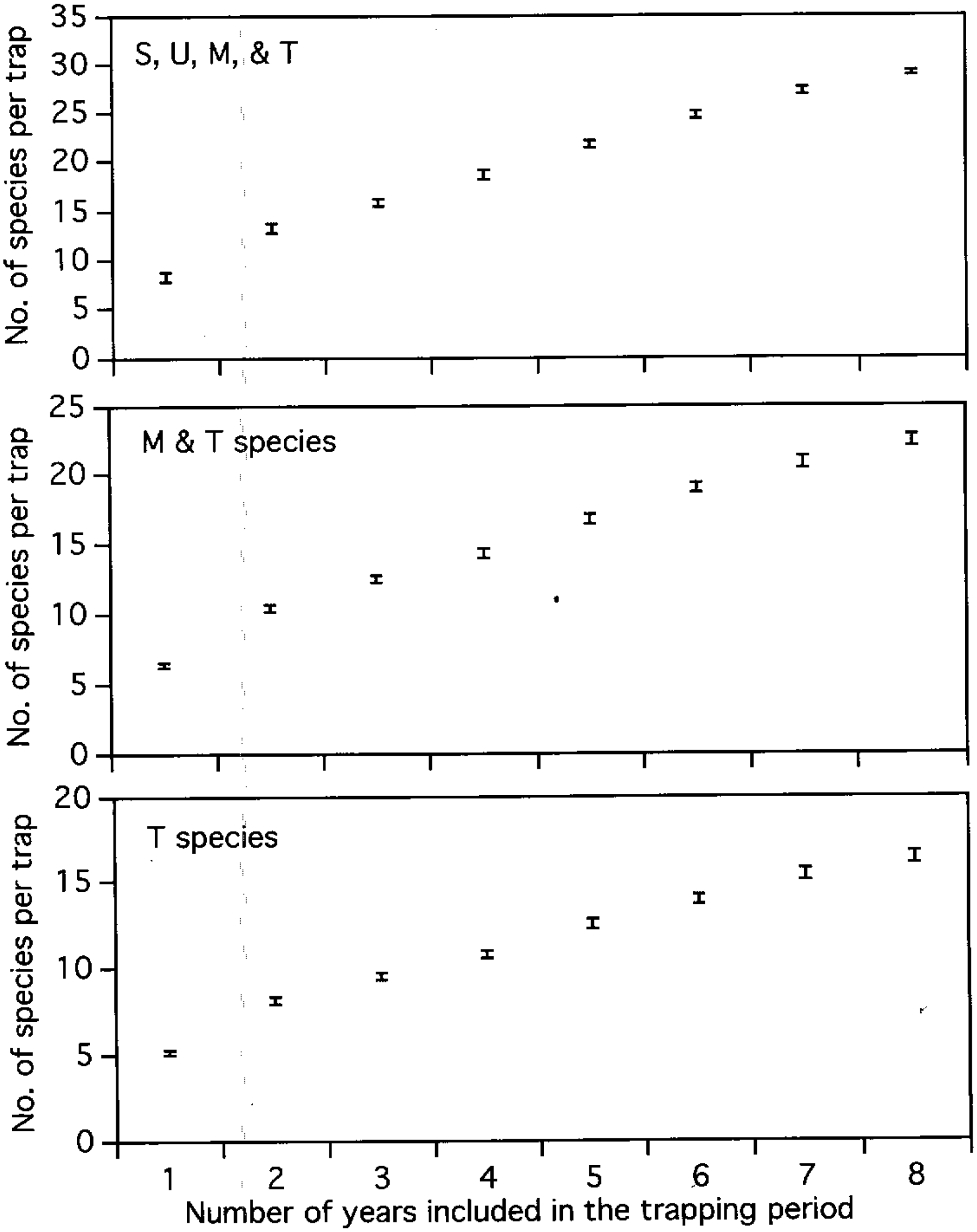


Figure 5.1. The mean number of species per trap versus the number of trapping-years including. Error bars are SE. See Appendix 1 for the species included in each growth form category.

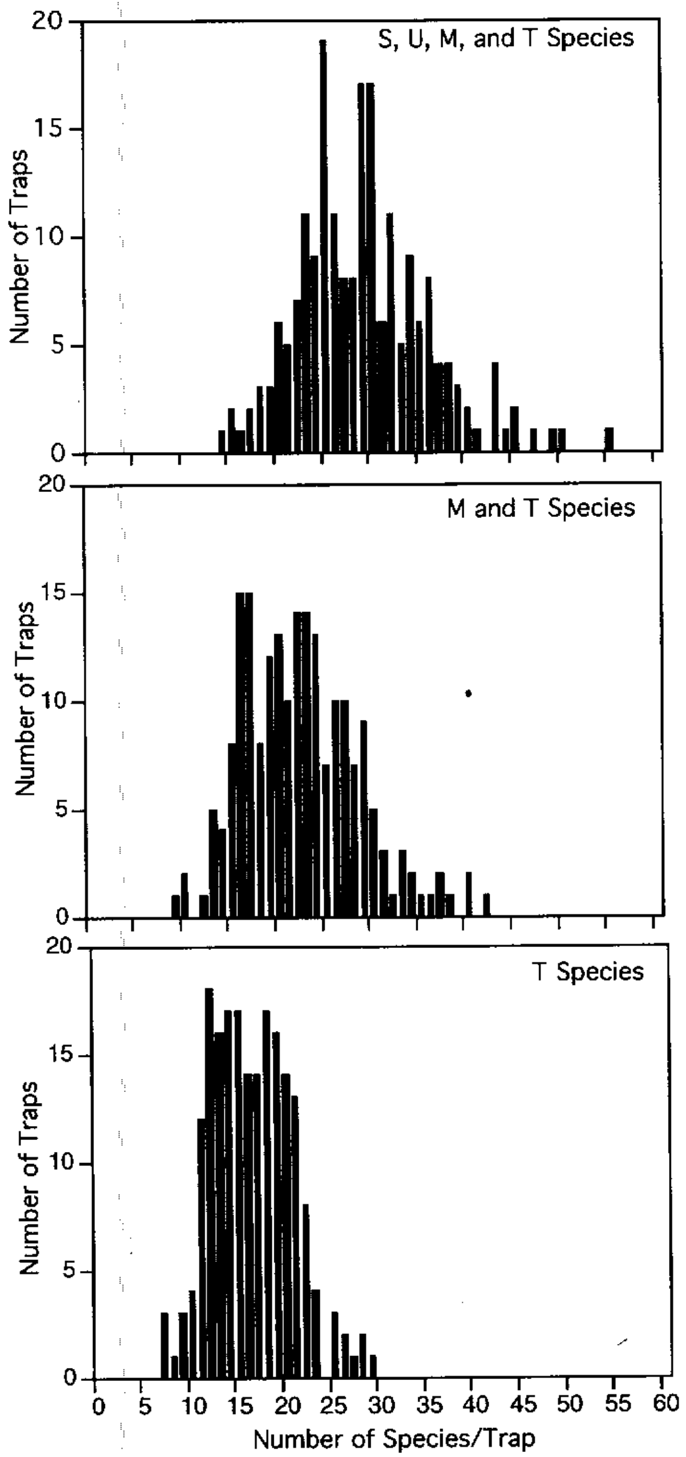


Figure 5.2 abc. Phenology trap contents by growth form for the period 1987-1994, inclusive.

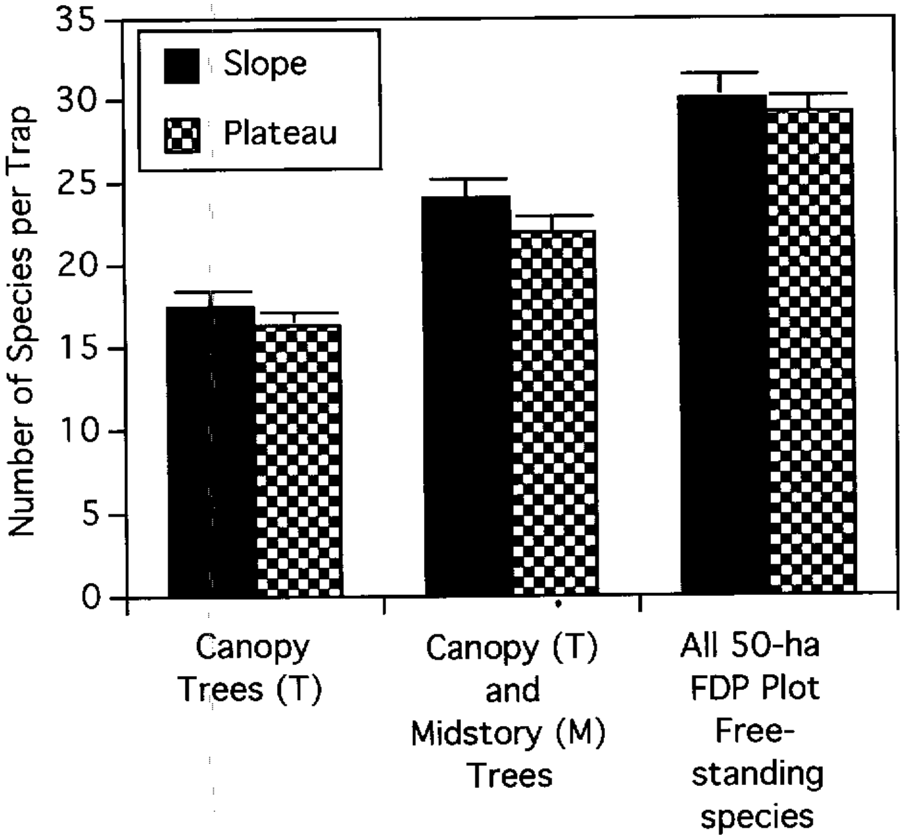


Figure 5.3. Comparison of the number of species found as seeds in phenology traps on the Slope and Low Plateau. N = 37 traps on Slope sites and N = 117 traps on the Low Plateau sites. Error bars show SE. See Appendix 1 for a list of species found within each growth form category.

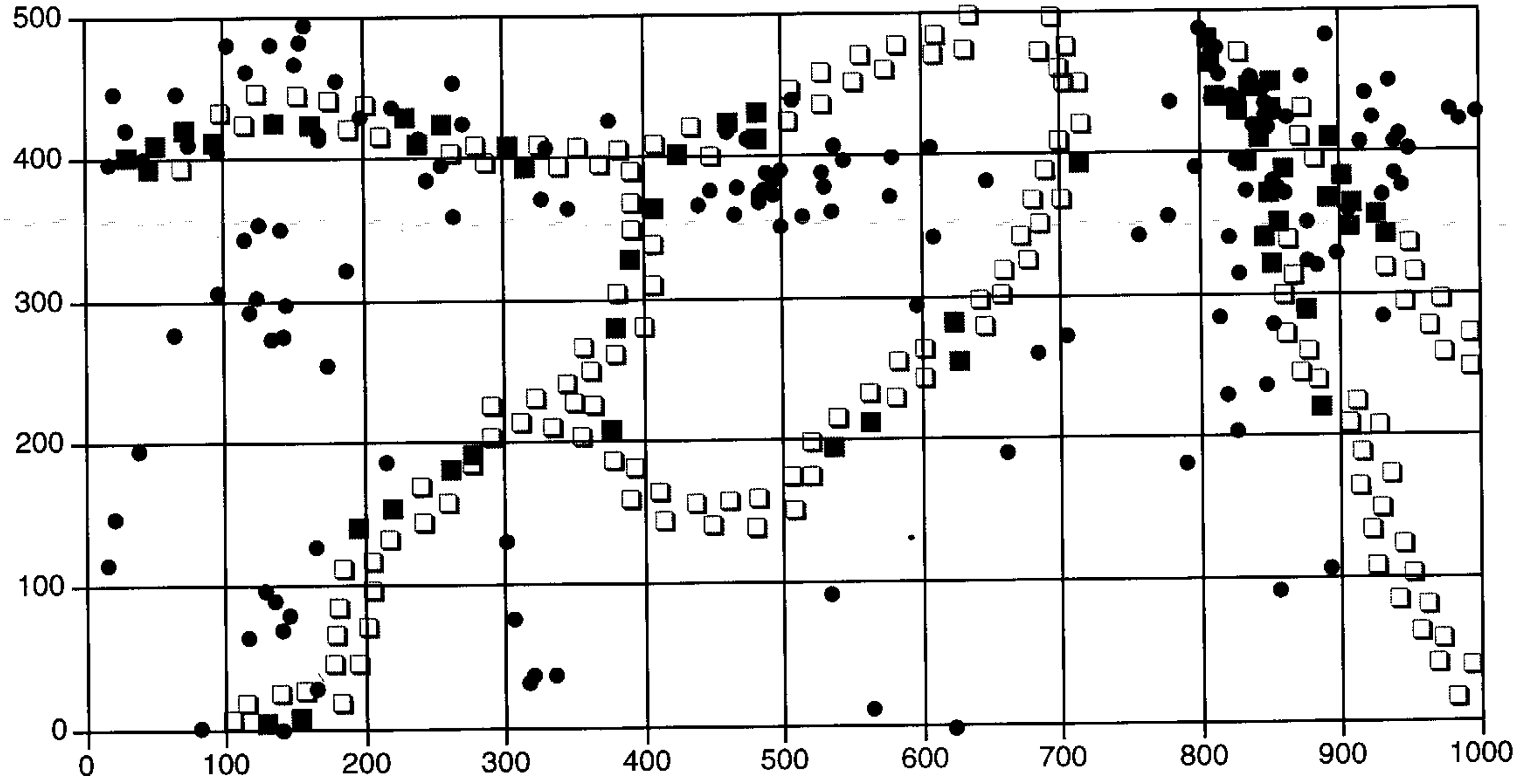


Figure 5.4. BEILPE trees ≥ 25-cm DBH in either the 1985 census or the 1990 census (solid circles), traps with at least one seed of BEILPE during the inclusive interval 1987-1994 (solid squares), and traps without any seeds of BEILPE during the same interval (open squares).

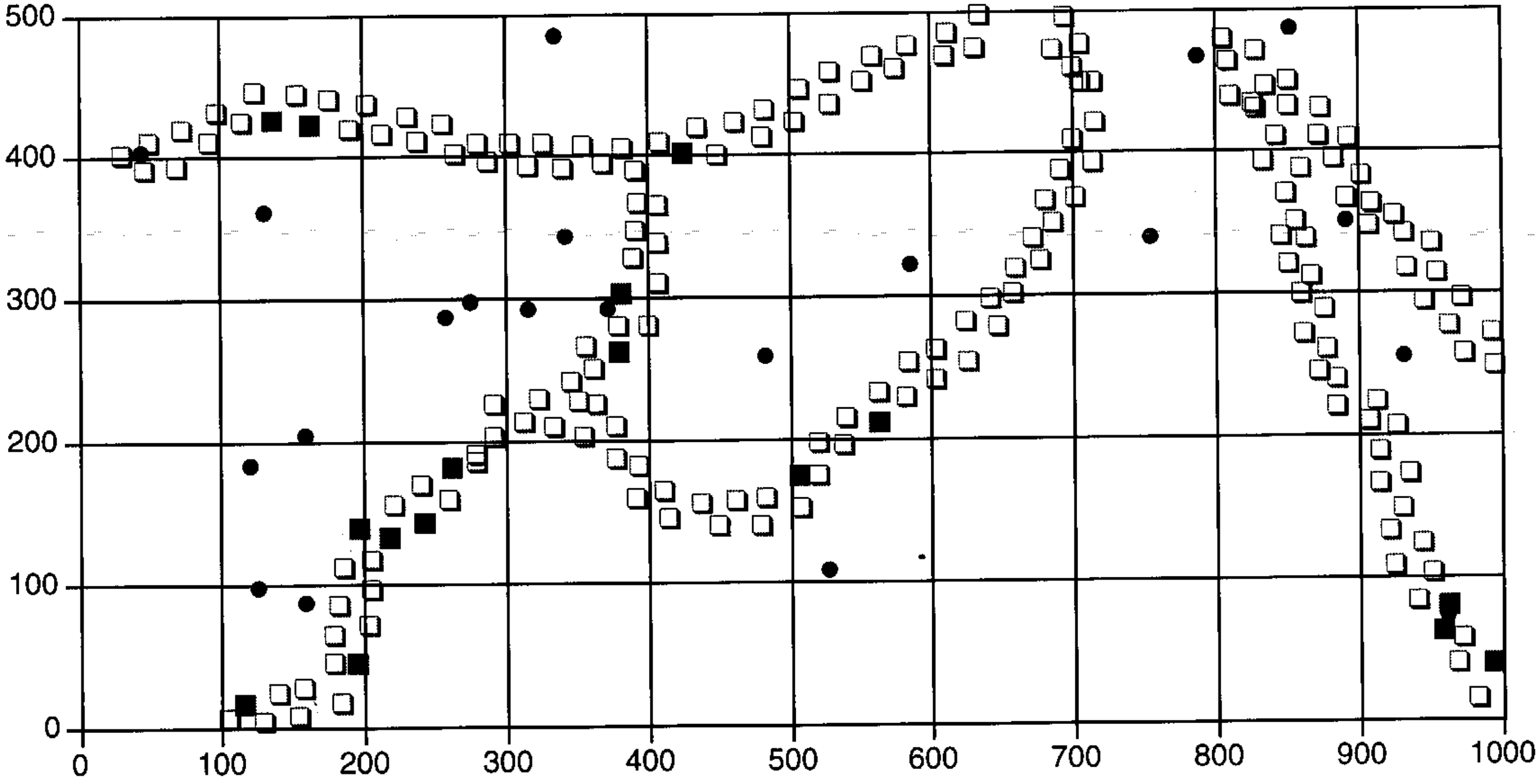


Figure 5.5. CALOLO trees ≥ 25-cm DBH in either the 1985 census or the 1990 census (solid circles), traps with at least one seed of CALOLO during the inclusive interval 1987-1994 (solid fruits), and traps without any seeds of CALOLO during the same interval (open squares).

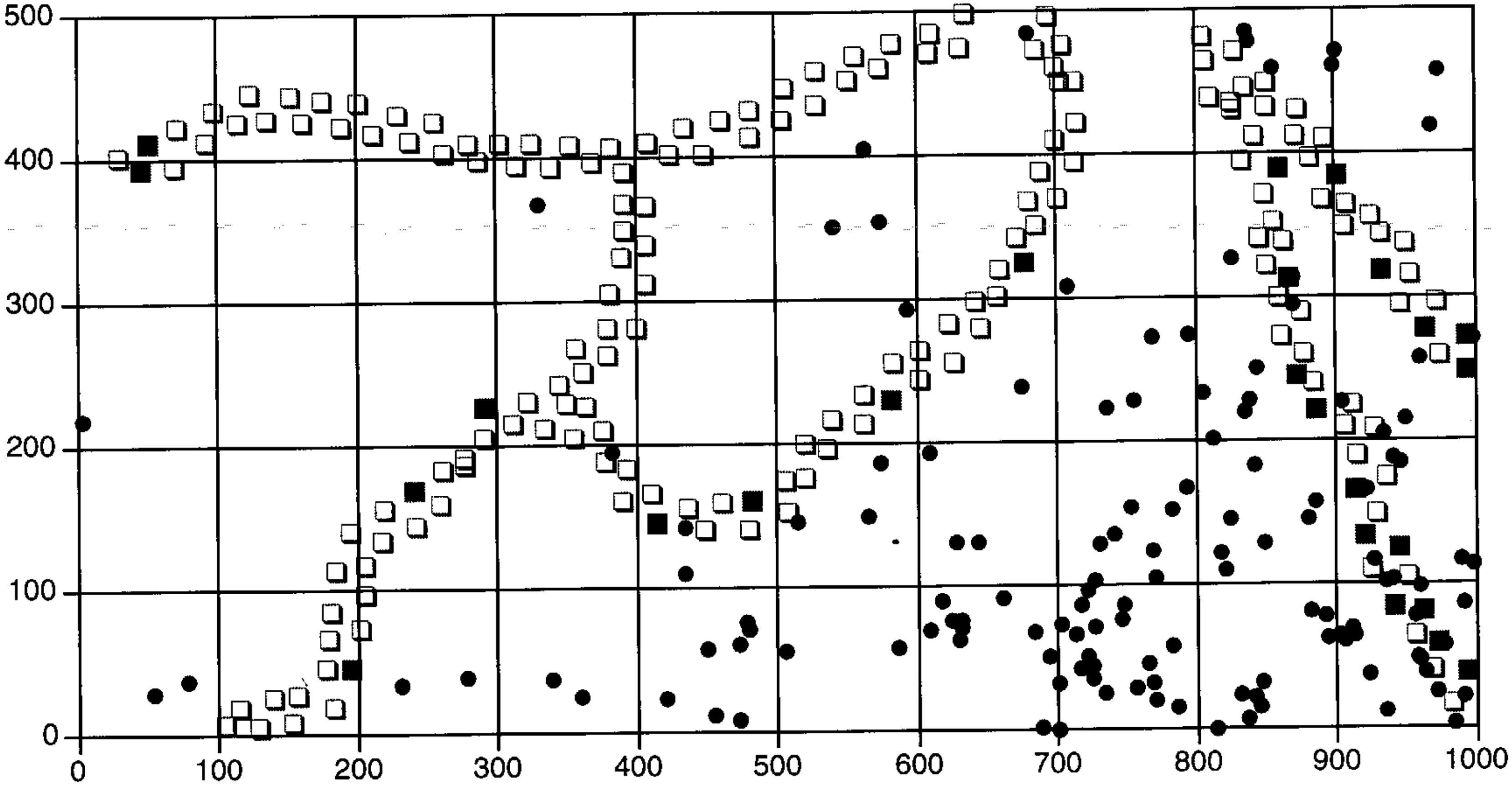


Figure 5.6. DRYPST trees ≥ 15-cm DBH in either the 1985 census or the 1990 census (solid circles), traps with at least one seed of DRYPST during the inclusive interval 1987-1994 (solid fruits), and traps without any seeds of DRYPST during the same interval (open squares).

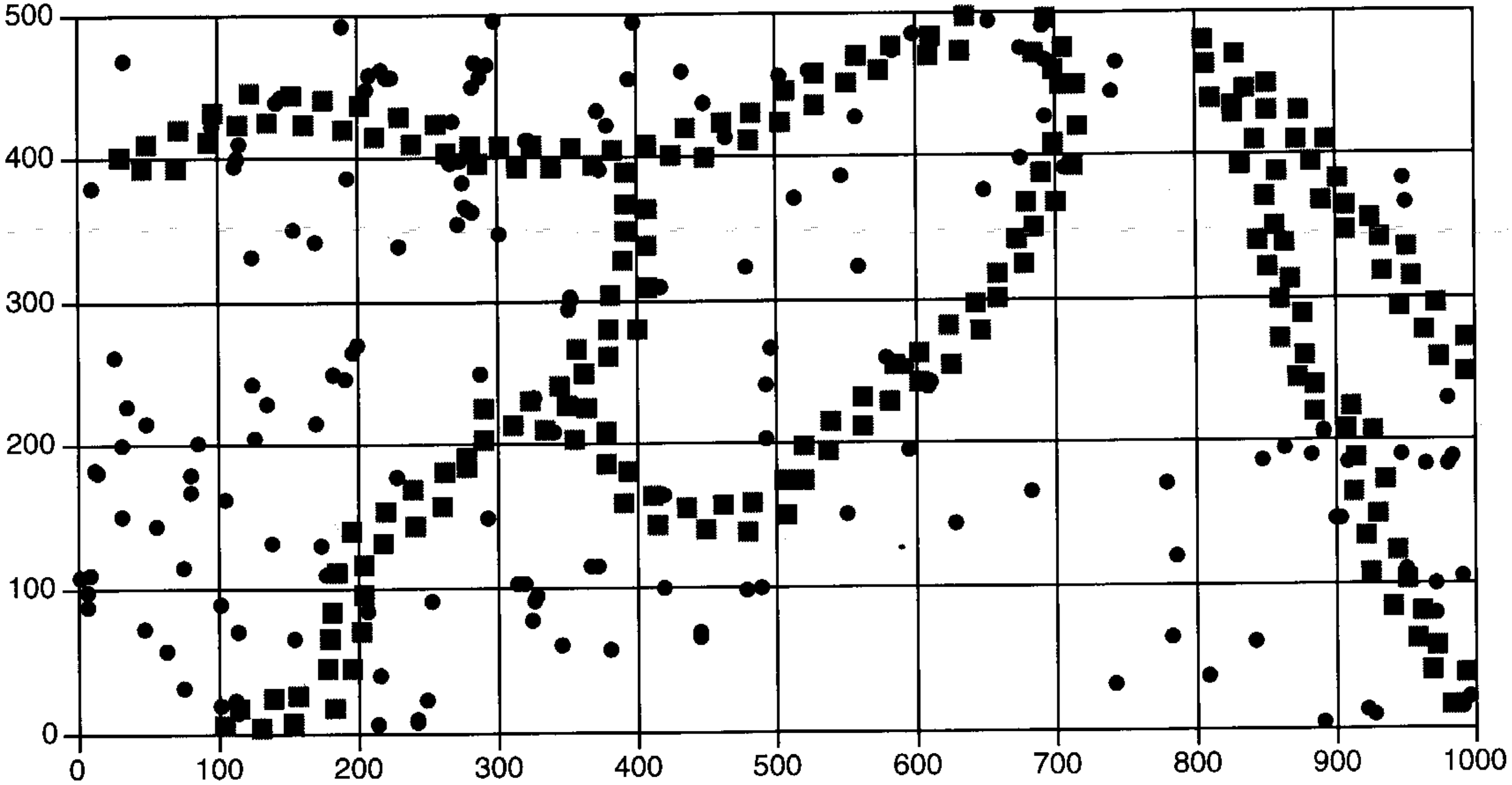


Figure 5.7. JAC1CO trees ≥ 25-cm DBH in either the 1985 census or the 1990 census (solid circles), traps with at least one seed of JAC1CO during the inclusive interval 1987-1994 (solid fruits), and traps without any seeds of JAC1CO during the same interval (open squares). Note that no traps went without seeds of JAC1CO during the trapping interval.

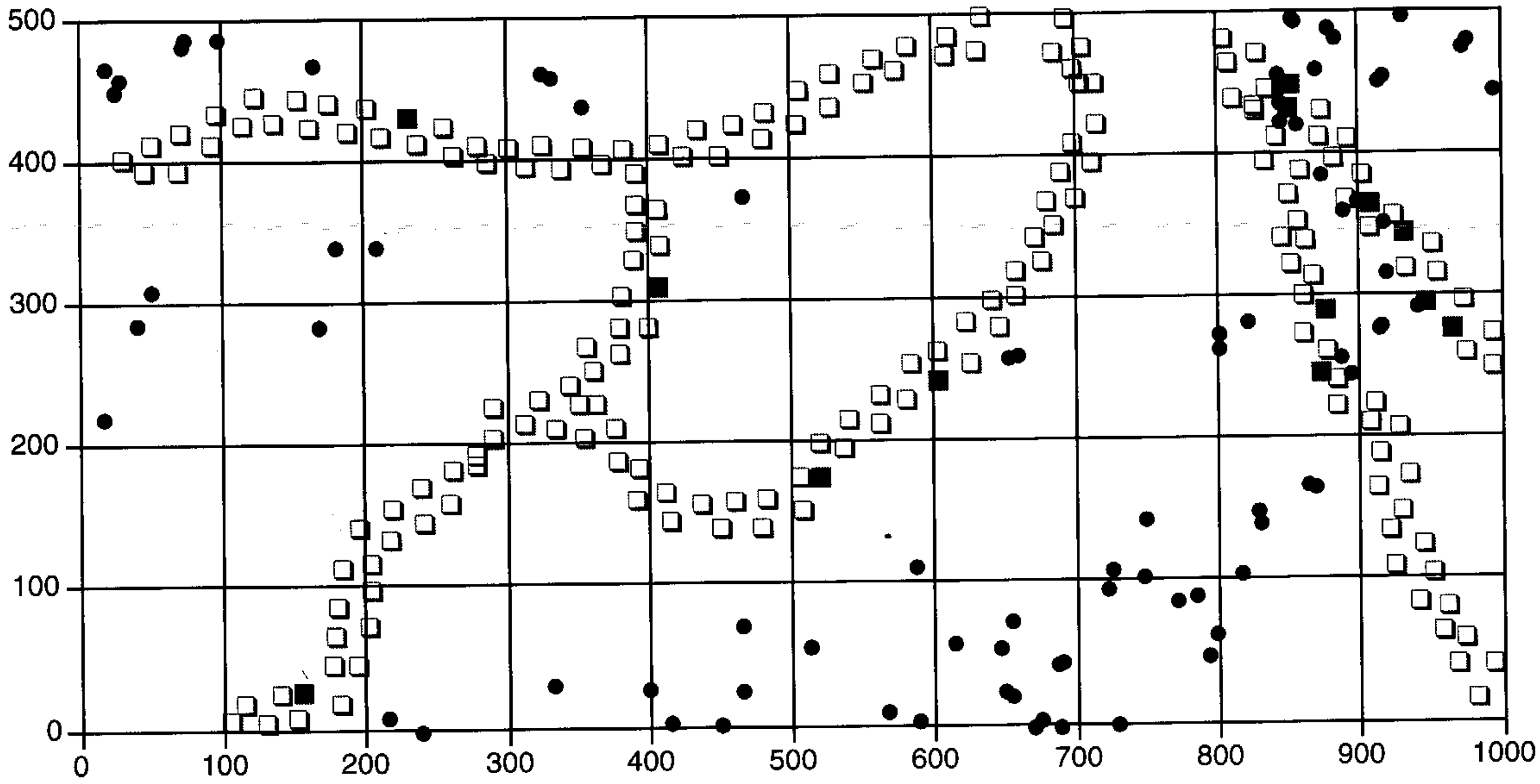


Figure 5.8. OCOTWH trees ≥ 25-cm DBH in either the 1985 census or the 1990 census (solid circles), traps with at least one seed of OCOTWH during the inclusive interval 1987-1994 (solid fruits), and traps without any seeds of OCOTWH during the same interval (open squares).

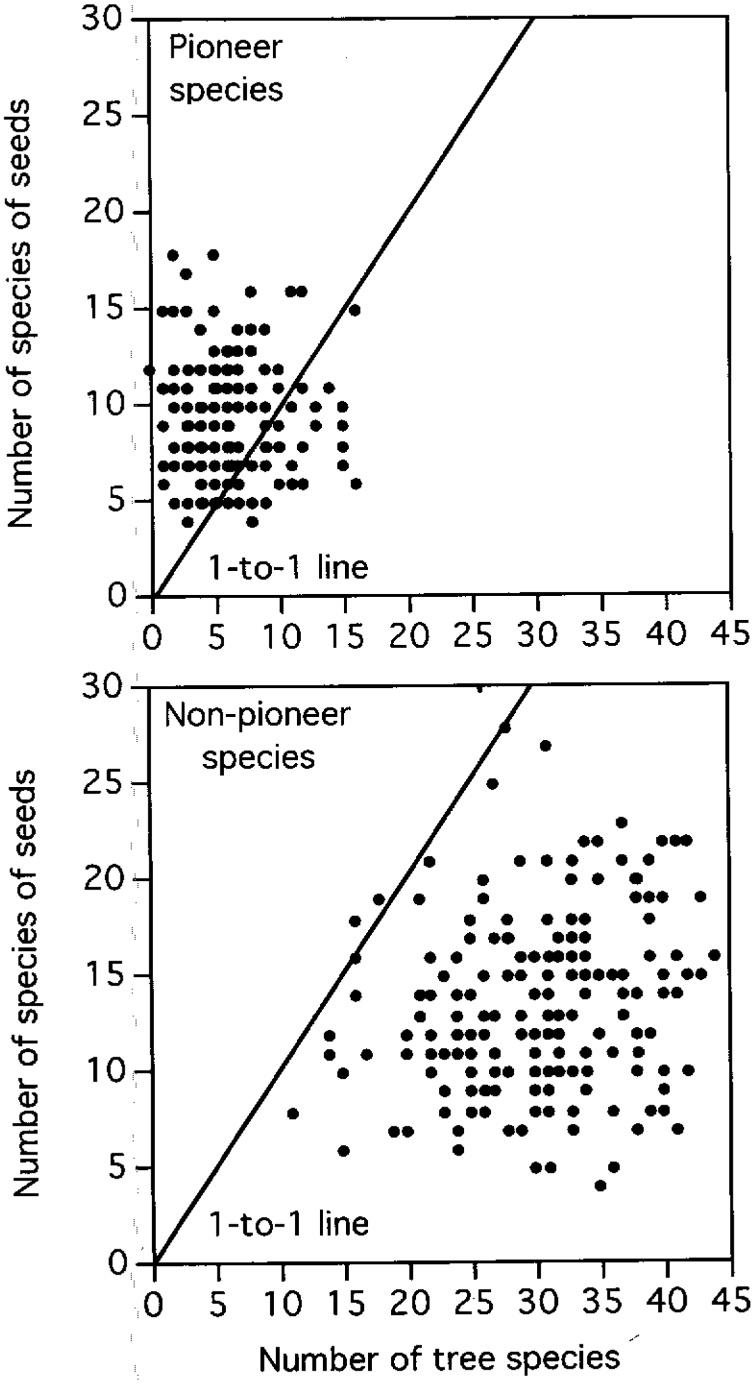


Figure 5.9 ab. Species-richness of seed-trap contents for pioneer versus non-pioneer midstory and canopy trees compared to the species-richness of each trap's tree-neighborhood, using all stems ≥ 1-cm DBH.

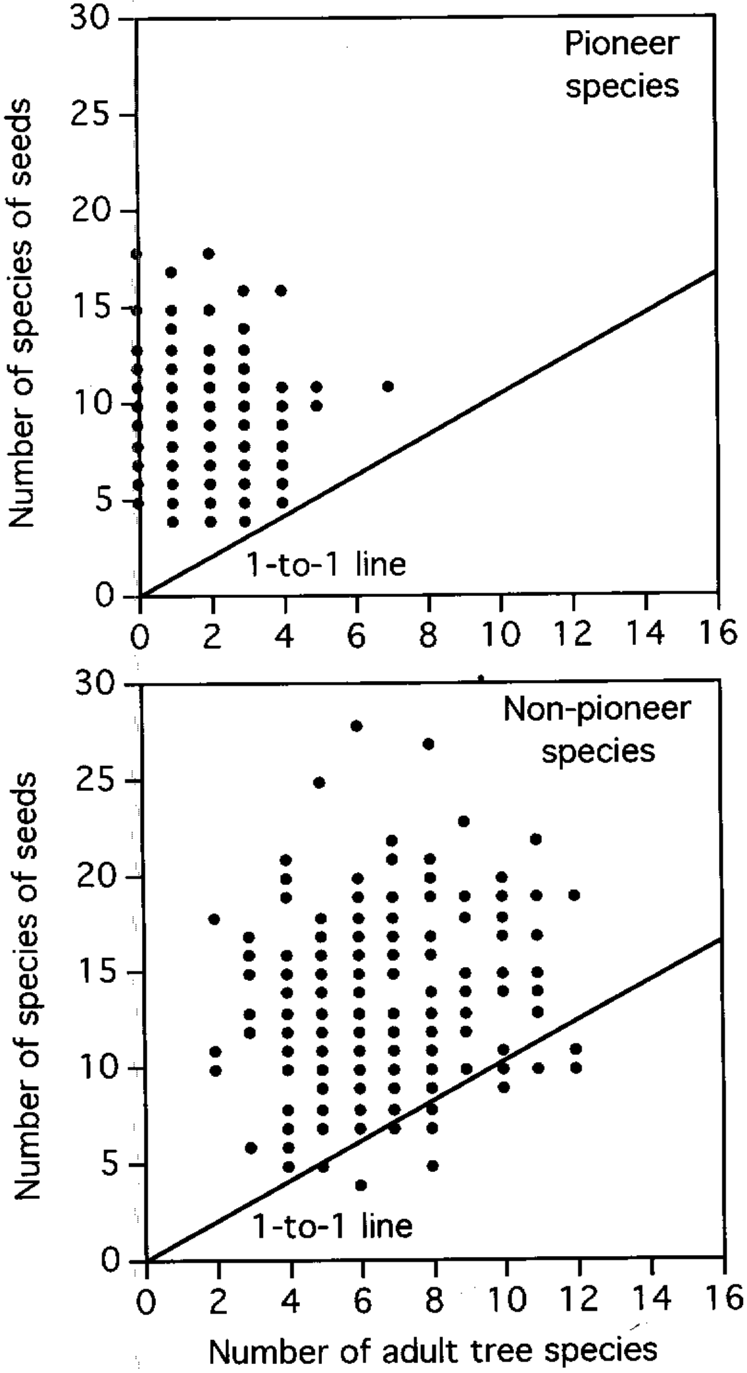


Figure 5.10 ab. Species-richness of seed-trap contents for pioneer versus non-pioneer midstory and canopy trees compared to the species-richness of each trap's adult tree-neighborhood.

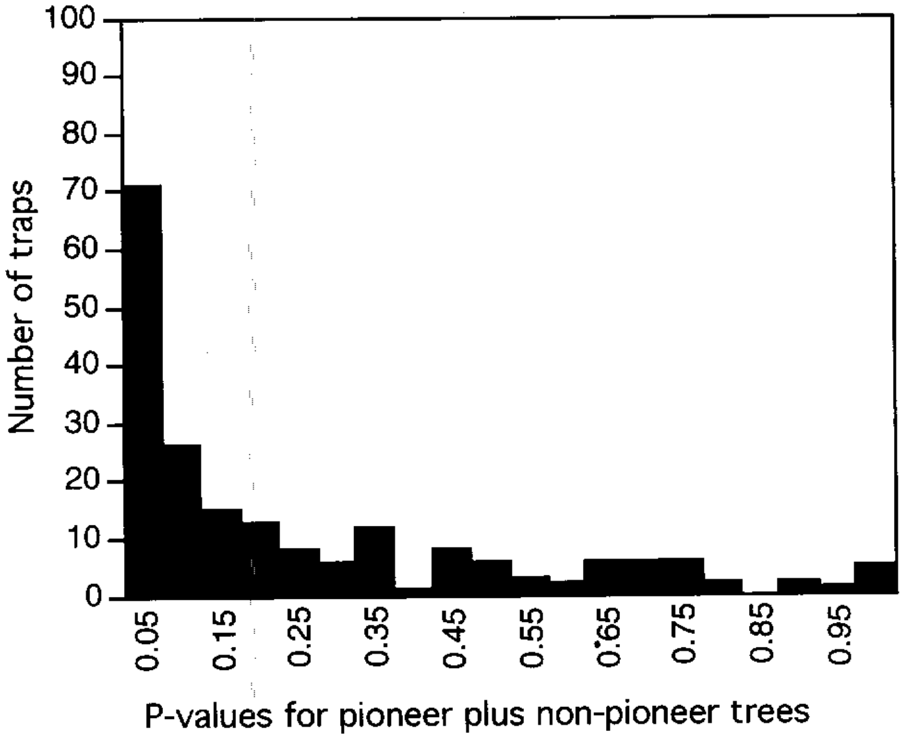


Figure 5.11. Frequency distribution of P-values for Jaccard's Similarity Index as a measure of the cross-correlation between trap-contents and adult tree-neighborhoods for the 200 seed-traps on the Forest Dynamics Project plot of Barro Colorado Island, Panamá. Each P-value is the probability that a Jaccard Index value as large or larger than that resulting from using the focal trap's own tree-neighborhood would arise by randomly sampling from among all other traps' tree-neighborhoods and calculating the Jaccard Index.

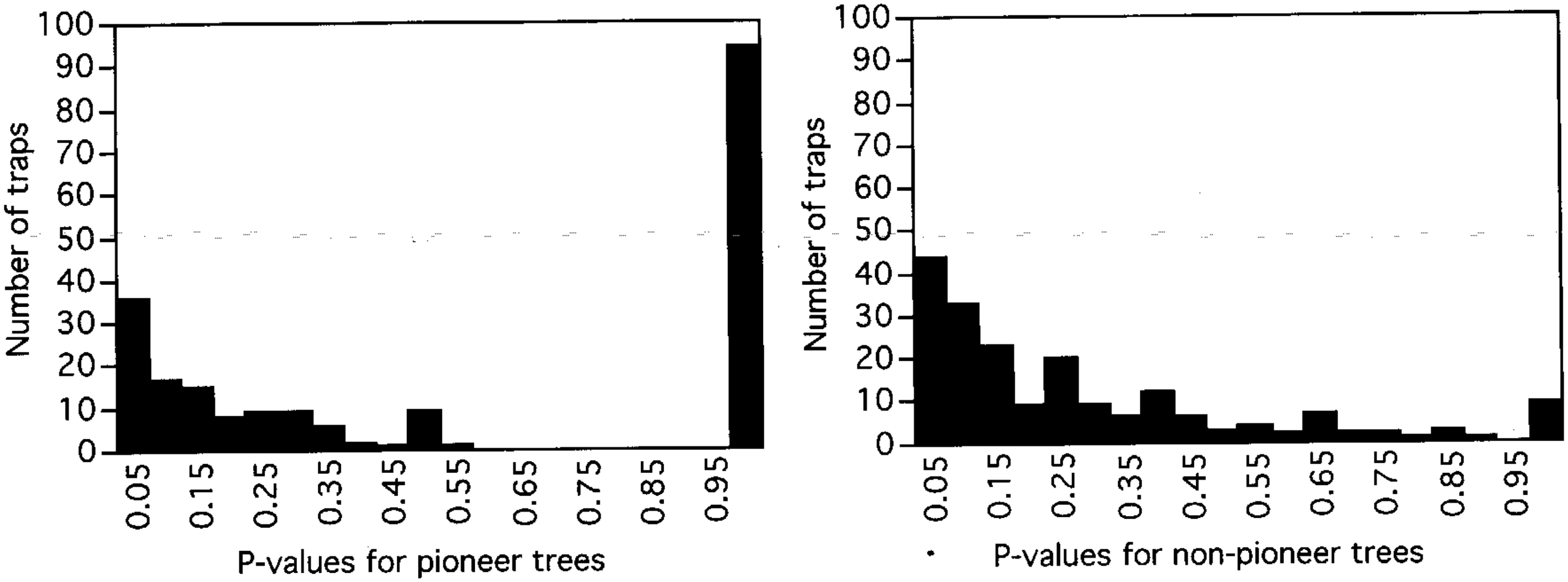
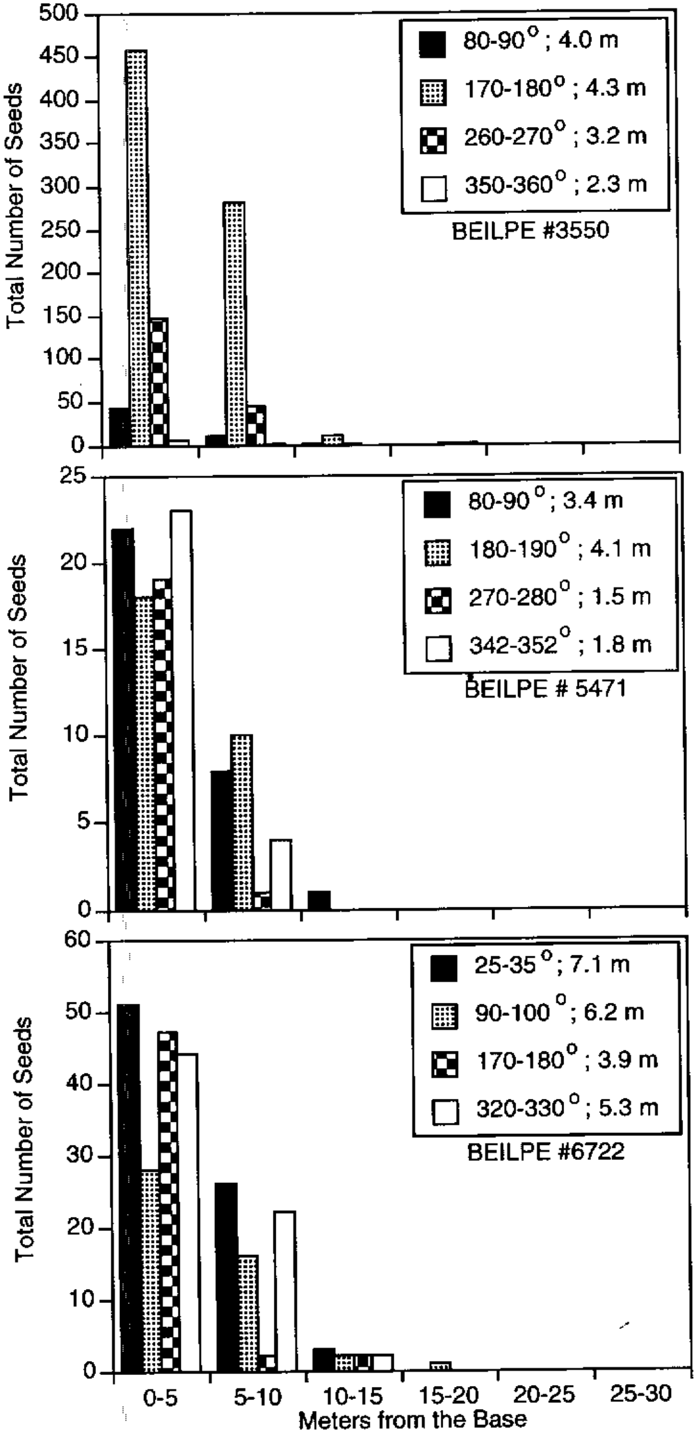
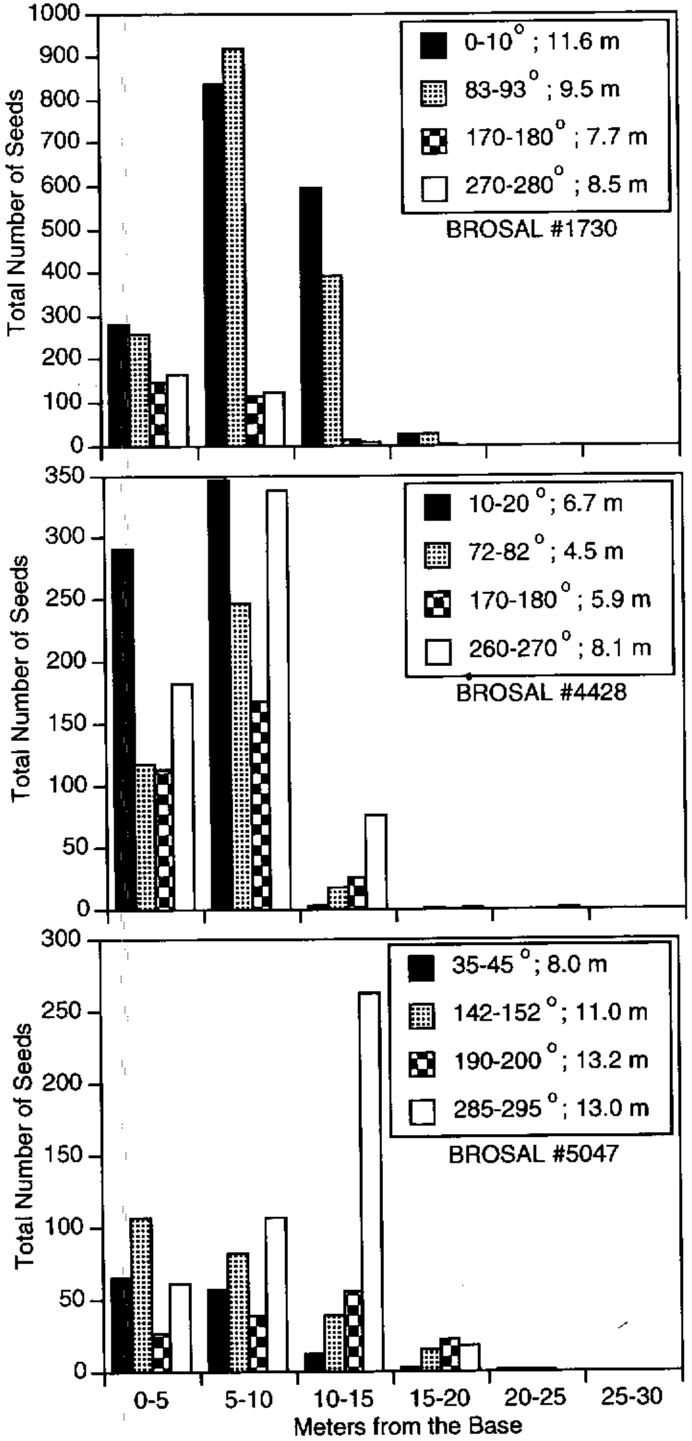


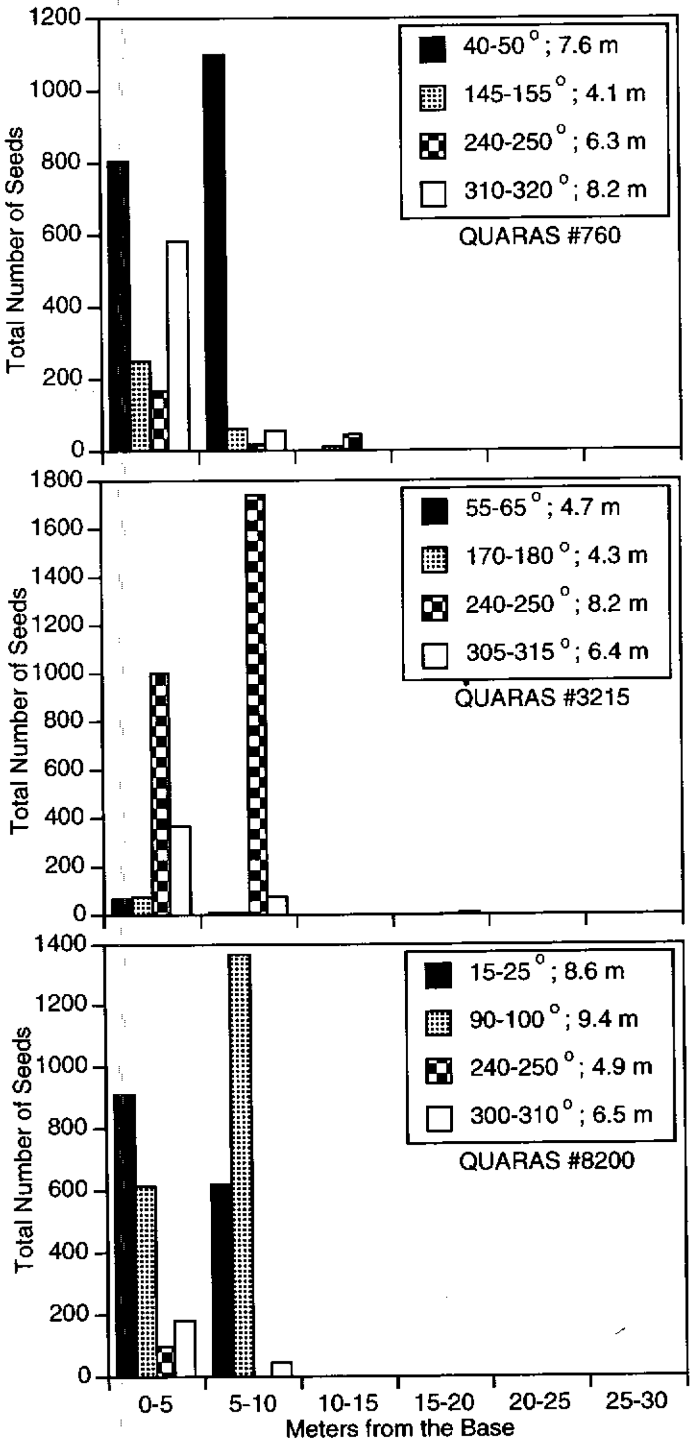
Figure 5.12 ab. Frequency distributions of P-values for Jaccard's Similarity Index as a measure of the cross-correlation between trap-contents and adult tree-neighborhoods for the 200 seed-traps on the Forest Dynamics Project plot of Barro Colorado Island, Panamá. Each P-value is the probability that a Jaccard Index value as large or larger than that resulting from using the focal trap's own tree-neighborhood would arise by randomly sampling from among all other traps' tree-neighborhoods and calculating the Jaccard Index.



Figures 5.13 abc. 10° seed dispersal transects from the bases of 3 separate individuals of BEILPE. Distances to the crown edge are given for each transect. The scale of the y-axis changes among figures.



Figures 5.14 abc. 10° seed dispersal transects from the bases of 3 separate individuals of BROSAL. Distances to the crown edge are given for each transect. The scale of the y-axis changes among figures.



Figures 5.15 abc. 10° seed dispersal transects from the bases of 3 separate individuals of QUARAS. Distances to the crown edge are given for each transect. The scale of the y-axis changes among figures.

LITERATURE CITED

Armesto, J. J., J. D. Mitchell & C. Villagran. 1986. A comparison of spatial patterns of trees in some tropical and temperate forests. Biotropica 18:1-11.

Ashton, P. Mark S., C. V. S. Gunatilleke & I. A. U. N. Gunatilleke. 1995. Seedling survival and growth of four *Shorea* species in a Sri Lankan rainforest. Journal of Tropical Ecology 11:263-279.

Ashton, Peter S. 1964. Ecological Studies in the Mixed Dipterocarp Forests of Brunei State. Oxford Forestry Memoirs 25:1-75.

Ashton, Peter S. 1969. Speciation among tropical forest trees: some deductions in light of recent evidence. Biological Journal of the Linnean Society 1;155-196.

Ashton, Peter S. 1977. A contribution of rain forest research to evolutionary theory. Annals of the Missouri Botanical Garden 64:694-705.

Augspurger, Carol K. 1983a. Offspring recruitment around tropical trees: Changes in cohort distance with time. Oikos 40:189-196.

Augspurger, Carol K. 1983b. Seed dispersal of the tropical tree, *Platypodium elegans*, and the escape of its seedlings from fungal pathogens. Journal of Ecology 71:759-771.

Augspurger, Carol K. 1984a. Light requirements of neotropical tree seedlings: A comparative study of growth and survival. Journal of Ecology 72:777-795.

Augspurger, Carol K. 1984b. Seedling survival of tropical tree seedlings: A comparative study of growth and survival. Journal of Ecology 77:777-796.

Augspurger, Carol K. 1984c. Seedling survival of tropical tree species: Interactions of dispersal distance, light-gaps, and pathogens. Ecology 65:1705-1712.

Austin, M. P., A. O. Nicholls & C. R. Margules. 1990. Measurement of the realized qualitative niche: Environmental niches of five *Eucalyptus* species. Ecological Monographs 60:161-177.

Basnet, Khadga. 1992. Effect of topography on the pattern of trees in Tabonuco (*Dacryodes excelsa*) dominated rain forest of Puerto Rico. Biotropica 24:31-42.

Bazzaz, F. A. 1991. Habitat selection in plants. The American Naturalist 137(Supplement):S116-S130.

Becker, Peter, Peter E. Rabenold, Jacquelyn R. Idol & Alan P. Smith. 1988. Water potential gradients for gaps and slopes in a Panamanian tropical moist forest's dry season. Journal of Tropical Ecology 4:173-184.

Black, G. A., Th. Dobzhansky & C. Pavan. 1950. Some attempts to estimate species diversity and population density of trees in Amazonian forests. Botanical Gazette 111:413-425.

Bormann, F. Herbert & Gene E. Likens. 1979. Pattern and Process in a Forested Ecosystem. Springer-Verlag, New York, NY, USA.

Brandani, Aldo, Gary S. Hartshorn & Gordon H. Orians. 1988. Internal heterogeneity of gaps and species richness in Costa Rican tropical wet forest. Journal of Tropical Ecology 4:99-19.

Bullock, Stephen H. 1992. Effects of sex, size and substrate on growth and mortality of trees in tropical wet forest. Oecologia 91:52-55.

Burger, William. 1992. Parapatric close-congeners in Costa Rica: Hypotheses for pathogen-mediated plant distribution and speciation. Biotropica 24:567-570.

Cavers, P. B. & J. L. Harper. 1967. Studies in the dynamics of plant populations. I. The fate of seed and transplants introduced into various habitats. Journal of Ecology 55:59-82.

Chambers, Jeanne C. & James A. MacMahon. 1994. A day in the life of a seed: Movements and fates of seeds and their implications for natural and managed systems. Annual Review of Ecology and Systematics 25:263-292.

Clark, David B. & Deborah A. Clark. 1985. Seedling dynamics of a tropical tree: Impacts of herbivory and meristem damage. Ecology 66:1884-1892.

Clark, David B. & Deborah A. Clark. 1987. Population ecology and microhabitat distribution of *Dipteryx panamensis*, a neotropical rain forest emergent tree. Biotropica 19:236-244.

Clark, Deborah A. & David B. Clark. 1984. Spacing dynamics of a tropial rain forest tree: Evaluation of the Janzen-Connell model. The American Naturalist 124:769-788.

Clark, Deborah A. & David B. Clark. 1992. Life history diversity of canopy and emergent trees in a Neotropical rain forest. Ecological Monographs 62:315-344.

Clark, Deborah A. & David B. Clark. 1994. Climate-induced annual variation in canopy tree growth in a Costa Rican tropical rain forest. Journal of Ecology 82:865-872.

Clark, James S. & Yuan Ji. 1995. Fecundity and dispersal in plant populations: Implications for structure and diversity. The American Naturalist 146:72-111.

Clinebell, Richard R., II, Oliver L. Phillips, Alwyn H. Gentry, Nellie Stark & Hans Zuuring. 1995. Prediction of neotropical tree and liana species richness from soil and climate data. Biodiversity and Conservation 4:56-90.

Colwell, Robert K. & Douglas J. Futuyma. 1971. On the measurement of niche breadth and overlap. Ecology 52:567-576.

Condit, Richard. 1995. Research in large, long-term tropical forest plots. Trends in Ecology and Evolution 10:18-22.

Condit, Richard. 1996. Defining and mapping vegetation types in mega-diverse tropical forests. Trends in Ecology and Evolution 11:4-5.

Condit, Richard, Stephen P. Hubbell & Robin B. Foster. 1992a. Recruitment near conspecific adults and the maintenance of tree and shrub diversity in a neotropical forest. The American Naturalist 140:261-286.

Condit, Richard, Stephen P. Hubbell & Robin B. Foster. 1992b. Short-term dynamics of a neotropical forest, change within limits. BioScience 42:822-828.

Condit, Richard, Stephen P. Hubbell & Robin B. Foster. 1993a. Identifying fast-growing native trees from the neotropics using data from a large, permanent census plot. Forest Ecology and Management 62:123-143.

Condit, Richard, Stephen P. Hubbell & Robin B. Foster. 1993b. Mortality and growth of a commercial hardwood, "El Cativo", *Prioria copaifera*, in Panama. Forest Ecology and Management 62:107-122.

Condit, Richard, Stephen P. Hubbell & Robin B. Foster. 1995. Mortality rates of 205 neotropical tree and shrub species and the impact of a severe drought. Ecological Monographs 65:419-439.

Condit, Richard, Suzanne Loo de Lao, Stephen P. Hubbell, Robin B. Foster & Egbert G. Leigh, Jr. *In press.* Microhabitat variation in tree diversity in a neotropical forest: Testing hypotheses about correlates of high diversity.

Connell, Joseph H. 1961. The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. Ecology 42:710-723.

Connell, Joseph H. 1971. On the role of enemies in preventing competitive exclusion in some marine animals and in rain forest trees. Pages 298-312 *in* P. J. den Boer and G. R. Gradwell, eds. Dynamics of Populations. Center for Agricultural Publication and Documentation, Wageningen, The Netherlands.

Connell, Joseph H. 1978. Diversity in tropical rain forests and coral reefs. Science 199:1302-1310.

Connell, Joseph H. 1980. Diversity and the coevolution of competitors, or the ghost of competition past. Oikos 35:131-138.

Cook, Robert Edward. 1979. Patterns of juvenile mortality and recruitment in plants. Pages 207-231 *in* O. T. Solbrig, S. Jain, G. B. Johnson, & P. H. Raven, eds. Topics in Plant Population Biology. Columbia University Press, New York, NY, USA.

Crawley, M. J. 1986. The structure of plant communities. Pages 1-50 *in* M. J. Crawley, ed. Plant Ecology. Blackwell Scientific Pubs., Oxford, UK. 496 pp.

Crawley, M. J. 1990. The population dynamics of plants. Philosophical Transactions of the Royal Society of London, Series B 330:125-140.

Croat, Thomas B. 1978. Flora of Barro Colorado Island. Stanford University Press, Stanford, CA, USA.

Curran, Lisa Marie. 1994. The ecology and evolution of mast-fruiting in Bornean Dipterocarpaceae: A general ectomycorrhizal theory. Ph.D. Dissertation, Princeton University, Princeton, NJ, USA.

Currie, David J. & Viviane Paquin. 1987. Large-scale biogeographical patterns of species richness of trees. Nature 329:326-327.

Denslow, Julie Sloan. 1980. Gap partitioning among tropical rainforest trees. Biotropica 12(Supplement):47-55.

De Steven, Diane. 1981. Predispersal seed predation in a tropical shrub (*Mabea occidentalis*, Euphorbiaceae). Biotropica 13:146-150.

De Steven, Diane. 1994. Tropical tree seedling dynamics: Recruitment patterns and their population consequences for three canopy species in Panamá. Journal of Tropical Ecology 10:369-383.

Dietrich, William E., Donald M. Windsor & Thomas Dunne. 1982. Geology, climate, and hydrology of Barro Colorado Island. Pages 21-46 *in* Egbert G. Leigh, Jr., A. Stanley Rand & Donald M. Windsor, eds. The Ecology of a Tropical Forest: Seasonal Rhythms and Long-term Changes. Smithsonian Institution Press, Washington, D. C., USA

Dixon, W. J. & F. J. Massey. 1969. Introduction to statistical analysis. Third edition. McGraw-Hill, New York, NY, USA.

Egler, Frank E. 1954. Vegetation science concepts. I. Initial floristic composition, a factor in old-field vegetation development. Vegetatio 4:412-417.

Eriksson, O. & J. Ehrlén. 1992. Seed and microsite limitation of recruitment in plant populations. Oecologia 91:360-364.

Fisher, Brian L., Henry F. Howe & S. Joseph Wright. 1991. Survival and growth of *Virola surinamensis* yearlings: Water augmentation in gap and understory. Oecologia 86:292-297.

Fleming, Theodore H. & E. Raymond Heithaus. 1981. Frugivorous bats, seed shadows, and the structure of tropical forests. Biotropica 13(Supplement):45-53.

Forget, Pierre-Michel. 1992. Seed removal and seed fate in *Gustavia superba* (Lecythidaceae). Biotropica 24:408-414.

Foster, Robin B. & Nicholas V. L. Brokaw. 1982. Structure and history of the vegetation of Barro Colorado Island. Pages 67-81 *in* E. G. Leigh, Jr., A. S. Rand, and D. M. Windsor, eds. The Ecology of a Tropical Forest: Seasonal Rhythms and Long-term Changes. Smithsonian Institution Press, Washington, D.C., USA.

Foster, Susan A. & Charles H. Janson. 1985. The relationship between seed size and establishment conditions in tropical woody plants. Ecology 66:773-780.

Futuyma, Douglas J. & Gabriel Moreno. 1988. The evolution of ecological specialization. Annual Review of Ecology & Systematics 19:207-233.

Gartlan, J. S., D. McC. Newbery, D. W. Thomas & P. G. Waterman. 1986. The influence of topography and soil phosphorus on the vegetation of Korup Forest Reserve, Cameroun. Vegetatio 65:131-148.

Gause, G. F. 1934. The Struggle for Existence. Williams & Wilkins, Baltimore, MD, USA.

Gentry, Alwyn H. 1988a. Changes in plant community diversity and floristic composition on environmental and geographical gradients. Annals of the Missouri Botanical Garden 75:1-34.

Gentry, Alwyn H. 1988b. Tree species richness of upper Amazonian forests. Proceedings of the National Academy of Sciences, USA. 85:156-159.

Gentry, Alwyn H. 1992. Tropical forest biodiversity: Distributional patterns and their conservational significance. Oikos 63:19-28.

Gilbert, Gregory S., Stephen P. Hubbell & Robin B. Foster. 1994. Density and distance-to-adult effects of a canker disease of trees in a moist tropical forest. Oecologia 98:100-108.

Gillett, J. B. 1962. Pest pressure, an underestimated factor in evolution. Systematics Association Publication 4:37-46.

Gleason, H. A. 1926. The individualistic concept of the plant association. Bulletin of the Torrey Botanical Club 53:7-26.

Goldberg, Deborah E. 1982. The distribution of evergreen and deciduous trees relative to soil type: An example from the Sierra Madre, Mexico, and a general model. Ecology 63:942-951.

Goldberg, Deborah E. 1985. Effects of soil pH, competition, and seed predation on the distributions of two tree species. Ecology 66:503-511.

Greene, D. F. & E. A. Johnson. 1996. Wind dispersal of seeds from a forest into a clearing. Ecology 77:595-609.

Greig-Smith, P. 1952. Ecological observations on degraded and secondary forest in Trinidad, British West Indies. II. Structure of the communities. Journal of Ecology 40:316-330.

Greig-Smith, P. 1983. Quantitative Plant Ecology, Third Edition. Blackwell Scientific Publications, Oxford, UK.

Hamill, David N. 1986. Selected studies on population dispersion, and species richness. Ph.D. Thesis, The University of Iowa, Iowa City, IA, USA.

Hardin, Garrett. 1960. The competitive exclusion principle. Science 131:1292-1297.

Harper, John L. 1977. Population Biology of Plants. Academic Press, London, UK.

Harper, J. L. & J. White. 1974. The demography of plants. Annual Review of Ecology and Systematics 5:419-463.

Hartshorn, Gary S. 1980. Neotropical forest dynamics. Biotropica (Supplement) 12:23-30.

Hartshorn, Gary S. 1990. An overview of Neotropical forest dynamics. Pages 585-599 *in* A. H. Gentry, ed. Four Neotropical Rainforests. Yale University Press, New Haven, CT, USA.

Hastings, Alan. 1980. Disturbance, coexistence, history, and competition for space. Theoretical Population Biology 18:363-373.

Hoppes, William G. 1988. Seedfall patterns of several species of bird-dispersed plants in an Illinois woodland. Ecology 69:320-329.

Horn, Henry S. 1975. Markovian properties of forest succession. Pages 196-211 *in* M. L. Cody and J. M. Diamond, eds. Ecology and Evolution of Communities. Harvard University Press, Cambridge, MA, USA.

Horn, Henry S. 1981. Some causes of variety in patterns of secondary succession. Pages 24-35 *in* D. C. West, H. H. Shugart and D. B. Botkin, eds. Forest Succession: Concepts and Application. Springer-Verlag, New York, NY, USA.

Horn, Henry S. & Robert H. MacArthur. 1972. Competition among fugitive species in a harlequin environment. Ecology 53:749-752.

Houle, G. 1992. Spatial relationship between seed and seedling abundance and mortality in a deciduous forest of northeastern North America. Journal of Ecology 80:99-108.

Howe, Henry F. 1986. Consequences of seed dispersal by birds: A case study from Central America. Journal of the Bombay Natural History Society 83(Supplement):19-42.

Howe, Henry F. 1990a. Seed dispersal by birds and mammals: Implications for seedling demography. Pages 191-218 *in* K. S. Bawa and M. Hadley, eds. Reproductive Ecology of Tropical Forest Plants. Volume 7, Man and the Biosphere Series, UNESCO, Paris, France.

Howe, Henry F. 1990b. Survival and growth of juvenile *Virola surinamensis* in Panama: Effects of herbivory and canopy closure. Journal of Tropical Ecology 6:259-280.

Howe, Henry F. & Lynn C. Westley. 1986. Ecology of pollination and seed dispersal. Pages 185-216 *in* M. J. Crawley, ed. Plant Ecology. Blackwell Scientific Publications, Oxford, UK.

Hubbell, Stephen P. 1979. Tree dispersion, abundance, and diversity in a tropical dry forest. Science 203:1299-1309.

Hubbell, Stephen P. 1995. Towards a theory of biodiversity and biogeography on continuous landscapes. Pages 171-199 *in* G. R. Carmichael, G. E. Folk and J. L. Schnoor, eds. Preparing for Global Change: A Midwestern Perspective. SPB Academic Publishing, Amsterdam, The Netherlands.

Hubbell, Stephen P. *In press.* A unified theory of biogeography and relative species abundance.

Hubbell, Stephen P. *In press.* A unified theory of biogeography and relative species abundance and its application to tropical rain forests and coral reefs. A Symposium on Coral Reefs.

Hubbell, Stephen P. & Robin B. Foster. 1983. Diversity of canopy trees in a neotropical forest and implications for conservation. Pages 25-41 *in* S. J. Sutton, T. C. Whitmore & A. C. Chadwick, eds. Tropical Rain Forest: Ecology and Management. Blackwell Scientific Publications, Oxford, UK.

Hubbell, Stephen P. & Robin B. Foster. 1986a. Biology, chance, and history and the structure of tropical rain forest tree communities. Pages 314-329 *in* J. Diamond and T. J. Case, eds. Community Ecology. Harper and Row, New York, NY, USA.

Hubbell, Stephen P. & Robin B. Foster. 1986b. Canopy gaps and the dynamics of a neotropical forest. Pages 77-96 *in* M. J. Crawley, ed. Plant Ecology. Blackwell Scientific Publications, Oxford, UK.

Hubbell, Stephen P. & Robin B. Foster. 1986c. Commonness and rarity in a neotropical forest: Implications for tropical tree conservation. Pages 205-231 *in* M. E. Soulé, ed. Conservation Biology: The Science of Scarcity and Diversity. Sinauer Associates, Sunderland, MA, USA.

Hubbell, Stephen P. & Robin B. Foster. 1990a. Structure, dynamics, and equilibrium status of old-growth forest on Barro Colorado Island. Pages 522-541 *in* A. H. Gentry, ed. Four Neotropical Rainforests. Yale University Press, New Haven, CT, USA.

Hubbell, Stephen P. & Robin B. Foster. 1990b. The fate of juvenile trees in a neotropical forest: Implications for the natural maintenance of tropical tree diversity. Pages 317-341 *in* and K. S. Bawa & M. Hadley, eds. Reproductive Ecology of Tropical Forest Plants. Parthenon Publishing, NJ, USA.

Hubbell, Stephen P. & Robin B. Foster. 1992. Short-term dynamics of a neotropical forest: Why ecological research matters to tropical conservation and management. Oikos 63:48-61.

Hubbell, Stephen P., Robin B. Foster, Richard Condit & Benjamin Wechsler. *In press.* Light gaps and tree diversity in a Neotropical forest.

Hurtt, George C. & Stephen W. Pacala. 1995. The consequences of recruitment limitation: Reconciling chance, history and competitive differences between plants. Journal of Theoretical Biology 176:1-12.

Huston, Michael A. 1979. A general hypothesis of species diversity. The American Naturalist 113:81-101.

Huston, Michael Alan. 1994. Biological Diversity: The Coexistence of Species on Changing Landscapes. Cambridge University Press, Cambridge, UK.

Hutchinson, G. E. 1951. Copepodology for the ornithologist. Ecology 32:571-577.

Hutchinson, G. E. 1957. Concluding remarks. Cold Spring Harbor Symposium on Quantitative Biology 22:415-427.

Hutchinson, G. E. 1961. The paradox of the plankton. The American Naturalist 95:137-145.

Jackson, James F. 1981. Seed size as a correlate of temporal and spatial patterns of seed fall in a neotropical forest. Biotropica 13:121-130.

Janos, David P. 1980. Vesicular-arbuscular mycorrhizae affect lowland tropical rain forest plant growth. Ecology 61:151-162.

Janzen, D. H. 1970. Herbivores and the number of tree species in tropical forests. The American Naturalist 104:501-528

Janzen, D. H. 1971. Seed predation by animals. Annual Review of Ecology and Systematics 2:465-492.

Janzen, D. H. 1978a. A bat-generated fig seed shadow in rainforest. Biotropica 10:121.

Janzen, D. H. 1978b. Seeding patterns of tropical trees. Pages 83-128 *in* P. B. Tomlinson and M. H. Zimmermann, eds. Tropical Trees as Living Systems. Cambridge University Press, Cambridge, UK.

Janzen, D. H. 1978c. The size of a local peak in a seed shadow. Biotropica 10:78.

Janzen, D. H., G. A. Miller, J. Hackforth-Jones, C. M. Pond, K. Hooper & D. P. Janos. 1976. Two Costa Rican bat-generated seed shadows of *Andira inermis* (Leguminosae). Ecology 57:1068-1075.

Jeffries, M. J. & J. H. Lawton. 1984. Enemy free space and the structure of ecological communities. Biological Journal of the Linnean Society 23:269-286.

Johnsson, Mark J. & Robert F. Stallard. 1989. Physiographic controls on the composition of sediments derived from volcanic and sedimentary terrains on Barro Colorado Island, Panama. Journal of Sedimentary Petrology 59:768-781.

Kitajima, Kaoru. & Carol K. Augspurger. 1989. Seed and seedling ecology of a monocarpic tropical tree, *Tachigalia versicolor*. Ecology 70:1102-1114.

Kobe, Richard K. 1996. Intraspecific variation in sapling mortality and growth predicts geographic variation in forest composition. Ecological Monographs 66:181-201.

Kwan, Wong Yew & T. C. Whitmore. 1970. On the influence of soil properties on species distribution in a Malayan lowland dipterocarp rain forest. The Malayan Forester 33:42-54.

Latham, Roger E. 1992. Co-occurring tree species change rank in seedling performance with resources varied experimentally. Ecology 73:2129-2144.

Leduc, A., P. Drapeau, Y. Bergeron & P. Legendre. 1992. Study of spatial components of forest cover using partial Mantel tests and path analysis. Journal of Vegetation Science 3:69-78.

Legendre, Pierre. 1993. Spatial autocorrelation: Trouble or new paradigm? Ecology 74:1659-1673.

Leigh, Egbert G., Jr. 1996. Epilogue: Research on Barro Colorado Island, 1980-94. Pp. 469-503 *in* Egbert G. Leigh, Jr., A. Stanley Rand, and Donald M. Windsor, eds. The Ecology of a Tropical Forest: Seasonal Rhythms and Long-term Changes, Second Edition. Smithsonian Institution Press, Washington, D. C., USA.

Leigh, E. G., Jr., A. S. Rand & D. M. Windsor (Eds.). 1982. The Ecology of a Tropical Forest: Seasonal Rhythms and Long-term Changes. Smithsonian Institution Press, Washinton, D. C., USA.

Leigh, E. G., Jr., A. S. Rand & D. M. Windsor (Eds.). 1990. Ecología de un Bosque Tropical: Ciclos estacionales y cambios a largo plazo. Smithsonian Institution Press, Washington, D. C., USA.

Leigh, E. G., Jr. D. M. Windsor, A. Stanley Rand & Robin B. Foster. 1990. The impact of the "El Niño" drought of 1982-83 on a Panamanian semideciduous forest. *In* P. W. Glynn, ed. Global Ecological Consequences of the 1982-83 El Niño-Southern Oscillation. Elsevier, NY, NY, USA.

Levin, Donald A. 1984. Immigration in plants: An exercise in the subjunctive. Pages 242-260 *in* R. Dirzo & J. Sarukhán, eds. Perspectives on Plant Population Ecology. Sinauer Associates, Sunderland, MA, USA.

Lewin, R. 1986. Supply-side ecology. Science 234:25-27.

Lieberman, Milton & Diana Lieberman. 1994. Patterns of density and dispersion of forest trees. Pages 106-119 *in* L. A. McDade, K. S. Bawa, H. A. Hespenheide and G. S. Harshorn, eds. La Selva: Ecology and Natural History of a Neotropical Rain Forest. University of Chicago Press, Chicago, IL, USA.

Lieberman, Milton, Diana Lieberman, G. S. Hartshorn & Roldolfo Peralta. 1985. Small-scale altitudinal variation in lowland wet tropical forest vegetation. Journal of Ecology 73:505-516.

Lieberman, Milton, Diana Lieberman, Rodolfo Peralta & Gary S. Harshorn. 1995. Canopy closure and the distribution of tropical forest tree species at La Selva, Costa Rica. Journal of Tropical Ecology 11:161-178.

Loiselle, Bette A., Eric Ribbens & Orlando Vargas. 1996. Spatial and temporal variation of seed rain in a tropical lowland wet forest. Biotropica 28:82-95.

Losos, Elizabeth C. 1993. The influence of seed dispersal on primary forest succession in an Amazonian floodplain forest. Ph.D. Dissertation, Princeton University, Princeton, NJ, USA.

Losos, Elizabeth C. 1995. Habitat specificity of two palm species: Experimental transplantation in Amazonian successional forests. Ecology 76:2595-2606.

Louda, Svata M. 1982a. Limitation of the recruitment of the shrub *Haplopappus squarrosus* (Asteraceae) by flower- and seed-feeding insects. Journal of Ecology 70:43-53.

Louda, Svata M. 1982b. Distribution ecology: Variation in plant recruitment over a gradient in relation to insect seed predation. Ecological Monographs 52:25-41.

MacArthur, Robert H. 1972. Geographical Ecology. Princeton University Press, Princeton, NJ, USA.

Magurran, Anne E. 1988. Ecological Diversity and its Measurement. Princeton University Press. Princeton, NJ, USA.

Matlack, Glenn R. 1994. Plant species migration in a mixed-history forest landscape in eastern North America. Ecology 75:1491-1502.

Meehan, Thomas E., Philip W. Rundel, Richard Ambrose, Gail Baker & Ann Rappaport. 1977. The influence of intense selective browsing by pocket mice (*Perognathus*) on the spatial distribution of *Polygala deserticum* in Baja California. American Midland Naturalist 97:489-495.

Molofsky, Jane & Carol K. Augspurger. 1992. The effect of leaf litter on early seedling establishment in a tropical forest. Ecology 73:68-77.

Molofsky, Jane & Brian L. Fisher. 1993. Habitat and predation effects on seedling survival and growth in shade-tolerant tropical trees. Ecology 74:261-265.

Murawski, Darlyne A. and James L. Hamrick. 1992. The mating system of Cavanillesia platanifolia under extremes of flowering-tree density: A test of predictions. Biotropica 24:99-101.

Mustart, Penelope J. & Richard M. Cowling. 1993. The role of regeneration stages in the distribution of edaphically restricted Fynbos Proteaceae. Ecology 74:1490-1499.

Neilson, R. P. & L. H. Wullstein. 1983. Biogeography of two southeast American oaks in relation to atmosphere dynamics. Journal of Biogeography 10:275-297.

O'Brien, Sean T. 1994. Guilds, structure and dynamics in the forest on Barro Colorado Island, Panama. Ph.D. Dissertation, University of Virginia, Charlottesville, VA, USA.

Oliveira-Filho, Ary T., James A. Ratter & George J. Shepherd. 1990. Floristic composition and community structure of a central Brazilian gallery forest. Flora 184:103-117.

Oliveira-Filho, Ary T., Enivanis A. Vilela, Douglas A. Carvalho & Manuel L. Gavilanes. 1994. Effects of soil and topography on the distribution of tree species in a tropical riverine forest in south-eastern Brazil. Journal of Tropical Ecology 10:483-508.

Orians, Gordon H. 1982. The influence of tree-falls in tropical forests on tree species richness. Tropical Ecology 23:255-279.

Osmond, C. B., K. Winter & H. Ziegler. 1982. Functional significance of different pathways of CO_2 fixation in photosynthesis. Pages 479-547 *in* O. L. Lange, P. S. Nobel, C. B. Osmond and H. Ziegler, eds. Physiological plant ecology. II. Water Relations and Carbon Assimilation. Encyclopedia of Plant Physiology, New Series, Vol. 12B. Springer-Verlag Publishers, New York, NY, USA.

Pacala, Stephen W., Charles D. Canham, John Saponara, John A. Silander, Jr., Richard K. Kobe & Eric Ribbens. 1996. Forest models defined by field measurements: Estimation, error analysis and dynamics. Ecological Monographs 66:1-43.

Paine, Robert T. 1966. Food web complexity and species diversity. The American Naturalist 100:65-75.

Phillips, O. L., P. Hall, A. H. Gentry, S. A. Sawyer & R. Vásquez. 1994. Dynamics and species richness of tropical rain forests. Proceedings of the National Academy of Science, USA 91:2805-2809.

Pianka, Eric R. 1966. Latitudinal gradients in species diversity: A review of concepts. The American Naturalist 100:33-46.

Pickett, S. T. A. & F. A. Bazzaz. 1978. Organization of an assemblage of early successional species on a soil moisture gradient. Ecology 59:1248-1255.

Pielou, E. C. 1960. A single mechanism to account for regular, random and aggregated populations. Journal of Ecology 48:575-584.

Piperno, Dolores R. 1990. Fitolitos, arqueología y cambios prehistóricos de la vegetación en un lote de cincuenta hectáreas de la isla de Barro Colorado. Pages 153-156 *in* E. G. Leigh, Jr., A. Stanley Rand, and Donald M. Windsor, eds. Ecología de un Bosque Tropical. Smithsonian Institution Press, Washington, D. C., USA.

Primack, Richard B. & S. L. Miao. 1992. Dispersal can limit local plant distribution. Conservation Biology 6:513-519.

Prince, S. D. & R. N. Carter. 1985. The geographical distribution of prickly lettuce (Lactuca serriola). III. Its performance in transplant sites beyond its distribution limit in Britain. Journal of Ecology 73:49-64.

Pulliam, H. Ronald. 1988. Sources, sinks, and population regulation. The American Naturalist 132:652-661.

Pulliam, H. Ronald & Brent J. Danielson. 1991. Sources, sinks, and habitat selection: A landscape perspective on population dynamics. The American Naturalist 137(Supplement):S50-S60.

Ribbens, Eric, John A. Silander, Jr. & Stephen W. Pacala. 1994. Seedling recruitment in forests: Calibrating models to predict patterns of tree seedling dispersion. Ecology 75:1794-1806.

Richards, P. W. 1969. Speciation in the tropical rain forest and the concept of the niche. Biological Journal of the Linnean Society 1:149-153.

Ricklefs, Robert E. 1977. Environmental heterogeneity and plant species diversity: A hypothesis. The American Naturalist 111:376-381.

Ricklefs, Robert E. 1987. Community diversity: Relative roles of local and regional processes. Science 235:167-171.

Ricklefs, Robert E. & Roger Earl Latham. 1993. Global patterns of diversity in mangrove floras. Pages 215-229 *in* R. E. Ricklefs & D. Schluter, eds. Species Diversity in Ecological Communities. The Univeristy of Chicago Press, Chicago, IL, USA.

Rosenzweig, Michael L. 1995. Species Diversity in Space and Time. Cambridge University Press, New York, NY, USA.

Roughgarden, Jonathan, Steven Gaines & Stephen Pacala. 1987. Supply side ecology: The role of physical transport processes. In J. H. R. Gee and P. S. Giller, eds. Organization of Communities: Past and Present. Blackwell Scientific Publications, Oxford, UK.

Roughgarden, Jonathan, Yoh Iwasa & Charles Baxter. 1985. Demographic theory for an open marine population with space-limited recruitment. Ecology 66:54-67.

Sarukhán, José. 1978. Studies on the demography of tropical trees. Pgs. 163-184 in P. B. Tomlinson & M. H. Zimmermann, Eds. Tropical trees as living systems. Cambridge University Press, Cambridge, UK.

Sarukhán, José. 1980. Demographic problems in tropical systems. Pgs. 161-188 in O. T. Solbrig, Ed. Demography and evolution in plant populations. Blackwell Scientific Publications, Oxford, UK.

Schluter, Dolph & Robert E. Ricklefs. 1993. Species diversity: An introduction to the problem. Pages 1-12 *in* R. E. Ricklefs and D. Schluter, eds. Species Diversity in Ecological Communities: Historical and Geographical Perspectives. University of Chicago Press, Chicago, IL, USA.

Schupp, Eugene W. 1988. Seed and early seedling predation in the forest understory and in treefall gaps. Oikos 51:71-78.

Schupp, Eugene W. 1992. The Janzen-Connell model for tropical tree diversity: Population implications and the importance of spatial scale. The American Naturalist 140:526-530.

Schupp, Eugene W. 1995. Seed-seedling conflicts, habitat choice, and patterns of plant recruitment. American Journal of Botany 82:399-409.

Schupp, Eugene W., Henry F. Howe, Carol K. Augspurger & Douglas J. Levey. 1989. Arrival and survival in tropical treefall gaps. Ecology 70:562-564.

Schupp, Eugene W. & Marcelino Fuentes. 1995. Spatial patterns of seed dispersal and the unification of plant population ecology. Ecoscience 2:267-275.

Sheil, Douglas, David F. R. P. Burslem & Denis Alder. 1995. The interpretation and misinterpretation of mortality rate measures. Journal of Ecology 83:331-333.

Silvertown, Jonathan. 1982. Introduction to Plant Population Ecology. Longman, London, UK.

Silvertown, Jonathan & Richard Law. 1987. Do plants need niches? Some recent developments in plant community ecology. Trends in Ecology and Evolution 2:24-26.

Skellam, J. G. 1951. Random dispersal in theoretical populations. Biometrika 38:196-218.

Snedecor, George W. & William G. Cochran. 1980. Statistical Methods, Seventh Edition. The Iowa State University Press, Ames, IA, USA.

Strong, Donald R., Jr. 1977. Epiphyte loads, tree falls, and perennial forest disruption: A mechanism for maintaining higher tree species richness in the tropics without animals. Journal of Biogeography 4:215-218.

SYSTAT. 1992. SYSTAT for Windows: Statistics, Version 5 Edition. Systat, Incorporated, Evanston, IL, USA.

Tansley, A. G. 1917. On competition between *Galium saxatile* L. (*G. hercynium* Weig.) and *Galium sylvestre* Poll. (*G. asperum* Schreb.) on different types of soil. Journal of Ecology 5:173-179.

Thomas, Donald W., Danielle Cloutier, Marc Provencher & Christian Houle. 1988. The shape of bird- and bat-generated seed shadows around a tropical fruiting tree. Biotropica 20:347-348.

Thomas, S. C. & J. V. LaFrankie. 1993. Sex, size, and interyear variation in flowering among dioecious trees of the Malayan rain forest. Ecology 74:1529-1537.

Thomson, James D., George Weiblen, Barbara A. Thomson, Satie Alfaro & Pierre Legendre. 1996. Untangling multiple factors in spatial distributions: Lilies, gophers, and rocks. Ecology 77:1698-1715.

Tilman, David. 1982. Resource Competition and Community Structure. Monographs in Population Biology, Princeton University Press, Princeton, NJ, USA.

Tilman, David. 1988. Plant Strategies and the Dynamics and Structure of Plant Communities. Monographs in Population Biology, Princeton University Press, Princeton, NJ, USA.

Tilman, David. 1994. Competition and biodiversity in spatially structured habitats. Ecology 75:2-16.

Tilman, David & Stephen Pacala. 1993. The maintenance of species richness in plant communities. Pages 13-25 *in* R. E. Ricklefs and D. Schluter, eds. Species Diversity in Ecological Communities: Historical and Geographical Perspectives. University of Chicago Press, Chicago, IL, USA.

Tuomisto, Hanna & Kalle Ruokolainen. 1994. Distribution of *Pteridophyta* and *Melastomataceae* along an edaphic gradient in an Amazonian rain forest. Journal of Vegetation Science 5:25-34.

Veenendaal, E. M., M. D. Swaine, R. T. Lecha, M. F. Walsh, I. K. Abebrese & K. Owusu-Afriyie. 1996. Responses of West African forest tree seedlings to irradiance and soil fertility. Functional Ecology 10:501-511.

Watt, Alex S. 1947. Pattern and process in the plant community. Journal of Ecology 35:1-22.

Webb, Sara L. & Mary F. Willson 1985. Spatial heterogeneity in post-dispersal predation on *Prunus* and *Uvularia* seeds. Oecologia 67:150-153.

Wechsler, Benjamin S. 1995. A Neotropical seedling census: Diversity, abundance, and dispersion. Bachelor of Arts Thesis, Princeton University, Princeton, NJ, USA.

Welden, Charles W., Steven W. Hewett, Stephen P. Hubbell & Robin B. Foster. 1991. Sapling survival, growth, and recruitment: relationship to canopy height in a Neotropical forest. Ecology 72:35-50.

Wesser, Sara D. & W. Scott Armbruster. 1991. Species distribution controls across a forest-steppe transition: A causal model and experimental test. Ecological Monographs 61:323-342.

Whelan, Christopher J., Mary F. Willson, Charles A. Tuma & Isabel Souza-Pinto. 1991. Spatial and temporal patterns of postdispersal seed predation. Canadian Journal of Botany 69: 428-436.

Whitmore, T. C. 1975. Tropical Rain Forests of the Far East. Clarendon Press, Oxford, UK.

Whitmore, T. C. 1984. Tropical Rain Forests of the Far East. Second Edition. Clarendon Press, Oxford, UK.

Whittaker, R. H. 1956. Vegetation of the Great Smoky Mountains. Ecological Monographs 26:1-80.

Whittaker, R. H. 1967. Gradient analysis of vegetation. Biological Review of the Cambridge Philosophical Society 42:207-264.

Whittaker, Robert H. 1970. Communities and Ecosystems. Macmillan, New York, NY, USA.

Wills, Christopher R., Richard Condit, Robin B. Foster & Stephen P. Hubbell. *In press.* Strong evidence for large intraspecific density-dependent effects, and for a beneficial effect of overall density, in a neotropical forest.

Willson, Mary F. 1992. The ecology of seed dispersal. Pages 61-85 in M. Fenner, ed. Seeds: The Ecology of Regeneration *in* Plant Communities. CAB International, Wallingford, Oxon, UK.

Wyatt-Smith, J. 1987. Foreward. Journal of Tropical Ecology 3(Special Issue):iv.

Yavitt, Joseph B. & R. Kelman Wieder. 1988. Nitrogen, phosphorus, and sulfur properties of some forest soils on Barro Colorado Island, Panama. Biotropica 20:2-10.

APPENDIX 1

Names, Codes, Growth Forms, and Reproductive Sizes for Species of the 50-ha FDP Plot on BCI, Panamá

Names, codes, growth forms, and estimated diameters at which individuals become reproductive for the 313 woody shrub and tree species found as ≥ 1-cm DBH stems on the 50-ha Forest Dynamics Project plot of Barro Colorado Island, Panamá between 1980 and 1990. Growth forms are defined as follows: S=shrubs, plants whose adults are < 4 m in height; U=understory treelets, adults 4-10 m; M=midstory trees, adults 10-20 m; T=canopy trees, adults > 20 m; H=hemiepiphytic figs; and Z=strangler figs. See Condit *et al.* (1995), Appendix 1, for previously used nomenclature for these species.

Species	Code	Growth form	Reproductive DBH (cm)
Acacia melanoceras	ACACME	U	4
Acalypha diversifolia	ACALDI	S	2
Acalypha macrostachya	ACALMA	U	2
Adelia triloba	ADE1TR	U	10
Aegiphila panamensis	AEGIPA	M	4
Alchornea costaricensis	ALCHCO	T	20
Alchornea latifolia	ALCHLA	M	16
Alibertia edulis	ALIBED	U	4
Allophyllus psilospermus	ALLOPS	M	4
Alseis blackiana	ALSEBL	T	20
Amaioua corymbosa	AMAICO	U	10
Anacardium excelsum	ANACEX	T	60
Anaxagorea panamensis	ANAXPA	S	1
Andira inermis	ANDIIN	T	20
Annona acuminata	ANNOAC	S	1
Annona hayesii	ANNOHA	U	4
Annona spraguei	ANNOSP	M	8
Apeiba membranacea	APEIME	T	30
Apeiba tibourbou	APEITI	M	8
Apeiba sp. nov. ("hybrid")	APEIHY	T	30
Aphelandra sinclairiana	APHESI	S	2
Appunia seibertii	APPUSE	S	2

Appendix 1 continued.

Species	Code	Growth form	Reproductive DBH (cm)
Ardisia bartlettii	ARDIBA	S	?
Ardisia fendleri	ARDIFE	U	4
Ardisia guianensis	ARDIGU	S	2
Aspidosperma cruenta	ASPICR	T	30
Astrocaryum standleyanum	AST1ST	M	8
Astronium graveolens	AST2GR	T	30
Bactris barronis	BACTBA	U	2
Bactris coloniata	BACTC1	S	2
Bactris coloradonis	BACTC2	U	2
Bactris major	BACTMA	U	2
Banara guianensis	BANAGU	U	?
Beilschmiedia pendula	BEILPE	T	30
Bertiera guianensis	BERTGU	S	1
Brosimum alicastrum	BROSAL	T	30
Brosimum guianense	BROSGU	T	30
Calophyllum longifolium	CALOLO	T	30
Capparis frondosa	CAPPFR	S	1
Casearia aculeata	CASEAC	U	5
Casearia arborea	CASEAR	T	20
Casearia commersoniana	CASECO	U	10
Casearia guianensis	CASEGU	U	4
Casearia sylvestris	CASESY	M	10
Cassipourea elliptica	CASSEL	M	8
Cavanillesia platanifolia	CAVAPL	T	50
Cecropia insignis	CECRIN	T	30
Cecropia obtusifolia	CECROB	M	8
Cedrela odorata	CEDROD	T	30
Ceiba pentandra	CEIBPE	T	60
Celtis schippii	CELTSC	M	16
Cespedezia macrophylla	CESPMA	T	30
Cestrum megalophyllum	CESTME	S	1
Chamaedorea tepejilote	CHA1TE	S	2
Chamguava schippii	CHA2SC	U	4
Chimarrhis parviflora	CHIMPA	T	30
Chrysochlamys eclipes	CHR1EC	S	2
Chrysophyllum argenteum	CHR2AR	T	30
Chrysophyllum cainito	CHR2CA	T	30
Clidemia dentata	CLIDDE	S	1
Clidemia octona	CLIDOC	S	1
Clidemia septuplinervia	CLIDSE	S	1
Cnemidaria petiolata	CNEMPE	S	1
Coccoloba coronata	COCCCO	M	8
Coccoloba manzanillensis	COCCMA	U	10
Colubrina glandulosa	COLUGL	T	30
Conostegia bracteata	CONOBR	S	1
Conostegia cinnamomea	CONOCI	S	1
Cordia alliodora	CORDAL	T	20

Appendix 1 continued.

Species	Code	Growth form	Reproductive DBH (cm)
Cordia bicolor	CORDBI	M	16
Cordia lasiocalyx	CORDLA	M	10
Coussarea curvigemmia	COU2CU	U	3
Coutarea hexandra	COUTHE	U	?
Croton billbergianus	CROTBI	U	5
Cupania cinerea	CUPACI	M	16
Cupania latifolia	CUPALA	T	30
Cupania rufescens	CUPARU	T	20
Cupania sylvatica	CUPASY	U	5
Cyphomandra hartwegii	CYPHHA	S	2
Dendropanax arboreus	DENDAR	T	30
Dendropanax stenodontus	DENDST	T	20
Desmopsis panamensis	DES2PA	U	3
Diospyros artanthifolia	DIO2AR	M	16
Dipteryx panamensis	DIPTPA	T	30
Drypetes standleyi	DRYPST	T	20
Elaeis oleifera	ELAEOL	M	40
Enterolobium schomburgkii	ENTESC	T	40
Erythrina costaricensis	ERY1CO	U	5
Erythroxylum multiflorum	ERY2MA	M	4
Erythroxylum panamense	ERY2PA	U	1
Eugenia coloradensis	EUGECO	T	30
Eugenia galalonensis	EUGEGA	U	4
Eugenia nesiotica	EUGENE	M	10
Eugenia oerstedeana	EUGEOE	M	20
Faramea occidentalis	FARAOC	U	5
Ficus bullenei	FICUBU	Z	?
Ficus citrifolia	FICUCI	H	?
Ficus colubrinae	FICUC1	H	?
Ficus costaricana	FICUC2	Z	30
Ficus insipida	FICUIN	T	40
Ficus maxima	FICUMA	T	30
Ficus obtusifolia	FICUOB	Z	30
Ficus pertusa	FICUPE	H	?
Ficus popenoei	FICUPO	Z	30
Ficus tonduzii	FICUTO	M	20
Ficus trigonata	FICUTR	Z	30
Ficus yoponensis	FICUYO	T	40
Garcinia intermedia	GAR2IN	M	10
Garcinia madruno	GAR2MA	M	20
Genipa americana	GENIAM	T	30
Geonoma interrupta	GEONIN	U	2
Guapira standleyanum	GUAPST	T	30
Guarea grandifolia	GUARGR	T	30
Guarea guidonia	GUARGU	M	4
Guarea sp. nov. ("fuzzy")	GUARSP	M	8
Guatteria dumetorum	GUATDU	T	30

Appendix 1 continued.

Species	Code	Growth form	Reproductive DBH (cm)
Guazuma ulmifolia	GUAZUL	T	30
Guettarda foliacea	GUETFO	U	10
Gustavia superba	GUSTSU	M	10
Hamelia axillaris	HAMEAX	S	1
Hamelia patens	HAMEPA	S	1
Hampea appendiculata	HAMPAP	M	8
Hasseltia floribunda	HASSFL	M	8
Heisteria acuminata	HEISAC	U	5
Heisteria concinna	HEISCO	M	15
Herrania purpurea	HERRPU	U	1
Hirtella americana	HIRTAM	T	30
Hirtella triandra	HIRTTR	M	8
Hura crepitans	HURACR	T	30
Hybanthus prunifolius	HYBAPR	S	1
Hyeronima alcheornoides	HYERAL	T	30
Inga cocleensis	INGACO	M	16
Inga fagifolia	INGAFA	T	30
Inga goldmanii	INGAGO	T	30
Inga marginata	INGAMA	T	30
Inga minutula	INGAMI	T	30
Inga mucuna	INGAM1	T	30
Inga pezizifera	INGAPE	T	30
Inga punctata	INGAPU	T	30
Inga quaternata	INGAQU	M	8
Inga ruiziana	INGARU	T	30
Inga sapindoides	INGASA	M	16
Inga spectabilis	INGASP	T	20
Inga umbellifera	INGAUM	M	8
Inga sp. nov. ("skinny")	INGAS1	U	8
Jacaranda copaia	JAC1CO	T	30
Koanophyllon wetmorei	KOANWE	S	3
Lacistema aggregatum	LACIAG	U	5
Lacmellea panamensis	LACMPA	M	16
Laetia procera	LAETPR	T	20
Laetia thamnia	LAETTH	U	8
Lafoensia punicifolia	LAFOPU	T	30
Leandra dichotoma	LEANDI	S	1
Licania hypoleuca	LICAHY	M	8
Licania platypus	LICAPL	T	30
Lindackeria laurina	LINDLA	M	10
Lonchocarpus latifolia	LONCLA	T	30
Lopimia dasypetala	LOPIDA	S	1
Lozania pittieri	LOZAPI	U	10
Luehea seemannii	LUEHSE	T	30
Lycianthes maxonii	LYCIMA	S	?
Maclura tinctoria	MACLTI	T	30
Macrocnemum glabrescens	MACRGL	M	8

Appendix 1 continued.

Species	Code	Growth form	Reproductive DBH (cm)
Malmea sp. nov. ("Garwood's")	MALMSP	M	4
Malpighia romeroana	MALPRO	S	1
Maquira costaricana	MAQUCO	M	10
Margaritaria nobilis	MARGNO	U	?
Marila laxiflora	MAR1LA	M	10
Maytenus schippii	MAYTSC	M	8
Miconia affinis	MICOAF	U	4
Miconia argentea	MICOAR	M	10
Miconia elata	MICOEL	U	10
Miconia hondurensis	MICOHO	U	10
Miconia impetiolaris	MICOIM	U	2
Miconia nervosa	MICONE	S	1
Miconia prasina	MICOPR	U	?
Mouriri myrtilloides	MOURMY	S	2
Myrcia gatunensis	MYRCGA	U	5
Myrospermum fructescens	MYROFR	T	30
Nectandra cissiflora	NECTCI	T	30
Nectandra globosa	NECTGL	M	16
Nectandra purpurea	NECTPU	M	8
Nectandra sp. nov. ("fuzzy")	NECTS1	T	30
Nectandra sp. nov. ("tiny leaf")	NECTS3	M	?
Neea amplifolia	NEEAAM	S	1
Ochroma pyramidale	OCHRPY	M	16
Ocotea cernua	OCOTCE	M	4
Ocotea oblonga	OCOTOB	T	30
Ocotea puberula	OCOTPU	T	30
Ocotea whitei	OCOTWH	T	30
Oenocarpus mapoura	OENOMA	M	8
Olmedia aspera	OLMEAS	U	4
Ormosia amazonica	ORMOAM	T	30
Ormosia croatii	ORMOCR	T	30
Ormosia macrocalyx	ORMOMA	T	30
Ouratea lucens	OURALU	S	3
Palicourea guianensis	PALIGU	S	1
Pentagonia macrophylla	PENTMA	U	2
Perebea xanthochyma	PEREXA	M	8
Phoebe cinnamomifolia	PHOECI	T	30
Picramnia latifolia	PICRLA	U	4
Piper aequale	PIPEAE	S	1
Piper arboreum	PIPEA1	U	3
Piper carrilloanum	PIPECA	S	1
Piper cordulatum	PIPECO	S	1
Piper culebranum	PIPECU	S	2
Piper imperiale	PIPEIM	U	2
Piper perlasense	PIPEPE	S	1
Piper reticulatum	PIPERE	U	4
Pithecellobium macradenium	PIT1MA	T	30

Appendix 1 continued.

Species	Code	Growth form	Reproductive DBH (cm)
Pithecellobium rufescens	PIT1RU	M	8
Platymiscium pinnatum	PLA1PI	T	30
Platypodium elegans	PLA2EL	T	30
Pochota quinata	POCHQU	T	30
Pochota sessilis	POCHSE	T	30
Posoqueria latifolia	POSOLA	M	8
Poulsenia armata	POULAR	T	30
Pourouma bicolor	POURBI	T	20
Pouteria fossicola	POUTFO	T	30
Pouteria reticulata	POUTRE	T	30
Pouteria stipitata	POUTST	M	16
Prioria copaifera	PRI2CO	T	60
Protium costaricense	PROTCO	M	16
Protium panamense	PROTPA	M	8
Protium tenuifolium	PROTTE	M	20
Protium sp. nov. ("skinny")	PROTSP	M	20
Pseudobombax septenatum	PSE1SE	T	40
Psidium friedrichsthalianum	PSIDFR	U	10
Psychotria acuminata	PSYCAC	S	1
Psychotria brachiata	PSYCB1	S	?
Psychotria chagrensis	PSYCCH	S	1
Psychotria deflexa	PSYCDE	S	1
Psychotria furcata	PSYCFU	S	1
Psychotria graciliflora	PSYCG1	S	1
Psychotria granadensis	PSYCG2	S	1
Psychotria grandis	PSYCG3	U	3
Psychotria horizontalis	PSYCHO	S	1
Psychotria limonensis	PSYCLI	S	1
Psychotria marginata	PSYCMA	S	1
Psychotria pittieri	PSYCPI	S	1
Psychotria racemosa	PSYCRA	S	1
Pterocarpus belizensis	PTERBE	T	30
Pterocarpus rohrii	PTERRO	T	30
Quararibea asterolepis	QUARAS	T	30
Quassia amara	QUASAM	U	4
Randia armata	RANDAR	U	5
Randia formosa	RANDFO	U	2
Rinorea sylvatica	RINOSY	S	2
Sapium aucuparium	SAPIAU	T	30
Sapium sp. nov. ("broadleaf")	SAPISP	T	30
Scheelea zonensis	SCH1ZO	M	16
Schefflera morototoni	SCH2MO	T	30
Schizolobium parahybum	SCHIPA	T	30
Senna dariensis	SENNDA	S	1
Simarouba amara	SIMAAM	T	30
Siparuna guianensis	SIPAGU	M	10
Siparuna pauciflora	SIPAPA	U	4

Appendix 1 continued.

Species	Code	Growth form	Reproductive DBH (cm)
Sloanea terniflora	SLOATE	T	40
Socratea exorrhiza	SOCREX	M	8
Solanum arboreum	SOLAAR	S	?
Solanum asperum	SOLAAS	S	?
Solanum hayesii	SOLAHA	M	4
Solanum steyemarkii	SOLAST	S	2
Sorocea affinis	SOROAF	S	3
Spachea membranacea	SPACME	U	10
Spondias mombin	SPONMO	T	30
Spondias radlkoferi	SPONRA	T	30
Stemmadenia grandiflora	STEMGR	U	4
Sterculia apetala	STERAP	T	40
Stylogyne standleyi	STYLST	S	3
Swartzia simplex var. grandiflora	SWARS1	U	8
Swartzia simplex var. ochnacea	SWARS2	U	4
Symphonia globulifera	SYMPGL	T	30
Tabebuia guayacan	TAB1GU	T	30
Tabebuia rosea	TAB1RO	T	30
Tabernaemontana arborea	TAB2AR	T	30
Tachigalia versicolor	TACHVE	T	70
Talisia nervosa	TALINE	U	3
Talisia princeps	TALIPR	M	8
Terminalia amazonica	TERMAM	T	30
Terminalia oblonga	TERMOB	T	30
Ternstroemia tepezapote	TERNTE	U	2
Tetragastris panamensis	TET2PA	T	30
Tetrathylacium johansenii	TET4JO	T	30
Theobroma cacao	THEOCA	U	10
Thevetia ahouai	THEVAH	U	2
Tocoyena pittieri	TOCOPI	M	16
Trattinnickia aspera	TRATAS	T	30
Trema micrantha	TREMMI	M	20
Tricanthera gigantea	TRI1GI	U	4
Trichilia pallida	TRI2PA	M	8
Trichilia tuberculata	TRI2TU	T	30
Trichospermum galeottii	TRI4GA	M	8
Triplaris cumingiana	TRIPCU	M	20
Trophis racemosa	TROPRA	M	8
Turpinia occidentalis	TURPOC	T	30
Unonopsis pittieri	UNONPI	M	8
Urera baccifera	URERBA	S	2
Virola sebifera	VIROSE	M	20
Virola surinamensis	VIROSU	T	30
Virola sp. nov. (“bozo”)	VIROSP	T	30
Vismia baccifera	VISMBA	U	2
Vismia billbergiana	VISMBI	U	5
Vismia macrophylla	VISMMA	M	?

Appendix 1 continued.

Species	Code	Growth form	Reproductive DBH (cm)
Vochysia ferruginea	VOCHFE	T	20
Xylopia macrantha	XYL1MA	M	10
Xylosma chloranthum	XYL2CH	U	4
Xylosma oligandrum	XYL2OL	S	3
Zanthoxylum belizense	ZANTBE	T	30
Zanthoxylum panamense	ZANTP1	T	30
Zanthoxylum procerum	ZANTPR	M	20
Zanthoxylum setulosum	ZANTSE	M	20
Zuelania guidonia	ZUELGU	M	20

APPENDIX 2

Tallies of Species by Growth Form for the 50-ha FDP Plot

The total number of species of each growth form found as ≥ 1-cm DBH stems on the 50-ha Forest Dynamics Project plot of Barro Colorado Island, Panamá between 1980 and 1990.

Growth form	Growth form code	Number of species
Canopy trees	T	108
Midstory trees	M	74
Understory trees	U	64
Shrubs	S	59
Figs - hemiepiphytes	H	3
Figs - stranglers	Z	5
All growth forms		313

APPENDIX 3

Total Number of Stems and Stem Density for Species on the 50-ha FDP Plot

The total number of stems ≥ 1-cm DBH and the stem density of all 303 species encountered during the 1990 census of the 50-ha Forest Dynamics Project plot of Barro Colorado Island, Panamá.

	Total number of stems					Number of stems/ha				
Species	High Plateau	Low Plateau	Slope	Stream	Swamp	High Plateau	Low Plateau	Slope	Stream	Swamp
ACACME	0	9	1	0	1	0.00	0.36	0.09	0.00	0.83
ACALDI	109	321	232	42	20	16.03	12.94	20.42	32.81	16.67
ACALMA	4	31	6	3	0	0.59	1.25	0.53	2.34	0.00
ADE1TR	94	97	29	3	0	13.82	3.91	2.55	2.34	0.00
AEGIPA	5	58	16	3	1	0.74	2.34	1.41	2.34	0.83
ALCHCO	26	148	57	2	0	3.82	5.97	5.02	1.56	0.00
ALCHLA	0	2	0	1	0	0.00	0.08	0.00	0.78	0.00
ALIBED	33	222	59	14	20	4.85	8.95	5.19	10.94	16.67
ALLOPS	30	74	30	4	0	4.41	2.98	2.64	3.13	0.00
ALSEBL	1151	4220	1636	134	50	169.26	170.16	144.01	104.69	41.67
AMAICO	0	24	7	0	0	0.00	0.97	0.62	0.00	0.00
ANACEX	0	9	7	1	4	0.00	0.36	0.62	0.78	3.33
ANAXPA	0	62	525	0	0	0.00	2.50	46.21	0.00	0.00
ANDIIN	47	148	75	5	2	6.91	5.97	6.60	3.91	1.67
ANNOAC	47	229	127	29	67	6.91	9.23	11.18	22.66	55.83
ANNOHA	0	1	0	0	0	0.00	0.04	0.00	0.00	0.00
ANNOSP	8	84	34	1	3	1.18	3.39	2.99	0.78	2.50
APEIME	34	166	74	15	6	5.00	6.69	6.51	11.72	5.00
APEITI	4	19	4	1	0	0.59	0.77	0.35	0.78	0.00
APHESI	0	2	1	3	1	0.00	0.08	0.09	2.34	0.83
APPUSE	0	0	4	0	0	0.00	0.00	0.35	0.00	0.00
ARDIBA	0	1	0	0	0	0.00	0.04	0.00	0.00	0.00
ARDIFE	11	30	34	3	0	1.62	1.21	2.99	2.34	0.00
ARDIGU	0	7	0	4	0	0.00	0.28	0.00	3.13	0.00
ASPICR	92	189	157	5	1	13.53	7.62	13.82	3.91	0.83
AST1ST	25	86	45	4	26	3.68	3.47	3.96	3.13	21.67
AST2GR	18	31	9	5	1	2.65	1.25	0.79	3.91	0.83
BACTBA	2	12	8	0	0	0.29	0.48	0.70	0.00	0.00
BACTC1	6	3	14	0	0	0.88	0.12	1.23	0.00	0.00
BACTC2	1	3	2	0	0	0.15	0.12	0.18	0.00	0.00
BACTMA	11	11	9	0	158	1.62	0.44	0.79	0.00	131.67

Appendix 3 continued.

	Total number of stems					Number of stems/ha				
Species	High Plateau	Low Plateau	Slope	Stream	Swamp	High Plateau	Low Plateau	Slope	Stream	Swamp
BANAGU	1	1	1	0	0	0.15	0.04	0.09	0.00	0.00
BEILPE	147	1521	963	41	1	21.62	61.33	84.77	32.03	0.83
BERTGU	0	1	0	0	0	0.00	0.04	0.00	0.00	0.00
BROSAL	138	449	195	47	6	20.29	18.10	17.17	36.72	5.00
BROSGU	0	0	1	0	0	0.00	0.00	0.09	0.00	0.00
CALOLO	26	381	426	12	11	3.82	15.36	37.50	9.38	9.17
CAPPFR	668	1387	897	146	34	98.24	55.93	78.96	114.06	28.33
CASEAC	90	207	103	13	2	13.24	8.35	9.07	10.16	1.67
CASEAR	22	114	29	4	1	3.24	4.60	2.55	3.13	0.83
CASECO	0	17	3	1	0	0.00	0.69	0.26	0.78	0.00
CASEGU	6	7	1	0	0	0.88	0.28	0.09	0.00	0.00
CASESY	19	106	46	7	6	2.79	4.27	4.05	5.47	5.00
CASSEL	80	503	173	12	72	11.76	20.28	15.23	9.38	60.00
CAVAPL	8	5	6	0	0	1.18	0.20	0.53	0.00	0.00
CECRIN	64	230	78	5	2	9.41	9.27	6.87	3.91	1.67
CECROB	4	24	11	0	4	0.59	0.97	0.97	0.00	3.33
CEDROD	0	4	5	0	0	0.00	0.16	0.44	0.00	0.00
CEIBPE	8	31	10	4	3	1.18	1.25	0.88	3.13	2.50
CELTSC	12	71	54	3	2	1.76	2.86	4.75	2.34	1.67
CESPMA	0	0	5	0	0	0.00	0.00	0.44	0.00	0.00
CESTME	10	65	62	10	6	1.47	2.62	5.46	7.81	5.00
CHA1TE	1	2	12	0	0	0.15	0.08	1.06	0.00	0.00
CHA2SC	1	261	2	1	9	0.15	10.52	0.18	0.78	7.50
CHIMPA	0	0	0	0	0	0.00	0.00	0.00	0.00	0.00
CHR1EC	6	128	245	27	0	0.88	5.16	21.57	21.09	0.00
CHR2AR	85	344	178	19	10	12.50	13.87	15.67	14.84	8.33
CHR2CA	23	35	22	1	8	3.38	1.41	1.94	0.78	6.67
CLIDDE	1	9	3	1	3	0.15	0.36	0.26	0.78	2.50
CLIDOC	3	5	1	0	0	0.44	0.20	0.09	0.00	0.00
CNEMPE	0	0	1	0	0	0.00	0.00	0.09	0.00	0.00
COCCCO	24	91	42	9	2	3.53	3.67	3.70	7.03	1.67
COCCMA	52	286	74	9	8	7.65	11.53	6.51	7.03	6.67
COLUGL	0	1	0	0	0	0.00	0.04	0.00	0.00	0.00
CONOBR	0	1	0	2	0	0.00	0.04	0.00	1.56	0.00
CONOCI	20	52	102	17	7	2.94	2.10	8.98	13.28	5.83
CORDAL	20	64	15	6	4	2.94	2.58	1.32	4.69	3.33
CORDBI	51	699	206	14	17	7.50	28.19	18.13	10.94	14.17
CORDLA	197	763	548	46	39	28.97	30.77	48.24	35.94	32.50
COU2CU	81	1544	146	14	26	11.91	62.26	12.85	10.94	21.67

Appendix 3 continued.

	Total number of stems					Number of stems/ha				
Species	High Plateau	Low Plateau	Slope	Stream	Swamp	High Plateau	Low Plateau	Slope	Stream	Swamp
COUTHE	0	0	1	0	0	0.00	0.00	0.09	0.00	0.00
CROTBI	55	565	120	54	95	8.09	22.78	10.56	42.19	79.17
CUPACI	1	6	1	1	0	0.15	0.24	0.09	0.78	0.00
CUPALA	3	25	20	1	0	0.44	1.01	1.76	0.78	0.00
CUPARU	2	66	9	0	10	0.29	2.66	0.79	0.00	8.33
CUPASY	157	671	203	31	0	23.09	27.06	17.87	24.22	0.00
CYPHHA	0	3	0	0	0	0.00	0.12	0.00	0.00	0.00
DENDAR	7	5	2	0	0	1.03	0.20	0.18	0.00	0.00
DENDST	3	74	28	1	3	0.44	2.98	2.46	0.78	2.50
DES2PA	2164	6107	2593	246	156	318.24	246.25	228.26	192.19	130.00
DIO2AR	1	52	15	1	1	0.15	2.10	1.32	0.78	0.83
DIPTPA	5	32	9	4	0	0.74	1.29	0.79	3.13	0.00
DRYPST	366	791	1026	11	3	53.82	31.90	90.32	8.59	2.50
ELAEOL	0	0	0	0	16	0.00	0.00	0.00	0.00	13.33
ENTESC	2	6	3	1	0	0.29	0.24	0.26	0.78	0.00
ERY1CO	14	87	60	6	1	2.06	3.51	5.28	4.69	0.83
ERY2MA	37	159	80	3	0	5.44	6.41	7.04	2.34	0.00
ERY2PA	11	45	29	3	4	1.62	1.81	2.55	2.34	3.33
EUGECO	127	441	189	17	5	18.68	17.78	16.64	13.28	4.17
EUGEGA	280	731	235	13	15	41.18	29.48	20.69	10.16	12.50
EUGENE	95	271	105	19	4	13.97	10.93	9.24	14.84	3.33
EUGEOE	320	1320	476	24	19	47.06	53.23	41.90	18.75	15.83
FARAOC	4234	15120	3817	551	424	622.65	609.68	336.00	430.47	353.33
FICUBU	1	0	0	0	0	0.15	0.00	0.00	0.00	0.00
FICUCI	0	1	0	0	0	0.00	0.04	0.00	0.00	0.00
FICUC1	0	0	0	1	0	0.00	0.00	0.00	0.78	0.00
FICUC2	3	2	1	0	1	0.44	0.08	0.09	0.00	0.83
FICUIN	0	1	1	1	2	0.00	0.04	0.09	0.78	1.67
FICUMA	0	5	4	0	1	0.00	0.20	0.35	0.00	0.83
FICUOB	1	4	0	0	2	0.15	0.16	0.00	0.00	1.67
FICUPE	0	1	0	0	0	0.00	0.04	0.00	0.00	0.00
FICUPO	1	5	0	0	1	0.15	0.20	0.00	0.00	0.83
FICUTO	3	19	16	4	0	0.44	0.77	1.41	3.13	0.00
FICUTR	1	0	2	1	0	0.15	0.00	0.18	0.78	0.00
FICUYO	0	2	0	2	0	0.00	0.08	0.00	1.56	0.00
GAR2IN	842	2194	892	59	49	123.82	88.47	78.52	46.09	40.83
GAR2MA	57	265	129	31	1	8.38	10.69	11.36	24.22	0.83
GENIAM	10	42	21	5	5	1.47	1.69	1.85	3.91	4.17
GEONIN	0	0	3	0	0	0.00	0.00	0.26	0.00	0.00

Appendix 3 continued.

	Total number of stems					Number of stems/ha				
Species	High Plateau	Low Plateau	Slope	Stream	Swamp	High Plateau	Low Plateau	Slope	Stream	Swamp
GUAPST	34	109	33	3	1	5.00	4.40	2.90	2.34	0.83
GUARGR	8	33	17	1	0	1.18	1.33	1.50	0.78	0.00
GUARGU	301	690	684	91	57	44.26	27.82	60.21	71.09	47.50
GUARSP	211	619	364	50	16	31.03	24.96	32.04	39.06	13.33
GUATDU	74	765	522	27	4	10.88	30.85	45.95	21.09	3.33
GUAZUL	10	15	7	0	1	1.47	0.60	0.62	0.00	0.83
GUETFO	47	174	63	15	7	6.91	7.02	5.55	11.72	5.83
GUSTSU	121	169	89	31	4	17.79	6.81	7.83	24.22	3.33
HAMEAX	5	51	25	7	6	0.74	2.06	2.20	5.47	5.00
HAMEPA	0	2	0	0	0	0.00	0.08	0.00	0.00	0.00
HAMPAP	3	25	7	0	1	0.44	1.01	0.62	0.00	0.83
HASSFL	77	410	232	43	33	11.32	16.53	20.42	33.59	27.50
HEISAC	4	56	33	2	2	0.59	2.26	2.90	1.56	1.67
HEISCO	145	528	225	32	12	21.32	21.29	19.81	25.00	10.00
HERRPU	40	309	130	22	6	5.88	12.46	11.44	17.19	5.00
HIRTAM	0	32	12	0	2	0.00	1.29	1.06	0.00	1.67
HIRTTR	248	2539	1758	123	32	36.47	102.38	154.75	96.09	26.67
HURACR	24	46	33	3	6	3.53	1.85	2.90	2.34	5.00
HYBAPR	5006	22026	8647	731	100	736.18	888.15	761.18	571.09	83.33
HYERAL	6	41	25	2	10	0.88	1.65	2.20	1.56	8.33
INGACO	1	199	18	8	3	0.15	8.02	1.58	6.25	2.50
INGAFA	6	33	9	2	11	0.88	1.33	0.79	1.56	9.17
INGAGO	33	227	138	9	20	4.85	9.15	12.15	7.03	16.67
INGAMA	86	308	263	14	8	12.65	12.42	23.15	10.94	6.67
INGAMI	0	4	4	0	0	0.00	0.16	0.35	0.00	0.00
INGAM1	0	1	0	0	0	0.00	0.04	0.00	0.00	0.00
INGAPE	31	35	98	15	0	4.56	1.41	8.63	11.72	0.00
INGAPU	10	2	4	1	0	1.47	0.08	0.35	0.78	0.00
INGAQU	78	325	263	19	5	11.47	13.10	23.15	14.84	4.17
INGARU	4	38	11	1	0	0.59	1.53	0.97	0.78	0.00
INGASA	39	176	80	11	1	5.74	7.10	7.04	8.59	0.83
INGASP	1	17	3	1	1	0.15	0.69	0.26	0.78	0.83
INGAUM	108	631	192	35	3	15.88	25.44	16.90	27.34	2.50
INGAS1	40	169	73	1	0	5.88	6.81	6.43	0.78	0.00
JAC1CO	18	194	51	6	4	2.65	7.82	4.49	4.69	3.33
KOANWE	0	5	2	5	0	0.00	0.20	0.18	3.91	0.00
LACIAG	114	1037	365	64	9	16.76	41.81	32.13	50.00	7.50
LACMPA	13	49	13	4	5	1.91	1.98	1.14	3.13	4.17
LAETPR	0	21	3	4	2	0.00	0.85	0.26	3.13	1.67

Appendix 3 continued.

Species	Total number of stems High Plateau	Low Plateau	Slope	Stream	Swamp	Number of stems/ha High Plateau	Low Plateau	Slope	Stream	Swamp
LAETTH	20	427	42	8	7	2.94	17.22	3.70	6.25	5.83
LAFOPU	0	4	0	0	1	0.00	0.16	0.00	0.00	0.83
LEANDI	0	1	0	0	0	0.00	0.04	0.00	0.00	0.00
LICAHY	11	90	24	0	0	1.62	3.63	2.11	0.00	0.00
LICAPL	4	137	153	11	1	0.59	5.52	13.47	8.59	0.83
LINDLA	8	48	8	1	11	1.18	1.94	0.70	0.78	9.17
LONCLA	55	534	204	18	8	8.09	21.53	17.96	14.06	6.67
LOZAPI	0	0	7	0	0	0.00	0.00	0.62	0.00	0.00
LUEHSE	27	104	34	6	19	3.97	4.19	2.99	4.69	15.83
MACLTI	0	0	0	0	1	0.00	0.00	0.00	0.00	0.83
MACRGL	8	31	29	17	0	1.18	1.25	2.55	13.28	0.00
MALMSP	12	221	88	6	16	1.76	8.91	7.75	4.69	13.33
MALPRO	7	27	11	10	0	1.03	1.09	0.97	7.81	0.00
MAQUCO	187	731	434	58	6	27.50	29.48	38.20	45.31	5.00
MARGNO	0	3	1	0	0	0.00	0.12	0.09	0.00	0.00
MAR1LA	0	1	9	12	0	0.00	0.04	0.79	9.38	0.00
MAYTSC	7	47	24	4	1	1.03	1.90	2.11	3.13	0.83
MICOAF	16	337	41	9	11	2.35	13.59	3.61	7.03	9.17
MICOAR	105	448	125	15	81	15.44	18.06	11.00	11.72	67.50
MICOEL	1	28	0	1	0	0.15	1.13	0.00	0.78	0.00
MICOHO	0	24	2	0	4	0.00	0.97	0.18	0.00	3.33
MICOIM	0	2	3	1	1	0.00	0.08	0.26	0.78	0.83
MICONE	16	239	21	1	19	2.35	9.64	1.85	0.78	15.83
MICOPR	0	1	0	0	0	0.00	0.04	0.00	0.00	0.00
MOURMY	891	4742	1091	176	96	131.03	191.21	96.04	137.50	80.00
MYRCGA	6	27	11	7	1	0.88	1.09	0.97	5.47	0.83
MYROFR	1	16	5	0	1	0.15	0.65	0.44	0.00	0.83
NECTCI	5	253	52	3	0	0.74	10.20	4.58	2.34	0.00
NECTGL	24	39	41	3	2	3.53	1.57	3.61	2.34	1.67
NECTPU	5	54	16	4	0	0.74	2.18	1.41	3.13	0.00
NECTS1	1	2	3	0	0	0.15	0.08	0.26	0.00	0.00
NEEAAM	5	44	14	2	0	0.74	1.77	1.23	1.56	0.00
OCHRPY	0	6	0	1	0	0.00	0.24	0.00	0.78	0.00
OCOTCE	35	190	69	8	6	5.15	7.66	6.07	6.25	5.00
OCOTCB	16	102	66	0	0	2.35	4.11	5.81	0.00	0.00
OCOTPU	8	148	40	6	3	1.18	5.97	3.52	4.69	2.50
OCOTWH	19	169	549	24	0	2.79	6.81	48.33	18.75	0.00
OENOMA	133	1043	378	44	70	19.56	42.06	33.27	34.38	58.33
OLMEAS	10	87	159	21	1	1.47	3.51	14.00	16.41	0.83

Appendix 3 continued.

	Total number of stems					Number of stems/ha				
Species	High Plateau	Low Plateau	Slope	Stream	Swamp	High Plateau	Low Plateau	Slope	Stream	Swamp
ORMOAM	1	0	1	0	0	0.15	0.00	0.09	0.00	0.00
ORMOCR	14	18	30	4	0	2.06	0.73	2.64	3.13	0.00
ORMOMA	1	2	0	0	0	0.15	0.08	0.00	0.00	0.00
OURALU	118	826	171	47	5	17.35	33.31	15.05	36.72	4.17
PALIGU	90	950	157	9	109	13.24	38.31	13.82	7.03	90.83
PENTMA	39	216	151	23	1	5.74	8.71	13.29	17.97	0.83
PEREXA	0	235	36	1	0	0.00	9.48	3.17	0.78	0.00
PHOECI	11	45	18	5	2	1.62	1.81	1.58	3.91	1.67
PICRLA	151	473	410	29	6	22.21	19.07	36.09	22.66	5.00
PIPEAE	2	24	42	15	0	0.29	0.97	3.70	11.72	0.00
PIPEA1	2	29	24	3	1	0.29	1.17	2.11	2.34	0.83
PIPECA	0	0	3	1	0	0.00	0.00	0.26	0.78	0.00
PIPECO	174	1156	329	27	4	25.59	46.61	28.96	21.09	3.33
PIPECU	2	19	17	3	8	0.29	0.77	1.50	2.34	6.67
PIPEIM	0	0	3	0	0	0.00	0.00	0.26	0.00	0.00
PIPEPE	5	11	52	0	0	0.74	0.44	4.58	0.00	0.00
PIPERE	9	64	55	2	7	1.32	2.58	4.84	1.56	5.83
PIT1MA	0	1	0	0	0	0.00	0.04	0.00	0.00	0.00
PIT1RU	0	2	0	0	0	0.00	0.08	0.00	0.00	0.00
PLA1PI	30	161	49	9	4	4.41	6.49	4.31	7.03	3.33
PLA2EL	17	88	27	7	5	2.50	3.55	2.38	5.47	4.17
POCHQU	0	0	0	1	0	0.00	0.00	0.00	0.78	0.00
POCHSE	9	0	0	0	0	1.32	0.00	0.00	0.00	0.00
POSOLA	4	46	14	4	2	0.59	1.85	1.23	3.13	1.67
POULAR	90	805	1074	82	3	13.24	32.46	94.54	64.06	2.50
POURBI	0	25	16	2	0	0.00	1.01	1.41	1.56	0.00
POUTFO	0	1	2	0	0	0.00	0.04	0.18	0.00	0.00
POUTRE	252	907	375	44	44	37.06	36.57	33.01	34.38	36.67
POUTST	6	48	2	1	0	0.88	1.94	0.18	0.78	0.00
PRI2CO	127	972	256	34	4	18.68	39.19	22.54	26.56	3.33
PROTCO	68	442	297	30	0	10.00	17.82	26.14	23.44	0.00
PROTPA	141	1948	730	113	4	20.74	78.55	64.26	88.28	3.33
PROTTE	233	1583	1031	106	8	34.26	63.83	90.76	82.81	6.67
PROTSP	0	1	2	0	0	0.00	0.04	0.18	0.00	0.00
PSE1SE	1	9	2	0	1	0.15	0.36	0.18	0.00	0.83
PSIDFR	9	15	18	0	2	1.32	0.60	1.58	0.00	1.67
PSYCAC	0	7	0	0	2	0.00	0.28	0.00	0.00	1.67
PSYCB1	0	0	0	0	0	0.00	0.00	0.00	0.00	0.00
PSYCCH	0	8	6	1	0	0.00	0.32	0.53	0.78	0.00

Appendix 3 continued.

	Total number of stems					Number of stems/ha				
Species	High Plateau	Low Plateau	Slope	Stream	Swamp	High Plateau	Low Plateau	Slope	Stream	Swamp
PSYCDE	1	53	2	0	2	0.15	2.14	0.18	0.00	1.67
PSYCFU	0	1	0	0	0	0.00	0.04	0.00	0.00	0.00
PSYCG1	0	1	0	0	26	0.00	0.04	0.00	0.00	21.67
PSYCG2	0	2	1	0	0	0.00	0.08	0.09	0.00	0.00
PSYCG3	0	32	30	0	12	0.00	1.29	2.64	0.00	10.00
PSYCHO	1140	2601	989	113	99	167.65	104.88	87.06	88.28	82.50
PSYCLI	0	17	2	0	0	0.00	0.69	0.18	0.00	0.00
PSYCMA	57	439	108	5	21	8.38	17.70	9.51	3.91	17.50
PSYCPI	0	1	2	0	0	0.00	0.04	0.18	0.00	0.00
PSYCRA	0	2	0	0	0	0.00	0.08	0.00	0.00	0.00
PTERBE	0	1	1	1	0	0.00	0.04	0.09	0.78	0.00
PTERRO	160	998	366	40	28	23.53	40.24	32.22	31.25	23.33
QUARAS	435	955	630	81	5	63.97	38.51	55.46	63.28	4.17
QUASAM	17	79	39	4	4	2.50	3.19	3.43	3.13	3.33
RANDAR	187	579	181	37	18	27.50	23.35	15.93	28.91	15.00
RANDFO	1	3	0	0	0	0.15	0.12	0.00	0.00	0.00
RINOSY	451	1053	675	53	5	66.32	42.46	59.42	41.41	4.17
SAPIAU	4	18	9	1	3	0.59	0.73	0.79	0.78	2.50
SAPISP	0	0	2	1	0	0.00	0.00	0.18	0.78	0.00
SCH1ZO	1	14	10	2	6	0.15	0.56	0.88	1.56	5.00
SCHIPA	0	15	1	0	0	0.00	0.60	0.09	0.00	0.00
SENNDA	15	52	33	6	2	2.21	2.10	2.90	4.69	1.67
SIMAAM	97	863	232	28	28	14.26	34.80	20.42	21.88	23.33
SIPAGU	0	18	9	4	1	0.00	0.73	0.79	3.13	0.83
SIPAPA	50	121	109	7	1	7.35	4.88	9.60	5.47	0.83
SLOATE	46	344	142	28	0	6.76	13.87	12.50	21.88	0.00
SOCREX	7	441	220	11	0	1.03	17.78	19.37	8.59	0.00
SOLAAS	0	2	1	0	1	0.00	0.08	0.09	0.00	0.83
SOLAHA	4	39	28	0	2	0.59	1.57	2.46	0.00	1.67
SOLAST	0	2	0	0	0	0.00	0.08	0.00	0.00	0.00
SOROAF	295	1789	810	101	31	43.38	72.14	71.30	78.91	25.83
SPACME	0	14	1	0	0	0.00	0.56	0.09	0.00	0.00
SPONMO	1	37	8	17	10	0.15	1.49	0.70	13.28	8.33
SPONRA	12	104	60	7	6	1.76	4.19	5.28	5.47	5.00
STERAP	6	31	14	0	9	0.88	1.25	1.23	0.00	7.50
STYLST	85	347	183	15	44	12.50	13.99	16.11	11.72	36.67
SWARS1	646	1173	391	27	26	95.00	47.30	34.42	21.09	21.67
SWARS2	230	1590	648	85	3	33.82	64.11	57.04	66.41	2.50
SYMPGL	5	58	88	16	0	0.74	2.34	7.75	12.50	0.00

Appendix 3 continued.

Species	Total number of stems					Number of stems/ha				
	High Plateau	Low Plateau	Slope	Stream	Swamp	High Plateau	Low Plateau	Slope	Stream	Swamp
TAB1GU	6	45	6	2	0	0.88	1.81	0.53	1.56	0.00
TAB1RO	30	124	70	15	44	4.41	5.00	6.16	11.72	36.67
TAB2AR	127	798	286	33	69	18.68	32.18	25.18	25.78	57.50
TACHVE	242	1782	887	49	11	35.59	71.85	78.08	38.28	9.17
TALINE	149	362	189	12	3	21.91	14.60	16.64	9.38	2.50
TALIPR	164	234	162	13	17	24.12	9.44	14.26	10.16	14.17
TERMAM	1	32	3	1	10	0.15	1.29	0.26	0.78	8.33
TERMOB	0	67	25	0	0	0.00	2.70	2.20	0.00	0.00
TERNTE	0	1	0	0	0	0.00	0.04	0.00	0.00	0.00
TET2PA	298	2490	889	86	46	43.82	100.40	78.26	67.19	38.33
TET4JO	1	1	0	0	4	0.15	0.04	0.00	0.00	3.33
THEOCA	3	5	9	2	0	0.44	0.20	0.79	1.56	0.00
THEVAH	2	15	18	9	40	0.29	0.60	1.58	7.03	33.33
TOCOPI	1	2	2	1	1	0.15	0.08	0.18	0.78	0.83
TRATAS	6	51	20	1	3	0.88	2.06	1.76	0.78	2.50
TREMMI	4	13	3	1	0	0.59	0.52	0.26	0.78	0.00
TRI1GI	0	2	1	0	0	0.00	0.08	0.09	0.00	0.00
TRI2PA	107	278	60	19	23	15.74	11.21	5.28	14.84	19.17
TRI2TU	2839	5030	3164	334	194	417.50	202.82	278.52	260.94	161.67
TRI4GA	0	2	0	0	0	0.00	0.08	0.00	0.00	0.00
TRIPCU	88	97	53	8	38	12.94	3.91	4.67	6.25	31.67
TROPRA	31	135	116	7	6	4.56	5.44	10.21	5.47	5.00
TURPOC	14	47	16	2	0	2.06	1.90	1.41	1.56	0.00
UNONPI	56	354	340	11	1	8.24	14.27	29.93	8.59	0.83
URERBA	4	7	6	0	0	0.59	0.28	0.53	0.00	0.00
VIROSE	204	1102	566	43	9	30.00	44.44	49.82	33.59	7.50
VIROSU	13	90	113	12	5	1.91	3.63	9.95	9.38	4.17
VIROSP	3	19	30	1	0	0.44	0.77	2.64	0.78	0.00
VISMBA	2	39	12	0	13	0.29	1.57	1.06	0.00	10.83
VISMBI	1	0	0	0	0	0.15	0.00	0.00	0.00	0.00
VOCHFE	0	22	1	0	1	0.00	0.89	0.09	0.00	0.83
XYL1MA	86	354	584	2	2	12.65	14.27	51.41	1.56	1.67
XYL2OL	29	72	30	14	0	4.26	2.90	2.64	10.94	0.00
ZANTBE	19	152	59	3	0	2.79	6.13	5.19	2.34	0.00
ZANTP1	27	138	44	3	1	3.97	5.56	3.87	2.34	0.83
ZANTPR	8	111	42	1	2	1.18	4.48	3.70	0.78	1.67
ZANTSE	0	0	1	0	0	0.00	0.00	0.09	0.00	0.00
ZUELGU	3	19	9	1	6	0.44	0.77	0.79	0.78	5.00

APPENDIX 4

Habitat Associations on the 50-ha FDP Plot Based on Chi-square Criteria

Habitat associations based on the Chi-square analysis of all individuals ≥ 1-cm DBH of all 303 species encountered during the 1990 census of the 50-ha Forest Dynamics Project plot of Barro Colorado Island, Panamá. The ratio of observed values over expected values is provided to distinguish positive from negative associations. * $P<0.05$; ** $P<0.01$.

	High Plateau		Low Plateau		Slope		Stream		Swamp	
Species	Obs/Exp	χ^2	Obs/Exp	χ^2	Obs/Exp	χ^2	Obs/Exp	χ^2	Obs/Exp	χ^2
ACACME	0/1.54	1.79	1.44	2.78	0.36	1.48	0/0.28	Insuff.	6.00	Insuff.
ACALDI	1.07	0.64	0.78	46.89 * *	1.28	19.37 * *	2.27	30.53 * *	1.82	7.55 * *
ACALMA	0.65	0.89	1.24	3.28	0.55	3.01	2.66	3.20	0/0.67	Insuff.
ADE1TR	3.01	146.36 * *	0.76	16.43 * *	0.52	17.03 * *	0.53	1.32	0/3.38	3.43
AEGIPA	0.43	4.40 *	1.23	5.67 *	0.77	1.43	1.41	0.37	0.80	0.05
ALCHCO	0.80	1.59	1.12	4.12 *	0.98	0.03	0.34	2.70	0/3.53	3.58
ALCHLA	0/0.42	Insuff.	1.17	0.12	0/0.75	Insuff.	13.03	Insuff.	0/0.05	Insuff.
ALIBED	0.68	5.95 *	1.12	6.67 * *	0.68	11.92 * *	1.57	2.99	3.79	41.77 * *
ALLOPS	1.55	6.82 * *	0.94	0.62	0.87	0.77	1.13	0.06	0/2.09	2.12
ALSEBL	1.14	23.46 * *	1.03	8.95 * *	0.91	18.83 * *	0.73	13.94 * *	0.46	32.39 * *
AMAICO	0/4.35	5.06 *	1.36	5.30 *	0.90	0.09	0/0.79	Insuff.	0/0.47	Insuff.
ANACEX	0/2.94	3.43	0.75	1.70	1.34	0.78	1.86	Insuff.	12.57	Insuff.
ANAXPA	0/82.31	95.74 * *	0.19	514.90 * *	3.58	1302.52 * *	0/15.02	15.41 * *	0/8.89	9.03 * *
ANDIIN	1.21	1.99	0.94	1.39	1.08	0.66	0.71	0.63	0.48	1.17
ANNOAC	0.67	8.77 * *	0.81	24.83 * *	1.02	0.06	2.27	21.18 * *	8.86	474.52 * *
ANNOHA	0/0.14	Insuff.	1.76	Insuff.	0/0.25	Insuff.	0/0.03	Insuff.	0/0.02	Insuff.
ANNOSP	0.44	6.68 * *	1.13	3.13	1.05	0.10	0.30	1.67	1.52	0.55
APEIME	0.82	1.53	0.99	0.05	1.00	0.00	1.99	7.55 * *	1.34	0.53
APEITI	1.02	0.00	1.19	1.36	0.57	1.70	1.40	Insuff.	0/0.42	Insuff.
APHESI	0/0.98	Insuff.	0.50	2.30	0.57	0.43	16.75	Insuff.	9.43	Insuff.
APPUSE	0/0.56	Insuff.	0/2.28	5.29 *	4.01	12.02 * *	0/0.10	Insuff.	0/0.06	Insuff.
ARDIBA	0/0.14	Insuff.	1.76	Insuff.	0/0.25	Insuff.	0/0.03	Insuff.	0/0.02	Insuff.
ARDIFE	1.01	0.00	0.68	10.86 * *	1.75	14.44 * *	1.50	0.52	0/1.18	1.20
ARDIGU	0/1.54	1.79	1.12	0.20	0/2.75	3.66	14.21	Insuff.	0/0.17	Insuff.
ASPICR	1.48	16.52 * *	0.75	37.40 * *	1.42	25.61 * *	0.44	3.65	0.15	4.95 *
AST1ST	0.96	0.05	0.81	8.69 * *	0.97	0.06	0.84	0.12	9.23	193.64 * *
AST2GR	2.01	10.56 * *	0.85	1.89	0.56	4.06 *	3.05	7.09 * *	1.03	Insuff.
BACTBA	0.65	0.44	0.96	0.05	1.46	1.53	0/0.56	Insuff.	0/0.33	Insuff.
BACTC1	1.86	2.78	0.23	18.07 * *	2.44	15.83 * *	0/0.59	Insuff.	0/0.35	Insuff.
BACTC2	1.19	Insuff.	0.88	0.12	1.34	0.22	0/0.15	Insuff.	0/0.09	Insuff.

Appendix 4 continued.

Species	High Plateau		Low Plateau		Slope		Stream		Swamp	
	Obs/Exp	χ^2	Obs/Exp	χ^2	Obs/Exp	χ^2	Obs/Exp	χ^2	Obs/Exp	χ^2
BACTMA	0.42	10.55 * *	0.10	201.42 * *	0.19	41.18 * *	0/4.84	4.96 *	55.18	8534.26 * *
BANAGU	2.38	Insuff.	0.59	0.68	1.34	Insuff.	0/0.08	Insuff.	0/0.05	Insuff.
BEILPE	0.39	161.06 * *	1.00	0.00	1.44	174.59 * *	0.60	11.26 * *	0.02	39.11 * *
BERTGU	0/0.14	Insuff.	1.76	Insuff.	0/0.25	Insuff.	0/0.03	Insuff.	0/0.02	Insuff.
BROSAL	1.18	4.34 *	0.94	3.41	0.94	1.16	2.20	31.56 * *	0.47	3.55
BROSGU	0/0.14	Insuff.	0/0.57	Insuff.	4.01	Insuff.	0/0.03	Insuff.	0/0.02	Insuff.
CALOLO	0.22	85.68 * *	0.78	53.93 * *	1.99	281.07 * *	0.55	4.59 *	0.85	0.30
CAPPFR	1.52	138.64 * *	0.78	204.52 * *	1.15	22.57 * *	1.82	55.55 * *	0.72	3.87 *
CASEAC	1.55	20.22 * *	0.88	8.43 * *	0.99	0.00	1.22	0.55	0.32	2.97
CASEAR	0.92	0.16	1.18	7.10 * *	0.68	5.67 *	0.92	0.03	0.39	0.98
CASECO	0/2.94	3.43	1.42	4.94 *	0.57	1.28	1.86	Insuff.	0/0.32	Insuff.
CASEGU	3.06	9.65 * *	0.88	0.27	0.29	2.37	0/0.36	Insuff.	0/0.21	Insuff.
CASESY	0.74	2.09	1.01	0.03	1.00	0.00	1.49	1.15	2.15	3.76
CASSEL	0.68	14.10 * *	1.05	2.97	0.82	8.56 * *	0.56	4.30 *	5.66	280.31 * *
CAVAPL	3.00	12.43 * *	0.46	7.27 * *	1.26	0.44	0/0.49	Insuff.	0/0.29	Insuff.
CECRIN	1.20	2.58	1.07	2.17	0.82	3.89 *	0.52	2.34	0.35	2.48
CECROB	0.66	0.79	0.98	0.02	1.02	0.01	0/1.10	1.13	6.14	Insuff.
CEDROD	0/1.26	1.47	0.78	0.57	2.23	4.50 *	0/0.23	Insuff.	0/0.14	Insuff.
CEIBPE	1.02	0.00	0.97	0.06	0.72	1.51	2.79	4.72 *	3.54	Insuff.
CELTSC	0.60	3.66	0.88	2.79	1.52	12.93 * *	0.83	0.11	0.93	0.01
CESPMA	0/0.70	Insuff.	0/2.85	6.61 *	4.01	15.03 * *	0/0.13	Insuff.	0/0.08	Insuff.
CESTME	0.47	7.11 * *	0.75	13.04 * *	1.62	19.77 * *	2.55	9.71 * *	2.59	5.94 *
CHA1TE	0.48	0.67	0.23	11.63 * *	3.20	24.25 * *	0/0.38	Insuff.	0/0.23	Insuff.
CHA2SC	0.03	42.39 * *	1.67	164.08 * *	0.03	85.91 * *	0.14	5.29 *	2.17	5.75 *
CHIMPA	0/0.00	Insuff.	Insuff.	Insuff.	0/0.00	Insuff.	0/0.00	Insuff.	0/0.00	Insuff.
CHR1EC	0.11	53.00 * *	0.55	106.92 * *	2.42	271.29 * *	2.60	27.26 * *	0/6.15	6.25 *
CHR2AR	0.95	0.23	0.95	2.11	1.12	3.10	1.17	0.47	1.04	0.01
CHR2CA	1.84	10.31 * *	0.69	11.26 * *	0.99	0.00	0.44	0.74	5.93	33.32 * *
CLIDDE	0.42	0.93	0.93	0.11	0.71	0.49	2.30	Insuff.	11.65	Insuff.
CLIDOC	2.38	2.78	0.98	0.01	0.45	0.92	0/0.23	Insuff.	0/0.14	Insuff.
CNEMPE	0/0.14	Insuff.	0/0.57	Insuff.	4.01	Insuff.	0/0.03	Insuff.	0/0.02	Insuff.
COCOCO	1.02	0.01	0.95	0.53	1.00	0.00	2.09	5.28 *	0.79	0.12
COCCMA	0.86	1.29	1.17	16.56 * *	0.69	13.63 * *	0.82	0.37	1.23	0.35
COLUGL	0/0.14	Insuff.	1.76	Insuff.	0/0.25	Insuff.	0/0.03	Insuff.	0/0.02	Insuff.
CONOBR	0/0.42	Insuff.	0.59	0.68	0/0.75	Insuff.	26.05	Insuff.	0/0.05	Insuff.
CONOCI	0.72	2.53	0.46	75.99 * *	2.06	74.50 * *	3.36	28.85 * *	2.33	5.42 *
CORDAL	1.31	1.69	1.03	0.14	0.55	7.30 * *	2.15	3.79	2.42	3.39
CORDBI	0.37	64.20 * *	1.24	77.58 * *	0.84	8.83 * *	0.55	5.15 *	1.14	0.28
CORDLA	0.88	3.62	0.84	53.11 * *	1.38	75.70 * *	1.13	0.69	1.62	9.30 * *
COU2CU	0.32	137.00 * *	1.50	592.34 * *	0.32	276.23 * *	0.30	23.16 * *	0.95	0.08

Appendix 4 continued.

Species	High Plateau		Low Plateau		Slope		Stream		Swamp	
	Obs/Exp	χ^2	Obs/Exp	χ^2	Obs/Exp	χ^2	Obs/Exp	χ^2	Obs/Exp	χ^2
COUTHE	0/0.14	Insuff.	0/0.57	Insuff.	4.01	Insuff.	0/0.03	Insuff.	0/0.02	Insuff.
CROTBI	0.44	45.28 * *	1.12	15.87 * *	0.54	62.40 * *	2.37	44.07 * *	7.05	501.12 * *
CUPACI	0.79	0.06	1.17	0.35	0.45	0.92	4.34	Insuff.	0/0.14	Insuff.
CUPALA	0.44	2.54	0.90	0.70	1.63	6.57 *	0.80	0.05	0/0.74	Insuff.
CUPARU	0.16	9.92 * *	1.33	12.71 * *	0.41	9.93 * *	0/2.23	2.28	7.59	58.06 * *
CUPASY	1.05	0.51	1.11	16.89 * *	0.77	19.41 * *	1.14	0.55	0/16.09	16.34 * *
CYPHHA	0/0.42	Insuff.	1.76	2.27	0/0.75	Insuff.	0/0.08	Insuff.	0/0.05	Insuff.
DENDAR	3.57	15.03 * *	0.63	2.57	0.57	0.85	0/0.36	Insuff.	0/0.21	Insuff.
DENDST	0.20	11.48 * *	1.19	5.33 *	1.03	0.03	0.36	1.18	1.82	1.12
DES2PA	1.37	251.26 * *	0.95	34.26 * *	0.92	22.85 * *	0.85	6.36 *	0.91	1.28
DIO2AR	0.10	9.21 * *	1.30	8.59 * *	0.86	0.47	0.56	0.36	0.94	0.00
DIPTPA	0.71	0.67	1.12	1.02	0.72	1.29	3.13	5.94 *	0/0.76	Insuff.
DRYPST	1.19	12.66 * *	0.63	392.69 * *	1.87	554.03 * *	0.20	37.32 * *	0.09	27.98 * *
ELAEOL	0/2.24	2.61	0/9.11	21.16 * *	0/3.99	5.32 *	0/0.41	Insuff.	66.00	Insuff.
ENTESC	1.19	0.07	0.88	0.24	1.00	0.00	3.26	Insuff.	0/0.18	Insuff.
ERY1CO	0.59	4.51 *	0.91	1.82	1.43	10.36 * *	1.40	0.69	0.39	0.95
ERY2MA	0.95	0.13	1.00	0.00	1.15	2.05	0.42	2.46	0/4.23	4.29 *
ERY2PA	0.85	0.33	0.86	2.42	1.26	2.11	1.27	0.18	2.87	4.95 *
EUGECO	1.16	3.36	0.99	0.03	0.97	0.21	0.85	0.44	0.42	3.98 *
EUGEGA	1.57	66.87 * *	1.01	0.10	0.74	28.91 * *	0.40	12.09 * *	0.78	0.97
EUGENE	1.37	11.11 * *	0.96	0.87	0.85	3.63	1.50	3.28	0.53	1.65
EUGEOE	1.06	1.14	1.07	15.54 * *	0.88	9.81 * *	0.43	18.13 * *	0.58	5.83 *
FARAOC	1.25	247.05 * *	1.10	317.84 * *	0.63	1080.92 * *	0.89	7.42 * *	1.16	9.39 * *
FICUBU	7.13	Insuff.	0/0.57	Insuff.	0/0.25	Insuff.	0/0.03	Insuff.	0/0.02	Insuff.
FICUCI	0/0.14	Insuff.	1.76	Insuff.	0/0.25	Insuff.	0/0.03	Insuff.	0/0.02	Insuff.
FICUC1	0/0.14	Insuff.	0/0.57	Insuff.	0/0.25	Insuff.	39.08	Insuff.	0/0.02	Insuff.
FICUC2	3.06	Insuff.	0.50	2.30	0.57	0.43	0/0.18	Insuff.	9.43	Insuff.
FICUIN	0/0.70	Insuff.	0.35	2.78	0.80	0.07	7.82	Insuff.	26.40	Insuff.
FICUMA	0/1.40	1.63	0.88	0.20	1.60	1.21	0/0.26	Insuff.	6.60	Insuff.
FICUOB	1.02	Insuff.	1.00	0.00	0/1.75	2.33	0/0.18	Insuff.	18.86	Insuff.
FICUPE	0/0.14	Insuff.	1.76	Insuff.	0/0.25	Insuff.	0/0.03	Insuff.	0/0.02	Insuff.
FICUPO	1.02	Insuff.	1.25	0.60	0/1.75	2.33	0/0.18	Insuff.	9.43	Insuff.
FICUTO	0.51	1.65	0.79	2.34	1.53	3.87 *	3.72	8.17 * *	0/0.64	Insuff.
FICUTR	1.78	Insuff.	0/2.28	5.29 *	2.00	1.34	9.77	Insuff.	0/0.06	Insuff.
FICUYO	0/0.56	Insuff.	0.88	0.08	0/1.00	1.33	19.54	Insuff.	0/0.06	Insuff.
GAR2IN	1.49	156.60 * *	0.95	10.93 * *	0.89	17.68 * *	0.57	19.48 * *	0.80	2.45
GAR2MA	0.84	1.98	0.96	0.85	1.07	0.78	2.51	28.86 * *	0.14	5.54 *
GENIAM	0.86	0.27	0.89	1.36	1.01	0.00	2.35	4.00 *	3.98	11.31 * *
GEONIN	0/0.42	Insuff.	0/1.71	3.97 *	4.01	Insuff.	0/0.08	Insuff.	0/0.05	Insuff.
GUAPST	1.35	3.54	1.06	0.96	0.73	4.23 *	0.65	0.57	0.37	1.11

Appendix 4 continued.

Species	High Plateau		Low Plateau		Slope		Stream		Swamp	
	Obs/Exp	χ^2	Obs/Exp	χ^2	Obs/Exp	χ^2	Obs/Exp	χ^2	Obs/Exp	χ^2
GUARGR	0.97	0.01	0.98	0.02	1.15	0.47	0.66	0.18	0/0.89	Insuff.
GUARGU	1.18	9.36 * *	0.66	270.91 * *	1.50	153.40 * *	1.95	43.28 * *	2.06	31.73 * *
GUARSP	1.19	7.75 * *	0.86	31.35 * *	1.16	10.35 * *	1.55	10.04 * *	0.84	0.51
GUATDU	0.38	87.52 * *	0.97	2.23	1.50	116.75 * *	0.76	2.14	0.19	14.06 * *
GUAZUL	2.16	7.25 * *	0.80	1.77	0.85	0.25	0/0.84	Insuff.	2.00	Insuff.
GUETFO	1.10	0.45	1.00	0.00	0.82	3.13	1.92	6.74 * *	1.51	1.22
GUSTSU	2.08	79.38 * *	0.72	43.86 * *	0.86	2.66	2.93	40.34 * *	0.64	0.84
HAMEAX	0.38	5.91 *	0.95	0.28	1.07	0.13	2.91	9.01 * *	4.21	14.93 * *
HAMEPA	0/0.28	Insuff.	1.76	1.51	0/0.50	Insuff.	0/0.05	Insuff.	0/0.03	Insuff.
HAMPAP	0.59	0.97	1.22	2.30	0.78	0.59	0/0.92	Insuff.	1.83	Insuff.
HASSFL	0.69	12.40 * *	0.91	9.34 * *	1.17	7.55 * *	2.11	25.90 * *	2.74	37.02 * *
HEISAC	0.29	7.88 * *	1.01	0.02	1.36	4.25 *	0.81	0.10	1.36	0.19
HEISCO	1.10	1.47	0.98	0.30	0.96	0.59	1.33	2.66	0.84	0.37
HERRPU	0.56	15.82 * *	1.07	3.32	1.03	0.12	1.70	6.45 *	0.78	0.37
HIRTAM	0/6.45	7.50 * *	1.22	2.99	1.04	0.03	0/1.18	1.21	2.87	Insuff.
HIRTTR	0.38	298.21 * *	0.95	16.31 * *	1.50	388.20 * *	1.02	0.06	0.45	21.92 * *
HURACR	1.53	5.10 *	0.72	11.50 * *	1.18	1.21	1.05	0.01	3.54	11.08 * *
HYBAPR	0.98	2.94	1.06	171.19 * *	0.95	32.01 * *	0.78	45.36 * *	0.18	376.94 * *
HYERAL	0.51	3.30	0.86	2.26	1.19	1.03	0.93	0.01	7.86	60.77 * *
INGACO	0.03	35.06 * *	1.53	83.84 * *	0.31	35.77 * *	1.37	0.80	0.86	0.06
INGAFA	0.70	0.89	0.95	0.20	0.59	3.40	1.28	0.13	11.90	Insuff.
INGAGO	0.55	14.03 * *	0.93	2.48	1.29	12.32 * *	0.82	0.35	3.09	28.73 * *
INGAMA	0.90	1.04	0.80	37.12 * *	1.55	68.71 * *	0.81	0.67	0.78	0.52
INGAMI	0/1.12	1.30	0.88	0.16	2.00	2.68	0/0.20	Insuff.	0/0.12	Insuff.
INGAM1	0/0.14	Insuff.	1.76	Insuff.	0/0.25	Insuff.	0/0.03	Insuff.	0/0.02	Insuff.
INGAPE	1.24	1.61	0.34	102.04 * *	2.19	84.76 * *	3.28	24.33 * *	0/2.71	2.75
INGAPU	4.19	28.30 * *	0.21	14.15 * *	0.94	0.02	2.30	Insuff.	0/0.26	Insuff.
INGAQU	0.81	4.23 *	0.83	27.23 * *	1.53	63.70 * *	1.08	0.11	0.48	2.89
INGARU	0.53	1.96	1.24	3.97 *	0.82	0.61	0.72	0.11	0/0.82	Insuff.
INGASA	0.91	0.44	1.01	0.02	1.04	0.20	1.40	1.29	0.21	2.91
INGASP	0.31	1.79	1.30	2.70	0.52	1.75	1.70	Insuff.	2.87	Insuff.
INGAUM	0.79	6.65 * *	1.14	26.45 * *	0.79	13.73 * *	1.41	4.31 *	0.20	9.44 * *
INGAS1	1.01	0.00	1.05	0.89	1.03	0.10	0.14	5.52 *	0/4.29	4.35 *
JAC1CO	0.47	12.50 * *	1.25	22.21 * *	0.75	5.76 *	0.86	0.14	0.97	0.00
KOANWE	0/1.68	1.96	0.73	1.14	0.67	0.44	16.28	Insuff.	0/0.18	Insuff.
LACIAG	0.51	61.81 * *	1.15	44.90 * *	0.92	3.38	1.57	13.75 * *	0.37	9.58 * *
LACMPA	1.10	0.15	1.02	0.07	0.62	4.04 *	1.86	1.64	3.93	11.08 * *
LAETPR	0/4.21	4.89 *	1.23	2.09	0.40	3.59	5.21	Insuff.	4.40	Insuff.
LAETTH	0.28	42.26 * *	1.49	158.68 * *	0.33	74.43 * *	0.62	1.91	0.92	0.05
LAFOPU	0/0.70	Insuff.	1.41	1.08	0/1.25	1.66	0/0.13	Insuff.	13.20	Insuff.

Appendix 4 continued.

Species	High Plateau		Low Plateau		Slope		Stream		Swamp	
	Obs/Exp	χ^2	Obs/Exp	χ^2	Obs/Exp	χ^2	Obs/Exp	χ^2	Obs/Exp	χ^2
LEANDI	0/0.14	Insuff.	1.76	Insuff.	0/0.25	Insuff.	0/0.03	Insuff.	0/0.02	Insuff.
LICAHY	0.63	2.83	1.26	11.57 * *	0.77	2.22	0/3.20	3.28	0/1.89	1.92
LICAPL	0.09	41.04 * *	0.79	18.47 * *	2.00	102.38 * *	1.40	1.32	0.22	2.90
LINDLA	0.75	0.77	1.11	1.20	0.42	8.46 * *	0.51	0.47	9.55	85.53 * *
LONCLA	0.48	36.27 * *	1.15	22.81 * *	1.00	0.00	0.86	0.43	0.64	1.59
LOZAPI	0/0.98	Insuff.	0/3.99	9.26 * *	4.01	21.04 * *	0/0.18	Insuff.	0/0.11	Insuff.
LUEHSE	1.01	0.01	0.96	0.38	0.72	5.07 *	1.23	0.27	6.60	91.67 * *
MACLTI	0/0.14	Insuff.	0/0.57	Insuff.	0/0.25	Insuff.	0/0.03	Insuff.	66.00	Insuff.
MACRGL	0.67	1.50	0.64	14.52 * *	1.37	3.80	7.82	103.71 * *	0/1.29	1.31
MALMSP	0.25	31.51 * *	1.13	7.86 * *	1.03	0.09	0.68	0.90	3.08	22.80 * *
MALPRO	0.91	0.08	0.86	1.38	0.80	0.72	7.11	53.84 * *	0/0.83	Insuff.
MAQUCO	0.94	0.78	0.91	16.31 * *	1.23	24.42 * *	1.60	13.42 * *	0.28	11.30 * *
MARGNO	0/0.56	Insuff.	1.32	0.53	1.00	0.00	0/0.10	Insuff.	0/0.06	Insuff.
MAR1LA	0/3.09	3.59	0.08	24.63 * *	1.64	2.99	21.32	Insuff.	0/0.33	Insuff.
MAYTSC	0.60	2.15	0.99	0.00	1.16	0.69	1.88	1.70	0.80	0.05
MICOAF	0.28	35.43 * *	1.43	101.05 * *	0.40	50.14 * *	0.85	0.25	1.75	3.62
MICOAR	0.97	0.13	1.02	0.28	0.65	32.11 * *	0.76	1.20	6.91	415.52 * *
MICOEL	0.24	2.84	1.64	16.21 * *	0/7.49	9.98 * *	1.30	Insuff.	0/0.45	Insuff.
MICOHO	0/4.21	4.89 *	1.41	6.51 *	0.27	5.36 *	0/0.77	Insuff.	8.80	Insuff.
MICOIM	0/0.98	Insuff.	0.50	2.30	1.72	1.20	5.58	Insuff.	9.43	Insuff.
MICONE	0.39	18.23 * *	1.42	68.41 * *	0.28	50.46 * *	0.13	5.86 *	4.24	47.71 * *
MICOPR	0/0.14	Insuff.	1.76	Insuff.	0/0.25	Insuff.	0/0.03	Insuff.	0/0.02	Insuff.
MOURMY	0.91	9.61 * *	1.19	335.51 * *	0.62	327.95 * *	0.98	0.05	0.91	0.96
MYRCGA	0.82	0.27	0.91	0.53	0.85	0.40	5.26	24.79 * *	1.27	Insuff.
MYROFR	0.31	1.79	1.22	1.50	0.87	0.13	0/0.59	Insuff.	2.87	Insuff.
NECTCI	0.11	40.08 * *	1.42	72.87 * *	0.67	11.66 * *	0.37	3.21	0/4.74	4.82 *
NECTGL	1.57	5.78 *	0.63	19.90 * *	1.51	9.31 * *	1.08	0.02	1.21	0.07
NECTPU	0.45	3.88 *	1.20	4.20 *	0.81	0.94	1.98	1.99	0/1.20	1.22
NECTS1	1.19	Insuff.	0.59	1.36	2.00	2.01	0/0.15	Insuff.	0/0.09	Insuff.
NEEAAM	0.55	2.16	1.19	3.07	0.86	0.41	1.20	0.07	0/0.98	Insuff.
OCHRPY	0/0.98	Insuff.	1.51	2.36	0/1.75	2.33	5.58	Insuff.	0/0.11	Insuff.
OCOTCE	0.81	1.81	1.08	2.83	0.90	1.08	1.02	0.00	1.29	0.39
OCOTOB	0.62	4.33 *	0.97	0.17	1.44	11.68 * *	0/4.71	4.83 *	0/2.79	2.83
OCOTPU	0.28	17.42 * *	1.27	19.46 * *	0.78	3.25	1.14	0.11	0.97	0.00
OCOTWH	0.18	83.85 * *	0.39	374.38 * *	2.89	904.14 * *	1.23	1.08	0/11.53	11.71 * *
OENOMA	0.57	50.63 * *	1.10	21.27 * *	0.91	4.72 *	1.03	0.04	2.77	80.39 * *
OLMEAS	0.26	25.06 * *	0.55	74.56 * *	2.29	154.15 * *	2.95	27.82 * *	0.24	2.49
ORMOAM	3.57	Insuff.	0/1.14	2.64	2.00	Insuff.	0/0.05	Insuff.	0/0.03	Insuff.
ORMOCR	1.51	2.83	0.48	23.69 * *	1.82	14.79 * *	2.37	3.25	0/1.00	1.02
ORMOMA	2.38	Insuff.	1.17	0.12	0/0.75	Insuff.	0/0.08	Insuff.	0/0.05	Insuff.

Appendix 4 continued.

Species	High Plateau		Low Plateau		Slope		Stream		Swamp	
	Obs/Exp	χ^2	Obs/Exp	χ^2	Obs/Exp	χ^2	Obs/Exp	χ^2	Obs/Exp	χ^2
OURALU	0.72	14.81 * *	1.24	91.19 * *	0.59	66.25 * *	1.57	10.10 * *	0.28	9.23 * *
PALIGU	0.49	56.21 * *	1.27	125.64 * *	0.48	119.11 * *	0.27	18.53 * *	5.47	404.39 * *
PENTMA	0.65	8.75 * *	0.88	7.89 * *	1.41	23.65 * *	2.09	13.43 * *	0.15	4.74 *
PEREXA	0/38.14	44.36 * *	1.52	96.27 * *	0.53	19.98 * *	0.14	5.24 *	0/4.12	4.18 *
PHOECI	0.97	0.01	0.98	0.06	0.89	0.33	2.41	4.24 *	1.63	0.49
PICRLA	1.01	0.01	0.78	70.22 * *	1.54	102.29 * *	1.06	0.10	0.37	6.52 *
PIPEAE	0.17	9.28 * *	0.51	26.58 * *	2.03	29.12 * *	7.06	80.12 * *	0/1.26	1.28
PIPEA1	0.24	5.53 *	0.86	1.46	1.63	7.78 * *	1.99	1.51	1.12	Insuff.
PIPECA	0/0.56	Insuff.	0/2.28	5.29 *	3.00	5.35 *	9.77	Insuff.	0/0.06	Insuff.
PIPECO	0.73	19.47 * *	1.20	90.59 * *	0.78	27.27 * *	0.62	6.26 *	0.16	18.51 * *
PIPECU	0.29	4.02 *	0.68	6.59 *	1.39	2.48	2.39	2.50	10.78	Insuff.
PIPEIM	0/0.42	Insuff.	0/1.71	3.97 *	4.01	Insuff.	0/0.08	Insuff.	0/0.05	Insuff.
PIPEPE	0.52	2.51	0.28	46.08 * *	3.06	96.30 * *	0/1.74	1.79	0/1.03	1.05
PIPERE	0.47	6.31 *	0.82	5.84 *	1.61	16.85 * *	0.57	0.66	3.37	11.86 * *
PIT1MA	0/0.14	Insuff.	1.76	Insuff.	0/0.25	Insuff.	0/0.03	Insuff.	0/0.02	Insuff.
PIT1RU	0/0.28	Insuff.	1.76	1.51	0/0.50	Insuff.	0/0.05	Insuff.	0/0.03	Insuff.
PLA1PI	0.85	0.98	1.12	4.63 *	0.78	4.23 *	1.39	1.01	1.04	0.01
PLA2EL	0.84	0.59	1.07	1.02	0.75	2.97	1.90	3.06	2.29	3.70
POCHQU	0/0.14	Insuff.	0/0.57	Insuff.	0/0.25	Insuff.	39.08	Insuff.	0/0.02	Insuff.
POCHSE	7.13	55.18 * *	0/5.12	11.90 * *	0/2.25	2.99	0/0.23	Insuff.	0/0.14	Insuff.
POSOLA	0.41	4.01 *	1.15	2.20	0.80	0.92	2.23	2.80	1.89	0.84
POULAR	0.31	158.36 * *	0.69	263.82 * *	2.09	818.56 * *	1.56	16.93 * *	0.10	25.80 * *
POURBI	0/6.03	7.01 * *	1.02	0.03	1.49	3.44	1.82	0.76	0/0.65	Insuff.
POUTFO	0/0.42	Insuff.	0.59	0.68	2.67	Insuff.	0/0.08	Insuff.	0/0.05	Insuff.
POUTRE	1.11	3.08	0.98	0.69	0.93	2.95	1.06	0.15	1.79	15.59 * *
POUTST	0.75	0.58	1.48	17.29 * *	0.14	14.01 * *	0.69	0.15	0/0.86	Insuff.
PRI2CO	0.65	27.81 * *	1.23	93.66 * *	0.74	32.27 * *	0.95	0.08	0.19	14.08 * *
PROTCO	0.58	24.15 * *	0.93	5.82 *	1.42	49.43 * *	1.40	3.53	0/12.68	12.88 * *
PROTPA	0.34	207.03 * *	1.17	106.05 * *	1.00	0.02	1.50	19.60 * *	0.09	37.41 * *
PROTTE	0.56	93.01 * *	0.94	14.59 * *	1.39	153.48 * *	1.40	12.38 * *	0.18	30.75 * *
PROTSP	0/0.42	Insuff.	0.59	0.68	2.67	Insuff.	0/0.08	Insuff.	0/0.05	Insuff.
PSE1SE	0.55	0.43	1.22	0.80	0.62	0.64	0/0.33	Insuff.	5.08	Insuff.
PSIDFR	1.46	1.51	0.60	9.37 * *	1.64	5.97 *	0/1.13	1.16	3.00	Insuff.
PSYCAC	0/1.26	1.47	1.37	1.59	0/2.25	2.99	0/0.23	Insuff.	14.67	Insuff.
PSYCB1	0/0.00	Insuff.	Insuff.	Insuff.	0/0.00	Insuff.	0/0.00	Insuff.	0/0.00	Insuff.
PSYCCH	0/2.10	2.45	0.94	0.08	1.60	1.81	2.61	Insuff.	0/0.23	Insuff.
PSYCDE	0.12	7.28 * *	1.60	28.06 * *	0.14	14.33 * *	0/1.48	1.52	2.28	Insuff.
PSYCFU	0/0.14	Insuff.	1.76	Insuff.	0/0.25	Insuff.	0/0.03	Insuff.	0/0.02	Insuff.
PSYCG1	0/3.79	4.40 *	0.07	31.21 * *	0/6.74	8.98 * *	0/0.69	Insuff.	63.56	Insuff.
PSYCG2	0/0.42	Insuff.	1.17	0.12	1.34	Insuff.	0/0.08	Insuff.	0/0.05	Insuff.

Appendix 4 continued.

Species	High Plateau		Low Plateau		Slope		Stream		Swamp	
	Obs/Exp	χ^2	Obs/Exp	χ^2	Obs/Exp	χ^2	Obs/Exp	χ^2	Obs/Exp	χ^2
PSYCG3	0/10.38	12.07 * *	0.76	5.66 *	1.62	9.58 * *	0/1.89	1.94	10.70	107.19 * *
PSYCHO	1.65	335.34 * *	0.92	37.40 * *	0.80	64.73 * *	0.89	1.47	1.32	7.89 * *
PSYCLI	0/2.66	3.10	1.57	8.20 * *	0.42	2.11	0/0.49	Insuff.	0/0.29	Insuff.
PSYCMA	0.65	12.93 * *	1.22	41.73 * *	0.69	20.58 * *	0.31	7.87 * *	2.20	13.96 * *
PSYCPI	0/0.42	Insuff.	0.59	0.68	2.67	Insuff.	0/0.08	Insuff.	0/0.05	Insuff.
PSYCRA	0/0.28	Insuff.	1.76	1.51	0/0.50	Insuff.	0/0.05	Insuff.	0/0.03	Insuff.
PTERBE	0/0.42	Insuff.	0.59	0.68	1.34	Insuff.	13.03	Insuff.	0/0.05	Insuff.
PTERRO	0.72	20.84 * *	1.10	21.47 * *	0.92	3.32	0.98	0.01	1.16	0.63
QUARAS	1.47	76.84 * *	0.80	115.41 * *	1.20	27.54 * *	1.50	14.00 * *	0.16	23.04 * *
QUASAM	0.85	0.54	0.97	0.17	1.09	0.41	1.09	0.03	1.85	1.58
RANDAR	1.33	17.89 * *	1.01	0.29	0.72	25.48 * *	1.44	5.17 *	1.19	0.53
RANDFO	1.78	Insuff.	1.32	0.53	0/1.00	1.33	0/0.10	Insuff.	0/0.06	Insuff.
RINOSY	1.44	69.91 * *	0.83	88.81 * *	1.21	32.40 * *	0.93	0.32	0.15	25.01 * *
SAPIAU	0.82	0.20	0.90	0.43	1.03	0.01	1.12	Insuff.	5.66	Insuff.
SAPISP	0/0.42	Insuff.	0/1.71	3.97 *	2.67	Insuff.	13.03	Insuff.	0/0.05	Insuff.
SCH1ZO	0.22	3.31	0.75	2.84	1.21	0.50	2.37	Insuff.	12.00	Insuff.
SCHIPA	0/2.24	2.61	1.65	8.84 * *	0.25	2.99	0/0.41	Insuff.	0/0.24	Insuff.
SENNDA	0.99	0.00	0.85	3.40	1.22	1.80	2.17	3.89 *	1.22	0.08
SIMAAM	0.55	40.44 * *	1.21	75.92 * *	0.74	27.08 * *	0.88	0.50	1.48	4.44 *
SIPAGU	0/4.49	5.22 *	0.99	0.01	1.13	0.17	4.89	Insuff.	2.06	Insuff.
SIPAPA	1.24	2.66	0.74	26.16 * *	1.52	25.51 * *	0.95	0.02	0.23	2.63
SLOATE	0.59	15.67 * *	1.08	4.61 *	1.02	0.05	1.95	13.39 * *	0/8.48	8.61 * *
SOCREX	0.07	95.06 * *	1.14	17.77 * *	1.30	20.04 * *	0.63	2.40	0/10.29	10.45 * *
SOLAAS	0/0.56	Insuff.	0.88	0.08	1.00	0.00	0/0.10	Insuff.	16.50	Insuff.
SOLAHA	0.39	4.42 *	0.94	0.37	1.54	6.99 * *	0/1.87	1.92	1.81	0.73
SOLAST	0/0.28	Insuff.	1.76	1.51	0/0.50	Insuff.	0/0.05	Insuff.	0/0.03	Insuff.
SOROAF	0.70	45.85 * *	1.04	5.88 *	1.07	5.25 *	1.30	7.37 * *	0.68	4.88 *
SPACME	0/2.10	2.45	1.64	8.10 * *	0.27	2.68	0/0.38	Insuff.	0/0.23	Insuff.
SPONMO	0.10	9.69 * *	0.89	1.16	0.44	7.65 * *	9.10	125.81 * *	9.04	72.62 * *
SPONRA	0.45	9.23 * *	0.97	0.28	1.27	4.64 *	1.45	0.99	2.10	3.49
STERAP	0.71	0.81	0.91	0.68	0.93	0.09	0/1.54	1.58	9.90	Insuff.
STYLST	0.90	1.11	0.90	8.18 * *	1.09	1.72	0.87	0.30	4.31	113.52 * *
SWARS1	2.04	395.92 * *	0.91	24.05 * *	0.69	71.39 * *	0.47	16.93 * *	0.76	2.03
SWARS2	0.64	53.52 * *	1.09	28.94 * *	1.02	0.20	1.30	6.03 *	0.08	33.46 * *
SYMPGL	0.21	16.85 * *	0.61	33.59 * *	2.11	68.55 * *	3.74	33.03 * *	0/2.53	2.57
TAB1GU	0.73	0.73	1.34	8.99 * *	0.41	6.90 * *	1.32	0.16	0/0.89	Insuff.
TAB1RO	0.76	2.75	0.77	19.87 * *	0.99	0.01	2.07	8.53 * *	10.26	373.48 * *
TAB2AR	0.69	20.61 * *	1.07	7.89 * *	0.87	7.10 * *	0.98	0.01	3.47	123.09 * *
TACHVE	0.58	85.12 * *	1.05	11.21 * *	1.20	37.92 * *	0.64	9.86 * *	0.24	26.10 * *
TALINE	1.49	27.55 * *	0.89	11.61 * *	1.06	0.82	0.66	2.22	0.28	5.75 *

Appendix 4 continued.

	High Plateau		Low Plateau		Slope		Stream		Swamp	
Species	Obs/Exp	χ^2	Obs/Exp	χ^2	Obs/Exp	χ^2	Obs/Exp	χ^2	Obs/Exp	χ^2
TALIPR	1.98	92.84 * *	0.70	71.83 * *	1.10	1.96	0.86	0.30	1.90	7.38 * *
TERMAM	0.15	5.52 *	1.20	2.38	0.26	8.66 * *	0.83	0.04	14.04	Insuff.
TERMOB	0/12.90	15.01 * *	1.28	9.47 * *	1.09	0.24	0/2.35	2.42	0/1.39	1.42
TERNTE	0/0.14	Insuff.	1.76	Insuff.	0/0.25	Insuff.	0/0.03	Insuff.	0/0.02	Insuff.
TET2PA	0.56	121.41 * *	1.15	110.49 * *	0.93	5.38 *	0.88	1.38	0.80	2.41
TET4JO	1.19	Insuff.	0.29	3.97 *	0/1.50	2.00	0/0.15	Insuff.	44.00	Insuff.
THEOCA	1.13	0.05	0.46	7.27 * *	1.90	5.09 *	4.11	Insuff.	0/0.29	Insuff.
THEVAH	0.17	9.44 * *	0.31	52.33 * *	0.86	0.56	4.19	22.41 * *	31.43	1196.62 * *
TOCOPI	1.02	Insuff.	0.50	2.30	1.14	0.05	5.58	Insuff.	9.43	Insuff.
TRATAS	0.53	2.94	1.11	1.20	0.99	0.00	0.48	0.57	2.44	2.60
TREMMI	1.36	0.44	1.09	0.21	0.57	1.28	1.86	Insuff.	0/0.32	Insuff.
TRI1GI	0/0.42	Insuff.	1.17	0.12	1.34	Insuff.	0/0.08	Insuff.	0/0.05	Insuff.
TRI2PA	1.57	25.52 * *	1.00	0.00	0.49	41.57 * *	1.52	3.52	3.12	33.58 * *
TRI2TU	1.75	1064.04 * *	0.76	850.41 * *	1.10	35.62 * *	1.13	5.06 *	1.11	2.06
TRI4GA	0/0.28	Insuff.	1.76	1.51	0/0.50	Insuff.	0/0.05	Insuff.	0/0.03	Insuff.
TRIPCU	2.21	67.78 * *	0.60	60.12 * *	0.75	6.02 *	1.10	0.08	8.83	267.96 * *
TROPRA	0.75	3.02	0.80	15.03 * *	1.58	32.46 * *	0.93	0.04	1.34	0.53
TURPOC	1.26	0.90	1.04	0.21	0.81	0.94	0.99	0.00	0/1.20	1.22
UNONPI	0.52	28.15 * *	0.82	34.14 * *	1.79	157.13 * *	0.56	3.80	0.09	9.78 * *
URERBA	1.68	1.27	0.72	1.72	1.41	0.97	0/0.43	Insuff.	0/0.26	Insuff.
VIROSE	0.76	18.66 * *	1.01	0.09	1.18	20.36 * *	0.87	0.81	0.31	14.14 * *
VIROSU	0.40	13.78 * *	0.68	31.86 * *	1.94	68.88 * *	2.01	6.28 *	1.42	0.62
VIROSP	0.40	3.07	0.63	9.61 * *	2.27	28.32 * *	0.74	0.10	0/0.80	Insuff.
VISMBA	0.22	6.61 *	1.04	0.12	0.73	1.62	0/1.69	1.73	13.00	146.23 * *
VISMBI	7.13	Insuff.	0/0.57	Insuff.	0/0.25	Insuff.	0/0.03	Insuff.	0/0.02	Insuff.
VOCHFE	0/3.37	3.91 *	1.61	11.81 * *	0.17	5.54 *	0/0.61	Insuff.	2.75	Insuff.
XYL1MA	0.60	27.29 * *	0.60	212.30 * *	2.28	556.47 * *	0.08	23.05 * *	0.13	12.01 * *
XYL2OL	1.43	4.30 *	0.87	3.14	0.83	1.42	3.77	29.29 * *	0/2.20	2.23
ZANTBE	0.58	6.66 * *	1.15	6.54 *	1.01	0.02	0.50	1.51	0/3.53	3.58
ZANTP1	0.90	0.32	1.14	5.35 *	0.83	2.11	0.55	1.13	0.31	1.56
ZANTPR	0.35	11.38 * *	1.19	7.72 * *	1.03	0.04	0.24	2.50	0.80	0.10
ZANTSE	0/0.14	Insuff.	0/0.57	Insuff.	4.01	Insuff.	0/0.03	Insuff.	0/0.02	Insuff.
ZUELGU	0.56	1.18	0.88	0.75	0.95	0.03	1.03	Insuff.	10.42	Insuff.

APPENDIX 5

Habitat Associations on the 50-ha FDP Plot Based on Torus-Randomization Criteria

Habitat associations based on the torus-randomization analysis of all individuals ≥ 1-cm DBH of all 303 species encountered during the 1990 census of the 50-ha Forest Dynamics Project plot of Barro Colorado Island, Panamá. A positive association for a given species with a particular habitat occurred when a significant proportion of torus-based maps had a stem-frequency of the focal species < its stem-frequency on the true map, where stem-frequency is the number of stems of the focal species over the number of stems of all species in a given habitat. A negative association with a particular habitat occurred when a significant proportion of torus-based maps had a stem-frequency of the focal species > its stem-frequency on the true map. Significant associations are those in which the proportion is > 0.975 (*i.e.*, P<0.025), and they are marked by an asterisk (*).

	High Plateau		Low Plateau		Slope		Stream		Swamp	
Species	Proportion of torus maps with stem-frequency > true map	Proportion of torus maps with stem-frequency < true map	Proportion of torus maps with stem-frequency > true map	Proportion of torus maps with stem-frequency < true map	Proportion of torus maps with stem-frequency > true map	Proportion of torus maps with stem-frequency < true map	Proportion of torus maps with stem-frequency > true map	Proportion of torus maps with stem-frequency < true map	Proportion of torus maps with stem-frequency > true map	Proportion of torus maps with stem-frequency < true map
ACACME	0.58	0.00	0.16	0.84	0.66	0.35	0.16	0.00	0.05	0.95
ACALDI	0.31	0.69	0.97	0.04	0.14	0.86	0.02	0.98 *	0.10	0.90
ACALMA	0.62	0.38	0.08	0.92	0.81	0.19	0.11	0.89	0.43	0.00
ADE1TR	0.03	0.98 *	0.86	0.14	0.93	0.07	0.58	0.42	0.85	0.00
AEGIPA	0.90	0.10	0.10	0.90	0.82	0.19	0.24	0.76	0.58	0.42
ALCHCO	0.78	0.22	0.23	0.77	0.61	0.39	0.87	0.13	0.97	0.00
ALCHLA	0.24	0.00	0.49	0.51	0.46	0.00	0.02	0.98 *	0.07	0.00
ALIBED	0.78	0.22	0.12	0.88	0.91	0.10	0.17	0.83	0.01	0.99 *
ALLOPS	0.09	0.91	0.67	0.33	0.73	0.27	0.35	0.65	0.93	0.00
ALSEBL	0.30	0.70	0.75	0.25	0.96	0.04	0.93	0.07	0.98 *	0.02
AMAICO	0.66	0.00	0.30	0.70	0.39	0.61	0.30	0.00	0.28	0.00
ANACEX	0.93	0.00	0.90	0.11	0.29	0.71	0.16	0.84	0.00	1.00 *
ANAXPA	0.24	0.00	0.63	0.38	0.10	0.90	0.10	0.00	0.07	0.00
ANDIIN	0.28	0.72	0.67	0.33	0.34	0.66	0.73	0.27	0.83	0.17
ANNOAC	0.86	0.14	0.94	0.06	0.44	0.56	0.05	0.95	0.00	1.00 *

Appendix 5 continued.

	High Plateau		Low Plateau		Slope		Stream		Swamp	
Species	Proportion of torus maps with stem-frequency > true map	Proportion of torus maps with stem-frequency < true map	Proportion of torus maps with stem-frequency > true map	Proportion of torus maps with stem-frequency < true map	Proportion of torus maps with stem-frequency > true map	Proportion of torus maps with stem-frequency < true map	Proportion of torus maps with stem-frequency > true map	Proportion of torus maps with stem-frequency < true map	Proportion of torus maps with stem-frequency > true map	Proportion of torus maps with stem-frequency < true map
ANNOHA	0.13	0.00	0.49	0.51	0.23	0.00	0.03	0.00	0.02	0.00
ANNOSP	0.84	0.16	0.28	0.72	0.41	0.59	0.72	0.28	0.18	0.82
APEIME	0.77	0.23	0.64	0.36	0.55	0.45	0.03	0.97	0.22	0.78
APEITI	0.54	0.46	0.24	0.76	0.94	0.06	0.26	0.74	0.55	0.00
APHESI	0.43	0.00	0.78	0.22	0.54	0.46	0.00	1.00 *	0.04	0.96
APPUSE	0.14	0.00	0.49	0.00	0.15	0.85	0.02	0.00	0.02	0.00
ARDIBA	0.13	0.00	0.49	0.51	0.23	0.00	0.03	0.00	0.02	0.00
ARDIFE	0.48	0.52	0.93	0.08	0.04	0.96	0.23	0.77	0.73	0.00
ARDIGU	0.46	0.00	0.57	0.43	0.77	0.00	0.03	0.97	0.13	0.00
ASPICR	0.22	0.78	0.77	0.24	0.15	0.86	0.72	0.28	0.92	0.08
AST1ST	0.59	0.41	0.99 *	0.01	0.66	0.34	0.62	0.38	0.00	1.00 *
AST2GR	0.08	0.92	0.69	0.31	0.82	0.19	0.06	0.94	0.38	0.62
BACTBA	0.53	0.47	0.52	0.49	0.14	0.86	0.39	0.00	0.37	0.00
BACTC1	0.07	0.93	1.00 *	0.00	0.01	0.99 *	0.37	0.00	0.36	0.00
BACTC2	0.22	0.78	0.68	0.32	0.26	0.74	0.15	0.00	0.14	0.00
BACTMA	0.36	0.64	1.00 *	0.00	0.78	0.22	0.51	0.00	0.00	1.00 *
BANAGU	0.12	0.88	0.90	0.11	0.38	0.62	0.10	0.00	0.10	0.00
BEILPE	0.92	0.08	0.26	0.74	0.01	0.99 *	0.70	0.30	0.98 *	0.02
BERTGU	0.14	0.00	0.48	0.52	0.23	0.00	0.03	0.00	0.03	0.00
BROSAL	0.17	0.83	0.84	0.16	0.72	0.28	0.00	1.00 *	0.96	0.04
BROSGU	0.13	0.00	0.49	0.00	0.12	0.88	0.02	0.00	0.03	0.00
CALOLO	0.98 *	0.02	0.87	0.13	0.00	1.00 *	0.68	0.32	0.35	0.65
CAPPFR	0.08	0.92	1.00 *	0.00	0.25	0.76	0.03	0.97	0.75	0.25
CASEAC	0.08	0.92	0.84	0.17	0.59	0.41	0.36	0.64	0.93	0.07
CASEAR	0.50	0.50	0.20	0.80	0.87	0.13	0.44	0.56	0.79	0.21
CASECO	0.46	0.00	0.21	0.80	0.62	0.38	0.16	0.84	0.24	0.00
CASEGU	0.00	1.00 *	0.73	0.27	0.93	0.07	0.34	0.00	0.31	0.00
CASESY	0.84	0.16	0.63	0.37	0.59	0.41	0.18	0.82	0.06	0.94
CASSEL	0.84	0.17	0.44	0.56	0.81	0.19	0.83	0.17	0.00	1.00 *
CAVAPL	0.06	0.94	0.93	0.07	0.33	0.67	0.36	0.00	0.35	0.00

Appendix 5 continued.

Species	High Plateau		Low Plateau		Slope		Stream		Swamp	
	Proportion of torus maps with stem-frequency > true map	Proportion of torus maps with stem-frequency < true map	Proportion of torus maps with stem-frequency > true map	Proportion of torus maps with stem-frequency < true map	Proportion of torus maps with stem-frequency > true map	Proportion of torus maps with stem-frequency < true map	Proportion of torus maps with stem-frequency > true map	Proportion of torus maps with stem-frequency < true map	Proportion of torus maps with stem-frequency > true map	Proportion of torus maps with stem-frequency < true map
CECRIN	0.21	0.79	0.24	0.76	0.73	0.27	0.78	0.22	0.81	0.19
CECROB	0.60	0.40	0.57	0.43	0.46	0.54	0.61	0.00	0.01	0.99 *
CEDROD	0.62	0.00	0.70	0.30	0.03	0.97	0.18	0.00	0.17	0.00
CEIBPE	0.48	0.52	0.53	0.47	0.79	0.21	0.06	0.94	0.02	0.98 *
CELTSC	0.87	0.13	0.74	0.26	0.00	1.00 *	0.52	0.48	0.45	0.55
CESPMA	0.27	0.00	0.81	0.00	0.02	0.98 *	0.05	0.00	0.05	0.00
CESTME	0.86	0.15	0.88	0.13	0.01	1.00 *	0.02	0.98 *	0.03	0.97
CHA1TE	0.59	0.41	1.00 *	0.00	0.00	1.00 *	0.32	0.00	0.29	0.00
CHA2SC	0.66	0.34	0.14	0.86	0.98 *	0.02	0.45	0.55	0.10	0.90
CHIMPA	0.14	0.00	0.49	0.00	0.23	0.00	0.03	0.00	0.02	0.00
CHR1EC	1.00 *	0.01	1.00 *	0.00	0.00	1.00 *	0.04	0.96	0.92	0.00
CHR2AR	0.55	0.45	0.54	0.46	0.17	0.83	0.26	0.74	0.43	0.57
CHR2CA	0.06	0.94	1.00 *	0.00	0.65	0.35	0.70	0.30	0.00	1.00 *
CLIDDE	0.63	0.37	0.49	0.51	0.63	0.37	0.10	0.90	0.00	1.00 *
CLIDOC	0.18	0.82	0.51	0.49	0.59	0.41	0.14	0.00	0.13	0.00
CNEMPE	0.14	0.00	0.49	0.00	0.11	0.89	0.03	0.00	0.02	0.00
COCCCO	0.44	0.56	0.74	0.26	0.49	0.51	0.02	0.98 *	0.60	0.40
COCCMA	0.66	0.34	0.04	0.96	0.99 *	0.01	0.62	0.38	0.26	0.74
COLUGL	0.14	0.00	0.50	0.50	0.23	0.00	0.03	0.00	0.02	0.00
CONOBR	0.29	0.00	0.81	0.19	0.49	0.00	0.01	0.99 *	0.06	0.00
CONOCI	0.63	0.37	1.00 *	0.00	0.00	1.00 *	0.01	0.99 *	0.08	0.92
CORDAL	0.24	0.76	0.40	0.60	0.98 *	0.02	0.10	0.90	0.06	0.94
CORDBI	0.90	0.10	0.12	0.88	0.63	0.37	0.65	0.35	0.33	0.67
CORDLA	0.54	0.46	0.88	0.12	0.00	1.00 *	0.29	0.71	0.05	0.95
COU2CU	0.78	0.22	0.01	0.99 *	0.99 *	0.01	0.77	0.23	0.33	0.67
COUTHE	0.14	0.00	0.49	0.00	0.11	0.89	0.02	0.00	0.02	0.00
CROTBI	0.70	0.30	0.38	0.62	0.88	0.12	0.13	0.87	0.00	1.00 *
CUPACI	0.45	0.56	0.61	0.39	0.85	0.15	0.05	0.95	0.21	0.00
CUPALA	0.83	0.17	0.60	0.40	0.03	0.97	0.37	0.63	0.65	0.00
CUPARU	0.88	0.12	0.10	0.90	0.92	0.08	0.70	0.00	0.01	0.99 *

Appendix 5 continued.

	High Plateau		Low Plateau		Slope		Stream		Swamp	
Species	Proportion of torus maps with stem-frequency > true map	Proportion of torus maps with stem-frequency < true map	Proportion of torus maps with stem-frequency > true map	Proportion of torus maps with stem-frequency < true map	Proportion of torus maps with stem-frequency > true map	Proportion of torus maps with stem-frequency < true map	Proportion of torus maps with stem-frequency > true map	Proportion of torus maps with stem-frequency < true map	Proportion of torus maps with stem-frequency > true map	Proportion of torus maps with stem-frequency < true map
CUPASY	0.38	0.62	0.08	0.92	0.92	0.08	0.30	0.70	1.00 *	0.00
CYPHHA	0.24	0.00	0.27	0.73	0.45	0.00	0.07	0.00	0.06	0.00
DENDAR	0.01	0.99 *	0.90	0.10	0.79	0.21	0.32	0.00	0.30	0.00
DENDST	0.83	0.17	0.27	0.73	0.51	0.49	0.65	0.35	0.20	0.80
DES2PA	0.05	0.96	0.66	0.34	0.72	0.28	0.72	0.28	0.52	0.48
DIO2AR	0.93	0.07	0.10	0.90	0.52	0.48	0.47	0.53	0.38	0.62
DIPTPA	0.69	0.31	0.18	0.82	0.81	0.19	0.03	0.97	0.69	0.00
DRYPST	0.37	0.63	0.85	0.15	0.01	0.99 *	0.85	0.15	0.87	0.13
ELAEOL	0.32	0.00	0.88	0.00	0.69	0.00	0.19	0.00	0.00	1.00 *
ENTESC	0.29	0.71	0.71	0.29	0.44	0.56	0.08	0.92	0.26	0.00
ERY1CO	0.93	0.08	0.83	0.17	0.01	1.00 *	0.25	0.75	0.83	0.17
ERY2MA	0.52	0.48	0.37	0.63	0.09	0.91	0.95	0.05	1.00 *	0.00
ERY2PA	0.64	0.36	0.86	0.14	0.29	0.72	0.29	0.71	0.05	0.95
EUGECO	0.24	0.76	0.40	0.60	0.52	0.48	0.57	0.43	0.90	0.10
EUGEGA	0.00	1.00 *	0.31	0.69	0.99 *	0.01	0.98 *	0.02	0.63	0.37
EUGENE	0.07	0.93	0.61	0.39	0.87	0.13	0.09	0.91	0.87	0.13
EUGEOE	0.42	0.58	0.20	0.80	0.79	0.21	0.99 *	0.01	0.81	0.19
FARAOC	0.18	0.82	0.14	0.86	1.00 *	0.00	0.66	0.34	0.32	0.68
FICUBU	0.01	0.99 *	0.49	0.00	0.23	0.00	0.02	0.00	0.02	0.00
FICUCI	0.13	0.00	0.51	0.49	0.22	0.00	0.02	0.00	0.02	0.00
FICUC1	0.13	0.00	0.49	0.00	0.23	0.00	0.00	1.00 *	0.02	0.00
FICUC2	0.02	0.98 *	0.88	0.12	0.62	0.38	0.17	0.00	0.02	0.98 *
FICUIN	0.61	0.00	1.00 *	0.00	0.66	0.34	0.05	0.95	0.00	1.00 *
FICUMA	0.77	0.00	0.65	0.35	0.11	0.89	0.24	0.00	0.03	0.97
FICUOB	0.36	0.64	0.64	0.36	0.83	0.00	0.17	0.00	0.00	1.00 *
FICUPE	0.13	0.00	0.51	0.49	0.22	0.00	0.02	0.00	0.02	0.00
FICUPO	0.28	0.72	0.25	0.75	0.85	0.00	0.16	0.00	0.01	0.99 *
FICUTO	0.79	0.21	0.88	0.12	0.06	0.94	0.02	0.98 *	0.61	0.00
FICUTR	0.18	0.82	0.91	0.00	0.22	0.78	0.02	0.98 *	0.12	0.00
FICUYO	0.58	0.00	0.92	0.09	0.79	0.00	0.00	1.00 *	0.14	0.00

Appendix 5 continued.

	High Plateau		Low Plateau		Slope		Stream		Swamp	
Species	Proportion of torus maps with stem-frequency > true map	Proportion of torus maps with stem-frequency < true map	Proportion of torus maps with stem-frequency > true map	Proportion of torus maps with stem-frequency < true map	Proportion of torus maps with stem-frequency > true map	Proportion of torus maps with stem-frequency < true map	Proportion of torus maps with stem-frequency > true map	Proportion of torus maps with stem-frequency < true map	Proportion of torus maps with stem-frequency > true map	Proportion of torus maps with stem-frequency < true map
GAR2IN	0.02	0.98 *	0.55	0.45	0.73	0.27	0.97	0.03	0.66	0.34
GAR2MA	0.65	0.36	0.57	0.43	0.36	0.64	0.02	0.98 *	0.96	0.04
GENIAM	0.51	0.50	0.59	0.41	0.34	0.66	0.03	0.97	0.00	1.00 *
GEONIN	0.25	0.00	0.75	0.00	0.02	0.98 *	0.07	0.00	0.06	0.00
GUAPST	0.08	0.92	0.14	0.86	0.91	0.09	0.68	0.32	0.90	0.10
GUARGR	0.47	0.53	0.41	0.59	0.23	0.77	0.45	0.55	0.71	0.00
GUARGU	0.27	0.73	1.00 *	0.01	0.00	1.00 *	0.02	0.98 *	0.03	0.97
GUARSP	0.14	0.86	0.98 *	0.03	0.07	0.93	0.03	0.97	0.69	0.31
GUATDU	1.00 *	0.01	0.49	0.52	0.00	1.00 *	0.57	0.43	0.97	0.03
GUAZUL	0.17	0.83	0.97	0.03	0.88	0.13	0.68	0.00	0.31	0.69
GUETFO	0.40	0.60	0.84	0.16	0.97	0.03	0.06	0.94	0.16	0.84
GUSTSU	0.22	0.78	1.00 *	0.00	0.89	0.12	0.13	0.87	0.72	0.28
HAMEAX	0.97	0.03	0.67	0.33	0.47	0.54	0.03	0.97	0.01	0.99 *
HAMEPA	0.13	0.00	0.51	0.49	0.23	0.00	0.03	0.00	0.02	0.00
HAMPAP	0.72	0.28	0.21	0.80	0.71	0.29	0.63	0.00	0.21	0.79
HASSFL	0.92	0.08	0.84	0.16	0.09	0.92	0.00	1.00 *	0.00	1.00 *
HEISAC	0.98 *	0.02	0.51	0.49	0.11	0.89	0.46	0.54	0.27	0.73
HEISCO	0.36	0.64	0.38	0.62	0.51	0.49	0.25	0.75	0.54	0.46
HERRPU	0.98 *	0.02	0.11	0.89	0.37	0.63	0.02	0.98 *	0.69	0.31
HIRTAM	0.95	0.00	0.22	0.78	0.36	0.64	0.52	0.00	0.09	0.91
HIRTTR	1.00 *	0.00	0.67	0.33	0.01	1.00 *	0.42	0.58	0.92	0.08
HURACR	0.18	0.82	0.78	0.22	0.24	0.76	0.38	0.62	0.01	0.99 *
HYBAPR	0.63	0.37	0.04	0.96	0.78	0.23	0.84	0.16	1.00 *	0.00
HYERAL	0.95	0.05	0.92	0.08	0.32	0.68	0.44	0.56	0.00	1.00 *
INGACO	0.97	0.03	0.00	1.00 *	0.98 *	0.02	0.26	0.74	0.38	0.62
INGAFA	0.66	0.34	0.66	0.34	0.92	0.08	0.28	0.72	0.00	1.00 *
INGAGO	0.99 *	0.01	0.84	0.16	0.01	0.99 *	0.66	0.34	0.00	1.00 *
INGAMA	0.49	0.51	0.95	0.05	0.00	1.00 *	0.59	0.41	0.58	0.42
INGAMI	0.57	0.00	0.72	0.28	0.25	0.75	0.22	0.00	0.19	0.00
INGAM1	0.14	0.00	0.48	0.52	0.23	0.00	0.03	0.00	0.03	0.00

Appendix 5 continued.

	High Plateau		Low Plateau		Slope		Stream		Swamp	
Species	Proportion of torus maps with stem-frequency > true map	Proportion of torus maps with stem-frequency < true map	Proportion of torus maps with stem-frequency > true map	Proportion of torus maps with stem-frequency < true map	Proportion of torus maps with stem-frequency > true map	Proportion of torus maps with stem-frequency < true map	Proportion of torus maps with stem-frequency > true map	Proportion of torus maps with stem-frequency < true map	Proportion of torus maps with stem-frequency > true map	Proportion of torus maps with stem-frequency < true map
INGAPE	0.32	0.68	0.82	0.18	0.05	0.95	0.10	0.90	0.46	0.00
INGAPU	0.00	1.00 *	1.00 *	0.00	0.56	0.45	0.13	0.87	0.37	0.00
INGAQU	0.62	0.38	0.81	0.20	0.01	0.99 *	0.33	0.67	0.87	0.13
INGARU	0.44	0.56	0.40	0.60	0.56	0.44	0.35	0.65	0.47	0.00
INGASA	0.58	0.42	0.32	0.69	0.26	0.74	0.13	0.87	0.98 *	0.02
INGASP	0.76	0.24	0.14	0.86	0.88	0.12	0.17	0.83	0.13	0.87
INGAUM	0.71	0.29	0.02	0.98 *	0.93	0.07	0.11	0.89	1.00 *	0.00
INGAS1	0.45	0.55	0.23	0.77	0.40	0.60	0.95	0.05	0.96	0.00
JAC1CO	0.85	0.15	0.10	0.90	0.83	0.17	0.51	0.49	0.41	0.59
KOANWE	0.34	0.00	0.56	0.44	0.36	0.65	0.01	0.99 *	0.09	0.00
LACIAG	0.98 *	0.02	0.04	0.96	0.65	0.36	0.06	0.94	0.98 *	0.02
LACMPA	0.40	0.60	0.59	0.41	0.98 *	0.02	0.13	0.87	0.01	0.99 *
LAETPR	0.58	0.00	0.32	0.68	0.75	0.25	0.03	0.97	0.06	0.94
LAETTH	0.83	0.17	0.00	1.00 *	1.00 *	0.00	0.62	0.38	0.42	0.58
LAFOPU	0.24	0.00	0.45	0.55	0.54	0.00	0.09	0.00	0.04	0.96
LEANDI	0.14	0.00	0.49	0.51	0.23	0.00	0.02	0.00	0.02	0.00
LICAHY	0.46	0.54	0.27	0.73	0.54	0.46	0.83	0.00	0.75	0.00
LICAPL	0.99 *	0.01	0.70	0.30	0.01	0.99 *	0.21	0.79	0.77	0.23
LINDLA	0.66	0.34	0.43	0.57	0.99 *	0.01	0.59	0.41	0.00	1.00 *
LONCLA	0.90	0.10	0.20	0.80	0.54	0.47	0.58	0.42	0.67	0.33
LOZAPI	0.27	0.00	0.80	0.00	0.02	0.99 *	0.09	0.00	0.07	0.00
LUEHSE	0.51	0.49	0.68	0.32	0.87	0.13	0.31	0.69	0.00	1.00 *
MACLTI	0.13	0.00	0.48	0.00	0.23	0.00	0.03	0.00	0.00	1.00 *
MACRGL	0.53	0.47	0.84	0.16	0.39	0.61	0.01	0.99 *	0.52	0.00
MALMSP	0.98 *	0.02	0.18	0.83	0.42	0.58	0.66	0.34	0.01	0.99 *
MALPRO	0.57	0.43	0.75	0.25	0.70	0.30	0.00	1.00 *	0.58	0.00
MAQUCO	0.53	0.47	0.71	0.29	0.00	1.00 *	0.02	0.98 *	1.00 *	0.00
MARGNO	0.26	0.00	0.49	0.51	0.35	0.65	0.05	0.00	0.05	0.00
MAR1LA	0.47	0.00	0.94	0.06	0.22	0.78	0.00	1.00 *	0.13	0.00
MAYTSC	0.77	0.23	0.46	0.54	0.26	0.74	0.11	0.89	0.57	0.43

Appendix 5 continued.

	High Plateau		Low Plateau		Slope		Stream		Swamp	
Species	Proportion of torus maps with stem-frequency > true map	Proportion of torus maps with stem-frequency < true map	Proportion of torus maps with stem-frequency > true map	Proportion of torus maps with stem-frequency < true map	Proportion of torus maps with stem-frequency > true map	Proportion of torus maps with stem-frequency < true map	Proportion of torus maps with stem-frequency > true map	Proportion of torus maps with stem-frequency < true map	Proportion of torus maps with stem-frequency > true map	Proportion of torus maps with stem-frequency < true map
MICOAF	0.69	0.31	0.04	0.96	0.93	0.07	0.44	0.56	0.18	0.82
MICOAR	0.46	0.54	0.60	0.41	0.98 *	0.02	0.61	0.39	0.00	1.00 *
MICOEL	0.56	0.44	0.01	0.99 *	0.96	0.00	0.22	0.78	0.32	0.00
MICOHO	0.65	0.00	0.37	0.63	0.92	0.08	0.46	0.00	0.02	0.98 *
MICOIM	0.65	0.00	0.97	0.03	0.19	0.81	0.04	0.96	0.02	0.98 *
MICONE	0.71	0.29	0.11	0.89	0.95	0.05	0.74	0.26	0.03	0.97
MICOPR	0.13	0.00	0.51	0.49	0.22	0.00	0.02	0.00	0.02	0.00
MOURMY	0.60	0.40	0.01	1.00 *	1.00 *	0.00	0.50	0.50	0.58	0.42
MYRCGA	0.50	0.50	0.54	0.46	0.56	0.44	0.03	0.97	0.30	0.70
MYROFR	0.56	0.44	0.32	0.68	0.38	0.63	0.29	0.00	0.10	0.90
NECTCI	0.89	0.11	0.08	0.92	0.65	0.35	0.54	0.46	0.79	0.00
NECTGL	0.20	0.80	0.96	0.04	0.06	0.94	0.36	0.64	0.35	0.65
NECTPU	0.73	0.27	0.17	0.83	0.59	0.41	0.13	0.87	0.71	0.00
NECTS1	0.25	0.75	0.77	0.24	0.12	0.88	0.12	0.00	0.14	0.00
NEEAAM	0.74	0.26	0.13	0.87	0.57	0.43	0.29	0.71	0.66	0.00
OCHRPY	0.56	0.00	0.20	0.81	0.79	0.00	0.04	0.96	0.13	0.00
OCOTCE	0.75	0.25	0.10	0.90	0.72	0.28	0.42	0.58	0.23	0.77
OCOTCB	0.83	0.17	0.36	0.64	0.01	0.99 *	0.97	0.00	0.96	0.00
OCOTPU	1.00 *	0.00	0.04	0.96	0.77	0.24	0.32	0.68	0.39	0.61
OCOTWH	0.86	0.15	0.98 *	0.02	0.00	1.00 *	0.28	0.72	0.86	0.00
OENOMA	0.88	0.12	0.25	0.75	0.71	0.29	0.44	0.56	0.00	1.00 *
OLMEAS	0.82	0.18	0.81	0.19	0.02	0.99 *	0.08	0.92	0.64	0.36
ORMOAM	0.09	0.91	0.68	0.00	0.26	0.74	0.05	0.00	0.04	0.00
ORMOCR	0.28	0.72	0.92	0.08	0.06	0.94	0.11	0.89	0.65	0.00
ORMOMA	0.08	0.92	0.72	0.29	0.64	0.00	0.10	0.00	0.09	0.00
OURALU	0.81	0.19	0.00	1.00 *	1.00 *	0.00	0.10	0.90	0.99 *	0.01
PALIGU	0.77	0.24	0.19	0.81	0.98 *	0.02	0.88	0.12	0.01	0.99 *
PENTMA	0.86	0.14	0.71	0.29	0.01	0.99 *	0.01	0.99 *	0.97	0.03
PEREXA	0.85	0.00	0.05	0.95	0.68	0.32	0.56	0.44	0.53	0.00
PHOECI	0.49	0.52	0.48	0.52	0.61	0.39	0.05	0.95	0.16	0.84

Appendix 5 continued.

	High Plateau		Low Plateau		Slope		Stream		Swamp	
Species	Proportion of torus maps with stem-frequency > true map	Proportion of torus maps with stem-frequency < true map	Proportion of torus maps with stem-frequency > true map	Proportion of torus maps with stem-frequency < true map	Proportion of torus maps with stem-frequency > true map	Proportion of torus maps with stem-frequency < true map	Proportion of torus maps with stem-frequency > true map	Proportion of torus maps with stem-frequency < true map	Proportion of torus maps with stem-frequency > true map	Proportion of torus maps with stem-frequency < true map
PICRLA	0.50	0.51	0.91	0.09	0.02	0.99 *	0.38	0.62	0.95	0.05
PIPEAE	0.86	0.14	0.90	0.10	0.01	0.99 *	0.01	0.99 *	0.59	0.00
PIPEA1	0.91	0.09	0.58	0.43	0.01	0.99 *	0.11	0.89	0.38	0.62
PIPECA	0.35	0.00	0.82	0.00	0.05	0.95	0.02	0.98 *	0.09	0.00
PIPECO	0.62	0.38	0.03	0.97	0.76	0.24	0.72	0.28	0.98 *	0.02
PIPECU	0.87	0.13	0.91	0.09	0.12	0.88	0.10	0.90	0.00	1.00 *
PIPEIM	0.27	0.00	0.81	0.00	0.03	0.97	0.05	0.00	0.05	0.00
PIPEPE	0.55	0.45	0.97	0.03	0.00	1.00 *	0.60	0.00	0.50	0.00
PIPERE	0.99 *	0.01	0.90	0.10	0.02	0.99 *	0.68	0.32	0.02	0.98 *
PIT1MA	0.14	0.00	0.49	0.51	0.22	0.00	0.03	0.00	0.02	0.00
PIT1RU	0.21	0.00	0.28	0.72	0.41	0.00	0.05	0.00	0.05	0.00
PLA1PI	0.68	0.32	0.00	1.00 *	0.90	0.10	0.13	0.87	0.38	0.62
PLA2EL	0.65	0.35	0.26	0.74	0.90	0.10	0.08	0.92	0.06	0.94
POCHQU	0.14	0.00	0.50	0.00	0.22	0.00	0.00	1.00 *	0.03	0.00
POCHSE	0.14	0.86	0.78	0.00	0.55	0.00	0.12	0.00	0.08	0.00
POSOLA	0.88	0.12	0.17	0.83	0.73	0.27	0.08	0.92	0.21	0.79
POULAR	0.96	0.04	0.90	0.10	0.00	1.00 *	0.14	0.86	0.95	0.05
POURBI	0.60	0.00	0.44	0.56	0.17	0.83	0.17	0.83	0.36	0.00
POUTFO	0.37	0.00	0.90	0.10	0.09	0.91	0.08	0.00	0.07	0.00
POUTRE	0.15	0.85	0.56	0.44	0.82	0.18	0.35	0.65	0.00	1.00 *
POUTST	0.59	0.41	0.01	0.99 *	1.00 *	0.00	0.46	0.54	0.71	0.00
PRI2CO	0.60	0.41	0.19	0.81	0.66	0.34	0.34	0.66	0.71	0.29
PROTCO	0.93	0.07	0.67	0.33	0.01	1.00 *	0.13	0.87	0.99 *	0.00
PROTPA	0.92	0.08	0.11	0.89	0.43	0.57	0.11	0.89	1.00 *	0.00
PROTTE	0.65	0.35	0.55	0.45	0.13	0.87	0.23	0.77	0.99 *	0.01
PROTSP	0.26	0.00	0.74	0.26	0.12	0.88	0.06	0.00	0.07	0.00
PSE1SE	0.53	0.48	0.55	0.45	0.78	0.22	0.29	0.00	0.11	0.89
PSIDFR	0.27	0.73	0.91	0.09	0.08	0.92	0.56	0.00	0.08	0.92
PSYCAC	0.60	0.00	0.62	0.38	0.91	0.00	0.28	0.00	0.03	0.97
PSYCB1	0.13	0.00	0.49	0.00	0.23	0.00	0.03	0.00	0.03	0.00

Appendix 5 continued.

	High Plateau		Low Plateau		Slope		Stream		Swamp	
Species	Proportion of torus maps with stem-frequency > true map	Proportion of torus maps with stem-frequency < true map	Proportion of torus maps with stem-frequency > true map	Proportion of torus maps with stem-frequency < true map	Proportion of torus maps with stem-frequency > true map	Proportion of torus maps with stem-frequency < true map	Proportion of torus maps with stem-frequency > true map	Proportion of torus maps with stem-frequency < true map	Proportion of torus maps with stem-frequency > true map	Proportion of torus maps with stem-frequency < true map
PSYCCH	0.78	0.00	0.53	0.47	0.09	0.91	0.08	0.92	0.28	0.00
PSYCDE	0.69	0.32	0.03	0.98 *	0.97	0.03	0.54	0.00	0.13	0.87
PSYCFU	0.28	0.00	0.80	0.20	0.40	0.00	0.05	0.00	0.05	0.00
PSYCG1	0.37	0.00	0.92	0.08	0.74	0.00	0.21	0.00	0.00	1.00 *
PSYCG2	0.39	0.00	0.61	0.39	0.42	0.58	0.08	0.00	0.09	0.00
PSYCG3	0.98 *	0.00	0.89	0.11	0.12	0.88	0.70	0.00	0.00	1.00 *
PSYCHO	0.20	0.80	0.74	0.26	0.93	0.07	0.54	0.46	0.31	0.69
PSYCLI	0.51	0.00	0.14	0.86	0.65	0.35	0.20	0.00	0.16	0.00
PSYCMA	0.59	0.41	0.25	0.75	0.81	0.19	0.87	0.13	0.10	0.90
PSYCPI	0.37	0.00	0.92	0.08	0.07	0.93	0.07	0.00	0.07	0.00
PSYCRA	0.27	0.00	0.19	0.82	0.42	0.00	0.05	0.00	0.05	0.00
PTERBE	0.31	0.00	0.84	0.16	0.29	0.71	0.01	0.99 *	0.06	0.00
PTERRO	0.86	0.14	0.07	0.93	0.70	0.30	0.45	0.55	0.25	0.75
QUARAS	0.06	0.94	0.99 *	0.01	0.09	0.91	0.11	0.89	1.00 *	0.00
QUASAM	0.41	0.59	0.46	0.54	0.35	0.65	0.32	0.68	0.18	0.82
RANDAR	0.07	0.93	0.60	0.40	0.99 *	0.01	0.10	0.90	0.34	0.66
RANDFO	0.20	0.80	0.30	0.70	0.57	0.00	0.08	0.00	0.07	0.00
RINOSY	0.21	0.79	0.95	0.05	0.29	0.71	0.54	0.46	0.82	0.18
SAPIAU	0.62	0.39	0.80	0.20	0.52	0.49	0.31	0.69	0.00	1.00 *
SAPISP	0.23	0.00	0.75	0.00	0.11	0.90	0.01	0.99 *	0.07	0.00
SCH1ZO	0.91	0.09	0.83	0.17	0.26	0.74	0.10	0.90	0.00	1.00 *
SCHIPA	0.64	0.00	0.04	0.96	0.88	0.12	0.29	0.00	0.24	0.00
SENNDA	0.39	0.61	0.85	0.15	0.19	0.81	0.07	0.93	0.29	0.71
SIMAAM	0.86	0.14	0.01	1.00 *	0.87	0.14	0.50	0.50	0.11	0.89
SIPAGU	0.59	0.00	0.45	0.55	0.34	0.66	0.04	0.96	0.17	0.83
SIPAPA	0.29	0.71	1.00 *	0.00	0.00	1.00 *	0.50	0.50	0.94	0.06
SLOATE	0.68	0.33	0.29	0.71	0.42	0.58	0.07	0.93	1.00 *	0.00
SOCREX	0.97	0.03	0.31	0.69	0.21	0.79	0.47	0.53	0.86	0.00
SOLAAS	0.43	0.00	0.71	0.29	0.41	0.59	0.10	0.00	0.01	0.99 *
SOLAHA	0.79	0.21	0.52	0.48	0.09	0.91	0.73	0.00	0.18	0.82

Appendix 5 continued.

Species	High Plateau		Low Plateau		Slope		Stream		Swamp	
	Proportion of torus maps with stem-frequency > true map	Proportion of torus maps with stem-frequency < true map	Proportion of torus maps with stem-frequency > true map	Proportion of torus maps with stem-frequency < true map	Proportion of torus maps with stem-frequency > true map	Proportion of torus maps with stem-frequency < true map	Proportion of torus maps with stem-frequency > true map	Proportion of torus maps with stem-frequency < true map	Proportion of torus maps with stem-frequency > true map	Proportion of torus maps with stem-frequency < true map
SOLAST	0.23	0.00	0.28	0.72	0.41	0.00	0.05	0.00	0.04	0.00
SOROAF	0.98 *	0.02	0.26	0.74	0.24	0.76	0.10	0.90	0.91	0.09
SPACME	0.27	0.00	0.50	0.50	0.35	0.65	0.05	0.00	0.05	0.00
SPONMO	0.89	0.11	0.66	0.34	0.88	0.13	0.03	0.97	0.03	0.97
SPONRA	0.92	0.08	0.49	0.51	0.10	0.90	0.20	0.80	0.06	0.94
STERAP	0.71	0.29	0.67	0.34	0.56	0.44	0.79	0.00	0.00	1.00 *
STYLST	0.74	0.26	0.97	0.04	0.24	0.76	0.67	0.33	0.00	1.00 *
SWARS1	0.00	1.00 *	0.69	0.31	0.93	0.07	0.84	0.16	0.63	0.37
SWARS2	0.89	0.11	0.34	0.66	0.46	0.54	0.22	0.78	1.00 *	0.00
SYMPGL	0.98 *	0.02	0.94	0.06	0.00	1.00 *	0.03	0.97	0.87	0.00
TAB1GU	0.73	0.27	0.15	0.85	0.97	0.04	0.33	0.67	0.62	0.00
TAB1RO	0.76	0.24	1.00 *	0.00	0.50	0.50	0.07	0.93	0.00	1.00 *
TAB2AR	0.71	0.30	0.36	0.64	0.69	0.31	0.44	0.56	0.00	1.00 *
TACHVE	0.94	0.06	0.10	0.90	0.06	0.94	0.79	0.21	0.96	0.04
TALINE	0.24	0.76	0.62	0.38	0.38	0.62	0.59	0.41	0.77	0.23
TALIPR	0.03	0.97	0.98 *	0.03	0.36	0.64	0.56	0.44	0.10	0.90
TERMAM	0.92	0.08	0.47	0.53	0.99 *	0.01	0.40	0.60	0.00	1.00 *
TERMOB	0.87	0.00	0.15	0.85	0.42	0.58	0.53	0.00	0.44	0.00
TERNTE	0.14	0.00	0.49	0.51	0.23	0.00	0.03	0.00	0.02	0.00
TET2PA	0.94	0.06	0.03	0.97	0.62	0.39	0.57	0.43	0.64	0.36
TET4JO	0.28	0.72	0.93	0.07	0.78	0.00	0.16	0.00	0.00	1.00 *
THEOCA	0.35	0.65	0.99 *	0.01	0.05	0.95	0.04	0.96	0.38	0.00
THEVAH	0.83	0.18	0.99 *	0.01	0.44	0.56	0.05	0.95	0.00	1.00 *
TOCOPI	0.23	0.77	0.92	0.08	0.33	0.67	0.03	0.97	0.01	0.99 *
TRATAS	0.79	0.21	0.16	0.84	0.38	0.62	0.55	0.45	0.08	0.92
TREMMI	0.21	0.79	0.37	0.63	0.66	0.34	0.13	0.87	0.27	0.00
TRI1GI	0.21	0.00	0.69	0.31	0.44	0.57	0.08	0.00	0.07	0.00
TRI2PA	0.16	0.84	0.62	0.38	1.00 *	0.00	0.25	0.75	0.02	0.98 *
TRI2TU	0.04	0.96	0.99 *	0.01	0.41	0.59	0.42	0.58	0.39	0.61
TRI4GA	0.16	0.00	0.38	0.62	0.34	0.00	0.04	0.00	0.04	0.00

Appendix 5 continued.

	High Plateau		Low Plateau		Slope		Stream		Swamp	
Species	Proportion of torus maps with stem-frequency > true map	Proportion of torus maps with stem-frequency < true map	Proportion of torus maps with stem-frequency > true map	Proportion of torus maps with stem-frequency < true map	Proportion of torus maps with stem-frequency > true map	Proportion of torus maps with stem-frequency < true map	Proportion of torus maps with stem-frequency > true map	Proportion of torus maps with stem-frequency < true map	Proportion of torus maps with stem-frequency > true map	Proportion of torus maps with stem-frequency < true map
TRIPCU	0.00	1.00 *	0.99 *	0.01	0.86	0.14	0.40	0.60	0.00	1.00 *
TROPRA	0.73	0.27	0.87	0.13	0.01	0.99 *	0.50	0.50	0.25	0.75
TURPOC	0.21	0.79	0.33	0.67	0.75	0.25	0.37	0.63	0.79	0.00
UNONPI	0.86	0.14	0.88	0.12	0.00	1.00 *	0.67	0.33	0.93	0.07
URERBA	0.20	0.80	0.66	0.34	0.23	0.77	0.20	0.00	0.20	0.00
VIROSE	0.87	0.13	0.40	0.60	0.07	0.94	0.61	0.39	0.97	0.03
VIROSU	0.96	0.05	0.99 *	0.01	0.00	1.00 *	0.04	0.96	0.21	0.79
VIROSP	0.76	0.24	0.88	0.12	0.01	0.99 *	0.35	0.65	0.54	0.00
VISMBA	0.73	0.27	0.53	0.47	0.71	0.29	0.65	0.00	0.01	0.99 *
VISMBI	0.05	0.95	0.89	0.00	0.53	0.00	0.08	0.00	0.07	0.00
VOCHFE	0.67	0.00	0.25	0.75	0.89	0.11	0.32	0.00	0.12	0.88
XYL1MA	0.50	0.50	0.82	0.18	0.01	1.00 *	0.88	0.12	0.71	0.29
XYL2OL	0.24	0.76	0.68	0.32	0.57	0.43	0.01	0.99 *	0.66	0.00
ZANTBE	0.75	0.25	0.09	0.92	0.36	0.65	0.62	0.38	0.92	0.00
ZANTP1	0.40	0.60	0.23	0.77	0.60	0.40	0.61	0.39	0.87	0.13
ZANTPR	0.91	0.09	0.10	0.90	0.37	0.63	0.83	0.17	0.43	0.57
ZANTSE	0.13	0.00	0.50	0.00	0.13	0.87	0.03	0.00	0.03	0.00
ZUELGU	0.75	0.26	0.64	0.36	0.49	0.51	0.30	0.70	0.00	1.00 *

APPENDIX 6

The Contribution of Habitat Location to Growth Rates for Species on the 50-ha FDP Plot

ANCOVA growth analysis from 1982 to 1990 for all stems ≥ 1-cm DBH of the 114 non-palm species for which ≥ 50 stems ≥ 1-cm DBH were alive in 1982 on both Slope and Plateau sites of the 50-ha Forest Dynamics Project plot of Barro Colorado Island, Panamá. The number of stems available for the growth analysis is < 50 if fewer than 50 stems survived to 1990. See Chapter 3 for a description of the terms included in each ANCOVA model. * $P<0.05$; ** $P<0.01$; *** $P<0.001$

Species	Significant habitat terms in the full model ANCOVA	Number of stems on Plateau sites alive in 1982 that survived to 1990	Number of stems on Slope sites alive in 1982 that survived to 1990	Habitat terms R^2	Full model R^2
ACALDI	NS	167	108	0.010	0.013
ALCHCO	NS	119	31	0.031	0.068
ALSEBL	*Hab; ***Hab x DBH82	3600	966	0.008	0.061
ANDIIN	NS	155	57	0.019	0.066
ANNOAC	NS	109	59	0.019	0.034
APEIME	NS	160	65	0.017	0.024
ASPICR	**Hab x DBH82; ***Hab x DBH82 x Dens20m82	210	113	0.041	0.536
BEILPE	*Hab x DBH82; ***Hab x DBH82 x Dens20m82	1043	549	0.018	0.150
BROSAL	NS	476	167	0.029	0.338
CALOLO	**Hab; ***Hab x DBH82	244	196	0.031	0.321
CAPPFR	NS	1205	508	0.001	0.015
CASEAC	NS	141	42	0.029	0.076
CASESY	NS	81	35	0.028	0.123
CASSEL	*Hab x DBH82	435	116	0.015	0.351
CECRIN	NS	162	53	0.024	0.116
CELTSC	*Hab x DBH82 x Dens20m82	77	45	0.053	0.161
CESTME	NS	30	35	0.013	0.039
CHR1EC	NS	70	126	0.038	0.061
CHR2AR	NS	203	97	0.004	0.106
COCCMA	NS	139	29	0.018	0.025
CONOCI	NS	11	28	0.171	0.190
CORDBI	NS	367	99	0.008	0.002
CORDLA	NS	688	422	0.001	0.020
COU2CU	*Hab; **Hab x DBH82; **Hab x Dens20m82; **Hab x DBH82 x Dens20m82	925	60	0.011	0.051
CROTBI	NS	76	38	0.021	0.049
CUPASY	**Hab; ***Hab x DBH82; *Hab x DBH82 x Dens20m82	355	79	0.090	0.214

Appendix 6 continued.

Species	Significant habitat terms in the full model ANCOVA	Number of stems on Plateau sites alive in 1982 that survived to 1990	Number of stems on Slope sites alive in 1982 that survived to 1990	Habitat terms R^2	Full model R^2
DES2PA	NS	4818	1435	0.001	0.003
DRYPST	*Hab x DBH82; ***Hab x Dens20m82; ***Hab x DBH82 x Dens20m82	975	831	0.018	0.183
ERY1CO	NS	74	47	0.006	0.037
ERY2MA	NS	139	51	0.039	0.268
EUGECO	NS	421	124	0.004	0.241
EUGEGA	NS	507	123	0.006	0.121
EUGENE	*Hab x DBH82 x Dens20m82	278	80	0.150	0.204
EUGEOE	*Hab	1043	305	0.003	0.175
FARAOC	*Hab x DBH82	13716	2535	0.001	0.018
GAR2IN	*Hab x DBH82	2298	672	0.008	0.146
GAR2MA	NS	234	98	0.001	0.129
GUARGU	**Hab; *Hab x Dens20m82	672	443	0.008	0.022
GUARSP	NS	635	267	0.003	0.028
GUATDU	NS	554	351	0.006	0.140
GUETFO	NS	108	27	0.021	0.043
GUSTSU	NS	241	69	0.006	0.034
HASSFL	*Hab x DBH82 x Dens20m82	357	172	0.018	0.115
HEISCO	NS	534	173	0.008	0.036
HERRPU	NS	231	86	0.012	0.031
HIRTTR	NS	1816	1128	0.001	0.060
HYBAPR	NS	14429	4266	0.001	0.002
INGAGO	NS	180	91	0.033	0.071
INGAMA	NS	165	118	0.012	0.193
INGAPE	NS	37	65	0.044	0.247
INGAQU	NS	297	180	0.009	0.018
INGAS1	NS	110	36	0.015	0.098
INGASA	NS	154	54	0.015	0.106
INGAUM	*Hab x DBH82; *Hab x Dens20m82; *Hab x DBH82 x Dens20m82	463	119	0.013	0.022
JAC1CO	NS	197	46	0.036	0.081
LACIAG	NS	728	206	0.007	0.041
LICAPL	NS	80	91	0.022	0.076
LONCLA	*Hab x DBH82	384	137	0.011	0.158
MALMSP	NS	152	57	0.011	0.012
MAQUCO	NS	695	324	0.007	0.034
MICOAR	NS	142	31	0.009	0.041
MOURMY	NS	3566	727	0.001	0.009
NECTCI	*Hab x DBH82; *Hab x Dens20m82; **Hab x DBH82 x Dens20m82	134	28	0.045	0.300
OCOTCE	NS	114	34	0.014	0.135

Appendix 6 continued.

Species	Significant habitat terms in the full model ANCOVA	Number of stems on Plateau sites alive in 1982 that survived to 1990	Number of stems on Slope sites alive in 1982 that survived to 1990	Habitat terms R^2	Full model R^2
COCOTOB	*Hab x DBH82; *Hab x DBH82 x Dens20m82	48	24	0.074	0.221
COCOTWH	NS	125	397	0.005	0.220
OLMEAS	NS	63	99	0.011	0.035
OURALU	NS	666	114	0.002	0.021
PALIGU	NS	57	13	0.027	0.095
PENTMA	NS	157	92	0.011	0.013
PICRLA	NS	384	259	0.002	0.128
PIPECO	NS	398	96	0.012	0.168
PIPERE	NS	31	28	0.026	0.117
PLA1PI	NS	123	33	0.023	0.219
POULAR	NS	811	958	0.004	0.022
POUTRE	*Hab x DBH82; **Hab x DBH82 x Dens20m82	806	251	0.015	0.211
PRI2CO	*Hab x DBH82 x Dens20m82	831	200	0.008	0.289
PROTCO	NS	319	200	0.009	0.028
PROTPA	*Hab x DBH82 x Dens20m82	1472	537	0.007	0.048
PROTTE	*Hab x DBH82; **Hab x Dens20m82	1196	715	0.012	0.073
PSYCHO	**Hab x DBH82	1730	471	0.008	0.011
PSYCMA	NS	180	47	0.015	0.029
PTERRO	*Hab x DBH82; **Hab x Dens20m82; ***Hab x DBH82 x Dens20m82	722	231	0.046	0.103
QUARAS	*Hab x DBH82 x Dens20m82	1058	398	0.005	0.055
RANDAR	NS	571	132	0.013	0.021
RINOSY	*Hab x Dens20m82	896	408	0.010	0.027
SENNDA	NS	26	18	0.068	0.201
SIMAAM	*Hab x DBH82 x Dens20m82	562	134	0.012	0.278
SIPAPA	*Hab x DBH82	54	44	0.164	0.237
SLOATE	**Hab x DBH82; **Hab x DBH82 x Dens20m82	330	115	0.018	0.109
SOROAF	NS	1523	594	0.002	0.017
SPONRA	NS	54	37	0.015	0.254
STY1ST	NS	203	102	0.020	0.038
SWARS1	*Hab x DBH82; **Hab x DBH82 x Dens20m82	1407	282	0.005	0.118
SWARS2	*Hab x DBH82	1529	540	0.004	0.019
SYMPGL	NS	54	55	0.023	0.291
TAB1RO	NS	114	40	0.040	0.073
TAB2AR	NS	663	193	0.032	0.136
TACHVE	***Hab x DBH82; *Hab x Dens20m82; ***Hab x DBH82 x Dens20m82	1383	586	0.006	0.492
TALINE	NS	430	167	0.005	0.034
TALIPR	**Hab x DBH82; **Hab x DBH82 x Dens20m82	267	116	0.024	0.025
TET2PA	NS	1788	585	0.002	0.094

Appendix 6 continued.

Species	Significant habitat terms in the full model ANCOVA	Number of stems on Plateau sites alive in 1982 that survived to 1990	Number of stems on Slope sites alive in 1982 that survived to 1990	Habitat terms R^2	Full model R^2
TRI2PA	NS	253	43	0.012	0.085
TRI2TU	NS	5453	1878	0.001	0.231
TRIPCU	NS	144	36	0.048	0.089
TROPRA	NS	128	86	0.018	0.064
UNONPI	NS	309	230	0.013	0.064
VIROSE	NS	1170	500	0.003	0.067
VIROSU	NS	91	90	0.017	0.159
XYL1MA	NS	304	362	0.021	0.062
ZANTBE	NS	83	35	0.027	0.254
ZANTP1	NS	116	33	0.020	0.381
ZANTPR	NS	91	35	0.039	0.048

APPENDIX 7

Mortality Rates on Slope and Plateau Sites of the 50-ha FDP Plot

Comparison of mortality on Slope versus Plateau sites of the 50-ha Forest Dynamics Project plot of Barro Colorado Island, Panamá. Two size-classes were used: Stems 10-99 mm DBH and stems ≥ 100 mm DBH. *N* is the number of stems alive in the 1982 census. *D* is the number of stems that died or turned up missing by the 1990 census. The *Mean t* is the mean length of the inter-census interval. See Chapter 3 for calculation of mortality rates for the 1982-1990 inter-census interval (reported here as percentages, as in Condit *et al.* [1995]). Only species/size-class combinations for which there were ≥ 20 stems on both Slope and Plateau sites are included. Asterisks (*) mark the comparisons whose 84% confidence intervals, reported as confidence limits (CL) *do not* overlap for mortality on Slope versus Plateau sites, giving an overall test for differences in mortality between Plateau and Slope sites at the alpha=0.05 level.

	Size	Plateau						Slope					
Species	class (mm)	Mean t (yr)	N	D	Mortality rate	Lower 84% CL	Upper 84% CL	Mean t (yr)	N	D	Mortality rate	Lower 84% CL	Upper 84% CL
ACALDI	10-99	8.69	830	184	2.88	2.59	3.19	9.06	479	124	3.31	2.90	3.73
ADE1TR	10-99	8.66	152	27	2.26	1.66	2.88	9.07	32	9	3.64	2.05	5.50
AEGIPA	10-99	8.11	66	13	2.70	1.69	3.80	8.77	28	7	3.28	1.66	5.17
ALCHCO *	10-99	8.45	167	33	2.61	1.99	3.26	8.81	48	20	6.12	4.33	8.24
ALCHCO	≥100	8.61	78	5	0.77	0.39	1.08	8.90	41	4	1.15	0.56	2.41
ALIBED	10-99	8.42	205	9	0.53	0.29	0.78	8.99	47	4	0.99	0.49	2.07
ALLOPS	10-99	8.57	95	17	2.30	1.54	3.11	9.13	34	2	0.66	0.25	1.89
ALSEBL	10-99	8.40	4225	221	0.64	0.58	0.70	8.76	1268	66	0.61	0.51	0.72
ALSEBL	≥100	8.72	544	17	0.36	0.24	0.49	8.97	105	1	0.11	0.00	0.41
ANAXPA	10-99	7.71	42	2	0.63	0.24	1.79	7.69	430	24	0.75	0.54	0.96
ANDIIN	10-99	8.66	182	4	0.26	0.13	0.53	9.17	66	1	0.17	0.00	0.65
ANNOAC *	10-99	8.50	266	27	1.26	0.92	1.60	8.76	122	6	0.58	0.25	0.91
APEIME	10-99	8.21	100	9	1.15	0.62	1.70	8.58	39	2	0.61	0.23	1.74
APEIME	≥100	8.60	138	7	0.61	0.29	0.93	9.03	49	4	0.94	0.46	1.98
ARDIFE	10-99	8.79	38	2	0.62	0.24	1.74	9.22	27	0	0.00	0.00	1.04
ASPICR	10-99	8.84	231	6	0.30	0.13	0.47	9.21	131	8	0.68	0.35	1.03
AST1ST	≥100	8.67	111	3	0.32	0.14	0.74	8.90	46	4	1.02	0.50	2.14
BACTBA	10-99	8.21	72	7	1.25	0.60	1.92	9.09	34	1	0.33	0.00	1.28
BACTC1	10-99	8.76	125	9	0.85	0.46	1.26	8.81	106	12	1.36	0.83	1.93
BACTMA	10-99	8.70	54	13	3.17	1.99	4.47	9.34	23	4	2.05	0.99	4.30
BEILPE *	10-99	8.18	1340	93	0.88	0.75	1.01	8.80	639	26	0.47	0.34	0.60

Appendix 7 continued.

Species	Size class (mm)	Plateau Mean t (yr)	Plateau N	Plateau D	Plateau Mortality rate	Plateau Lower 84% CL	Plateau Upper 84% CL	Slope Mean t (yr)	Slope N	Slope D	Slope Mortality rate	Slope Lower 84% CL	Slope Upper 84% CL
BEILPE	≥100	8.55	196	13	0.80	0.50	1.12	9.30	94	5	0.59	0.31	1.14
BROSAL	10-99	8.64	430	10	0.27	0.15	0.39	8.80	144	2	0.16	0.06	0.45
BROSAL	≥100	8.64	116	6	0.61	0.27	0.97	8.99	43	2	0.53	0.20	1.50
CALOLO	10-99	8.32	301	33	1.40	1.06	1.74	8.85	250	23	1.09	0.78	1.41
CAPPFR	10-99	8.72	2057	72	0.41	0.34	0.48	9.04	888	34	0.43	0.33	0.54
CASEAC	10-99	8.59	271	25	1.13	0.82	1.45	8.98	94	4	0.48	0.24	1.01
CASEAR	10-99	8.09	90	15	2.25	1.46	3.10	8.83	21	3	1.75	0.77	4.10
CASEAR	≥100	8.36	94	10	1.35	0.76	1.96	8.81	20	1	0.58	0.00	2.28
CASESY	10-99	8.24	113	17	1.98	1.32	2.67	8.83	32	3	1.11	0.49	2.62
CASESY	≥100	8.57	33	4	1.51	0.73	3.16	8.98	21	3	1.72	0.75	4.04
CASSEL	10-99	8.26	453	12	0.33	0.19	0.46	8.71	125	5	0.47	0.25	0.91
CECRIN	10-99	8.48	147	30	2.69	2.02	3.40	8.65	61	14	3.01	1.94	4.20
CECRIN	≥100	8.61	210	32	1.92	1.45	2.41	8.70	51	4	0.94	0.46	1.96
CELTSC	10-99	8.50	74	10	1.71	0.97	2.49	9.09	54	5	1.07	0.56	2.06
CESTME	10-99	8.35	157	39	3.42	2.67	4.21	9.13	106	37	4.70	3.66	5.85
CHR1EC	10-99	8.39	157	15	1.20	0.77	1.64	8.91	258	14	0.63	0.39	0.86
CHR2AR	10-99	8.44	214	9	0.51	0.27	0.75	8.82	97	1	0.12	0.00	0.46
CHR2AR	≥100	8.34	48	2	0.51	0.20	1.44	9.01	22	2	1.06	0.40	3.00
COCCCO	10-99	8.41	104	6	0.71	0.31	1.12	8.90	33	2	0.70	0.27	1.99
COCCMA	10-99	8.38	310	11	0.43	0.25	0.61	8.82	73	5	0.80	0.42	1.56
CONOCI	10-99	8.57	116	25	2.83	2.06	3.66	8.83	224	65	3.88	3.22	4.58
CORDBI *	10-99	8.04	355	67	2.60	2.16	3.06	8.47	85	27	4.51	3.35	5.80
CORDBI	≥100	8.16	180	10	0.70	0.39	1.01	8.62	63	3	0.57	0.26	1.33
CORDLA	10-99	8.53	708	62	1.07	0.88	1.27	8.90	437	38	1.02	0.79	1.26
CORDLA	≥100	8.70	254	27	1.29	0.95	1.65	9.02	114	7	0.70	0.34	1.08
COU2CU	10-99	8.28	1242	50	0.50	0.40	0.59	8.72	91	2	0.25	0.10	0.72
CROTBI	10-99	8.16	308	93	4.41	3.78	5.07	8.39	87	26	4.23	3.12	5.46
CUPASY	10-99	8.40	682	8	0.14	0.07	0.21	8.92	157	2	0.14	0.05	0.41
DES2PA	10-99	8.50	8065	1068	1.67	1.60	1.74	8.82	2370	322	1.66	1.53	1.79
DRYPST	10-99	8.99	1010	56	0.63	0.52	0.75	9.10	879	35	0.45	0.34	0.55
DRYPST	≥100	9.13	108	2	0.20	0.07	0.58	9.26	78	4	0.57	0.28	1.19
ERY1CO	10-99	8.23	124	19	2.02	1.39	2.69	8.70	87	19	2.83	1.95	3.78
ERY2MA *	10-99	8.52	205	35	2.20	1.69	2.73	8.79	77	7	1.08	0.52	1.67
ERY2PA	10-99	8.44	56	6	1.34	0.60	2.14	8.36	26	1	0.47	0.00	1.83
EUGECO	10-99	8.48	514	53	1.28	1.04	1.53	8.98	152	17	1.32	0.88	1.78
EUGECO	≥100	8.80	45	4	1.06	0.51	2.22	9.21	21	4	2.29	1.11	4.82
EUGEGA	10-99	8.52	678	36	0.64	0.49	0.79	9.02	161	5	0.35	0.18	0.68
EUGENE	10-99	8.58	310	5	0.19	0.10	0.37	8.86	90	2	0.25	0.10	0.72

Appendix 7 continued.

		Plateau						Slope					
Species	Size class (mm)	Mean t (yr)	N	D	Mortality rate	Lower 84% CL	Upper 84% CL	Mean t (yr)	N	D	Mortality rate	Lower 84% CL	Upper 84% CL
EUGEOE	10-99	8.43	1377	137	1.24	1.10	1.39	8.91	402	33	0.96	0.73	1.20
FARAOC *	10-99	8.45	16323	760	0.56	0.54	0.59	8.85	2988	117	0.45	0.39	0.51
FARAOC	≥100	8.58	890	101	1.40	1.21	1.60	8.82	159	17	1.28	0.85	1.73
GAR2IN	10-99	8.68	2551	111	0.51	0.44	0.58	9.02	756	35	0.53	0.40	0.65
GAR2MA	10-99	8.49	384	112	4.06	3.53	4.61	8.76	154	43	3.74	2.96	4.57
GUAPST	10-99	8.50	110	14	1.60	1.02	2.22	8.81	21	1	0.55	0.00	2.16
GUARGU	10-99	8.72	695	44	0.75	0.59	0.91	8.98	494	28	0.65	0.48	0.82
GUARGU	≥100	8.92	232	6	0.29	0.13	0.46	9.17	98	4	0.45	0.22	0.95
GUARSP	10-99	8.49	878	100	1.42	1.23	1.63	8.97	361	55	1.84	1.50	2.20
GUARSP	≥100	8.61	61	12	2.54	1.56	3.62	9.03	37	5	1.61	0.84	3.12
GUATDU	10-99	8.26	765	76	1.27	1.06	1.47	8.79	444	34	0.91	0.69	1.13
GUATDU	≥100	8.42	159	20	1.60	1.11	2.11	9.01	105	11	1.23	0.72	1.76
GUETFO *	10-99	8.51	177	8	0.54	0.28	0.82	8.84	57	8	1.71	0.89	2.59
GUSTSU	10-99	8.70	81	1	0.14	0.00	0.55	8.13	32	2	0.79	0.30	2.25
GUSTSU	≥100	8.85	230	6	0.30	0.13	0.47	8.76	62	0	0.00	0.00	0.48
HAMEAX	10-99	8.44	72	21	4.09	2.89	5.41	9.23	33	8	3.01	1.61	4.62
HASSFL	10-99	8.32	481	74	2.01	1.69	2.34	8.79	252	40	1.97	1.54	2.41
HASSFL	≥100	8.39	150	19	1.61	1.11	2.14	8.85	59	7	1.43	0.70	2.21
HEISAC	10-99	8.56	58	0	0.00	0.00	0.53	8.97	26	1	0.44	0.00	1.71
HEISCO	10-99	8.58	435	15	0.41	0.26	0.56	9.02	151	11	0.84	0.49	1.20
HEISCO	≥100	8.61	173	13	0.91	0.56	1.27	9.13	53	1	0.21	0.00	0.81
HERRPU	10-99	8.42	329	12	0.44	0.26	0.62	8.76	128	11	1.03	0.60	1.47
HIRTTR	10-99	8.54	2000	84	0.50	0.43	0.58	8.90	1276	63	0.57	0.47	0.67
HIRTTR	≥100	8.70	298	20	0.80	0.55	1.05	9.13	155	8	0.58	0.30	0.87
HURACR	≥100	9.18	59	1	0.19	0.00	0.72	9.34	30	1	0.36	0.00	1.42
HYBAPR *	10-99	8.40	26902	3118	1.47	1.43	1.50	8.92	7909	792	1.18	1.12	1.24
INGAGO	10-99	8.43	250	32	1.62	1.23	2.03	8.97	130	12	1.08	0.65	1.53
INGAMA	10-99	8.55	394	76	2.51	2.11	2.92	8.94	328	72	2.77	2.32	3.24
INGAMA	≥100	8.49	51	7	1.74	0.85	2.70	8.82	24	7	3.91	2.00	6.21
INGAPE	10-99	9.35	70	13	2.20	1.38	3.09	9.47	96	9	1.04	0.57	1.54
INGAQU	10-99	8.66	392	33	1.02	0.77	1.27	9.06	242	21	1.00	0.70	1.31
INGAS1	10-99	8.57	137	11	0.98	0.57	1.40	9.10	50	2	0.45	0.17	1.27
INGASA	10-99	8.40	209	17	1.01	0.67	1.36	8.68	85	8	1.14	0.59	1.72
INGAUM *	10-99	8.40	659	62	1.18	0.97	1.39	8.85	170	8	0.54	0.28	0.82
JAC1CO	10-99	8.15	78	9	1.50	0.82	2.23	8.51	21	3	1.81	0.80	4.26
JAC1CO	≥100	8.25	157	8	0.63	0.32	0.95	8.70	38	4	1.28	0.62	2.68
LACIAG	10-99	8.25	1051	118	1.44	1.26	1.63	8.68	290	30	1.26	0.94	1.58
LAETTH	10-99	8.37	424	54	1.63	1.32	1.94	8.84	38	7	2.30	1.14	3.60

Appendix 7 continued.

Species	Size class (mm)	Plateau						Slope					
		Mean t (yr)	N	D	Mortality rate	Lower 84% CL	Upper 84% CL	Mean t (yr)	N	D	Mortality rate	Lower 84% CL	Upper 84% CL
LICAPL	10-99	9.11	102	8	0.90	0.46	1.35	9.13	126	14	1.29	0.82	1.78
LONCLA	10-99	8.22	466	40	1.09	0.85	1.34	8.63	165	14	1.03	0.65	1.42
LONCLA	≥100	8.30	88	14	2.09	1.33	2.90	8.64	31	6	2.49	1.15	4.01
MALMSP	10-99	8.37	167	0	0.00	0.00	0.19	8.81	65	1	0.18	0.00	0.69
MAQUCO	10-99	8.47	732	30	0.49	0.37	0.62	9.01	321	12	0.42	0.25	0.60
MAQUCO	≥100	8.36	135	21	2.02	1.42	2.66	8.80	66	12	2.28	1.39	3.24
MICOAF	10-99	8.04	292	58	2.75	2.26	3.27	8.35	46	6	1.67	0.75	2.67
MICOAR	10-99	8.40	292	83	3.98	3.38	4.61	8.49	59	16	3.73	2.48	5.11
MICONE	10-99	7.99	284	96	5.16	4.44	5.93	7.88	35	16	7.75	5.26	10.86
MOURMY *	10-99	8.31	5195	727	1.81	1.72	1.91	8.76	1023	98	1.15	0.99	1.31
NECTCI	10-99	7.89	264	14	0.69	0.43	0.95	8.27	56	4	0.90	0.44	1.87
NECTGL	10-99	8.67	50	5	1.22	0.64	2.35	9.13	46	6	1.53	0.69	2.44
OCOTCE	10-99	8.35	213	12	0.69	0.42	0.98	8.92	72	4	0.64	0.31	1.34
OCOTOB	10-99	8.20	113	20	2.38	1.65	3.14	8.81	62	13	2.67	1.68	3.76
OCOTPU	10-99	8.09	193	21	1.42	1.00	1.87	8.82	41	5	1.47	0.77	2.86
OCOTWH	10-99	8.77	202	39	2.45	1.91	3.01	9.14	731	127	2.09	1.83	2.35
OCOTWH	≥100	8.65	59	4	0.81	0.40	1.70	9.05	100	10	1.16	0.66	1.69
OENOMA	10-99	8.26	669	13	0.24	0.15	0.33	8.86	197	6	0.35	0.15	0.55
OENOMA	≥100	8.41	507	4	0.09	0.05	0.14	8.95	160	2	0.14	0.05	0.40
OLMEAS	10-99	8.87	141	28	2.50	1.85	3.18	9.13	217	47	2.67	2.14	3.24
ORMOCR	10-99	8.86	21	0	0.00	0.00	1.39	9.00	20	0	0.00	0.00	1.44
OURALU	10-99	8.61	849	41	0.57	0.45	0.70	9.01	153	4	0.29	0.14	0.61
PALIGU *	10-99	8.07	261	119	7.54	6.60	8.57	8.65	64	21	4.60	3.26	6.11
PENTMA	10-99	8.50	315	26	1.01	0.74	1.30	8.90	190	17	1.05	0.70	1.42
PEREXA	10-99	7.87	217	16	0.97	0.64	1.32	7.88	35	2	0.75	0.29	2.11
PICRLA	10-99	8.76	595	63	1.28	1.05	1.51	9.01	399	54	1.61	1.31	1.93
PIPEA1	10-99	8.08	54	8	1.98	1.04	3.01	8.65	39	10	3.43	2.00	5.06
PIPEAE	10-99	8.33	76	23	4.33	3.12	5.67	8.75	111	31	3.74	2.83	4.73
PIPECO *	10-99	8.14	2390	719	4.40	4.17	4.63	8.64	544	142	3.50	3.10	3.92
PIPECU	10-99	8.13	49	5	1.32	0.69	2.57	8.30	38	8	2.85	1.51	4.35
PIPEPE	10-99	8.56	33	9	3.72	2.10	5.61	9.21	74	19	3.22	2.23	4.31
PIPERE	10-99	8.49	77	12	2.00	1.21	2.83	8.74	66	13	2.51	1.57	3.53
PLA1PI *	10-99	8.39	124	11	1.11	0.65	1.58	8.85	46	12	3.42	2.11	4.89
POULAR *	10-99	8.48	1180	207	2.27	2.05	2.50	9.07	1142	173	1.81	1.62	2.01
POULAR *	≥100	8.41	412	82	2.64	2.24	3.05	9.06	451	67	1.78	1.48	2.08
POUTRE	10-99	8.48	1009	68	0.82	0.68	0.96	8.96	302	25	0.96	0.70	1.24
POUTRE	≥100	8.69	99	7	0.84	0.41	1.30	8.97	26	0	0.00	0.00	1.11
PRI2CO	10-99	8.18	817	22	0.33	0.23	0.43	8.12	192	4	0.26	0.13	0.55

Appendix 7 continued.

Species	Size class (mm)	Plateau						Slope					
		Mean t (yr)	N	D	Mortality rate	Lower 84% CL	Upper 84% CL	Mean t (yr)	N	D	Mortality rate	Lower 84% CL	Upper 84% CL
PRI2CO	≥100	8.21	215	3	0.17	0.08	0.40	8.20	44	3	0.86	0.38	2.02
PROTCO *	10-99	8.35	474	61	1.65	1.36	1.95	8.86	263	20	0.89	0.62	1.18
PROTCO	≥100	8.57	71	15	2.77	1.81	3.82	8.56	28	3	1.32	0.59	3.11
PROTPA *	10-99	8.16	1832	138	0.96	0.85	1.07	8.71	632	33	0.62	0.47	0.77
PROTTE	10-99	8.79	1310	75	0.67	0.56	0.78	9.12	849	62	0.83	0.68	0.98
PROTTE	≥100	8.89	222	22	1.17	0.83	1.53	9.11	89	9	1.17	0.64	1.73
PSYCG3	10-99	9.11	41	12	3.80	2.36	5.46	9.09	47	15	4.23	2.79	5.89
PSYCHO	10-99	8.63	3949	809	2.66	2.53	2.79	8.89	1014	197	2.43	2.19	2.68
PSYCMA *	10-99	8.25	410	107	3.67	3.18	4.17	8.78	102	18	2.21	1.50	2.97
PTERRO	10-99	8.29	983	82	1.05	0.89	1.21	8.68	309	24	0.93	0.67	1.20
PTERRO	≥100	8.74	66	11	2.09	1.24	3.00	9.12	36	3	0.95	0.42	2.23
QUARAS	10-99	8.62	1013	60	0.71	0.58	0.84	8.99	411	29	0.81	0.60	1.03
QUARAS	≥100	8.86	432	24	0.65	0.46	0.83	9.25	194	11	0.63	0.37	0.90
QUASAM	10-99	8.99	98	1	0.11	0.00	0.44	9.11	40	3	0.86	0.38	2.01
RANDAR *	10-99	8.47	606	37	0.74	0.57	0.92	8.79	138	16	1.40	0.92	1.90
RANDAR	≥100	8.58	146	18	1.53	1.04	2.05	8.85	36	1	0.32	0.00	1.24
RINOSY	10-99	8.66	1480	112	0.91	0.79	1.03	8.50	648	38	0.71	0.55	0.87
SENNDA	10-99	8.37	121	39	4.65	3.64	5.75	9.01	60	15	3.19	2.09	4.42
SIMAAM	10-99	8.18	747	144	2.62	2.32	2.93	8.75	170	36	2.72	2.10	3.37
SIMAAM	≥100	8.24	198	42	2.89	2.28	3.54	8.68	33	4	1.49	0.72	3.12
SIPAPA	10-99	8.54	202	9	0.53	0.29	0.79	8.96	148	12	0.94	0.57	1.33
SLOATE	10-99	8.51	364	11	0.36	0.21	0.51	9.00	117	5	0.49	0.25	0.94
SLOATE	≥100	8.79	48	3	0.73	0.32	1.72	9.17	32	2	0.70	0.27	2.00
SOCREX *	10-99	7.95	301	58	2.69	2.21	3.20	8.54	127	16	1.58	1.04	2.14
SOCREX	≥100	7.94	261	44	2.33	1.84	2.83	8.17	106	15	1.87	1.21	2.56
SOLAHA	10-99	8.45	44	12	3.77	2.33	5.41	8.08	35	15	6.93	4.62	9.76
SOROAF	10-99	8.48	2050	170	1.02	0.91	1.13	8.93	788	58	0.86	0.70	1.01
SPONRA	10-99	8.32	84	15	2.36	1.54	3.25	8.64	42	7	2.11	1.04	3.29
STYLST	10-99	8.41	406	26	0.79	0.57	1.01	8.88	182	7	0.44	0.21	0.68
SWARS1	10-99	8.62	1449	13	0.10	0.06	0.15	8.82	310	7	0.26	0.12	0.40
SWARS1	≥100	8.58	155	3	0.23	0.10	0.53	8.75	24	1	0.49	0.00	1.90
SWARS2 *	10-99	8.47	1665	35	0.25	0.19	0.31	9.00	575	6	0.12	0.05	0.18
SWARS2	≥100	8.33	73	4	0.68	0.33	1.42	8.70	21	0	0.00	0.00	1.41
SYMPGL	10-99	8.26	56	6	1.37	0.61	2.18	9.00	66	10	1.83	1.04	2.67
TAB1RO	10-99	8.48	122	9	0.90	0.49	1.33	8.99	54	7	1.54	0.76	2.39
TAB1RO	≥100	8.97	44	5	1.34	0.70	2.60	9.07	22	3	1.62	0.71	3.80
TAB2AR	10-99	8.31	640	46	0.90	0.71	1.08	8.64	211	9	0.50	0.27	0.74
TAB2AR	≥100	8.40	211	16	0.94	0.61	1.27	8.65	41	3	0.88	0.39	2.06

Appendix 7 continued.

Species	Size class (mm)	Plateau						Slope					
		Mean t (yr)	N	D	Mortality rate	Lower 84% CL	Upper 84% CL	Mean t (yr)	N	D	Mortality rate	Lower 84% CL	Upper 84% CL
TACHVE	10-99	8.26	1876	268	1.87	1.71	2.03	8.88	796	107	1.63	1.41	1.85
TACHVE	≥100	8.52	54	10	2.40	1.38	3.52	8.98	20	3	1.81	0.80	4.25
TALINE	10-99	9.05	510	16	0.35	0.23	0.48	9.36	199	9	0.49	0.27	0.73
TALIPR	10-99	8.82	364	8	0.25	0.13	0.38	9.14	147	3	0.23	0.10	0.53
TET2PA *	10-99	8.44	1947	97	0.61	0.52	0.69	8.84	675	50	0.87	0.70	1.04
TET2PA	≥100	8.51	228	6	0.31	0.14	0.49	9.20	64	2	0.35	0.13	0.98
TRI2PA	10-99	8.51	323	30	1.15	0.86	1.44	8.82	50	2	0.46	0.17	1.31
TRI2TU *	10-99	8.75	6448	729	1.37	1.30	1.44	9.06	2467	227	1.07	0.97	1.16
TRI2TU	≥100	8.50	1528	181	1.48	1.33	1.64	8.94	287	33	1.37	1.04	1.70
TRIPCU	10-99	8.97	147	15	1.20	0.77	1.64	9.10	58	5	0.99	0.52	1.92
TROPRA	10-99	8.70	136	9	0.79	0.43	1.16	9.04	94	4	0.48	0.24	1.01
UNONPI	10-99	8.34	313	20	0.79	0.55	1.04	9.03	289	28	1.13	0.83	1.43
UNONPI	≥100	8.25	84	2	0.29	0.11	0.83	9.15	46	2	0.49	0.19	1.38
VIROSE *	10-99	8.27	1128	112	1.26	1.10	1.43	8.85	468	31	0.77	0.58	0.97
VIROSE	≥100	8.44	397	30	0.93	0.70	1.17	8.75	161	11	0.81	0.47	1.16
VIROSU	10-99	8.28	55	5	1.15	0.60	2.23	8.85	54	6	1.33	0.59	2.12
VIROSU	≥100	8.78	77	4	0.61	0.30	1.27	9.07	78	6	0.88	0.39	1.40
VISMBA	10-99	8.06	43	8	2.55	1.35	3.89	8.31	21	4	2.54	1.24	5.34
XYL1MA	10-99	8.89	309	6	0.22	0.10	0.35	8.96	416	17	0.47	0.31	0.62
XYL1MA	≥100	8.84	39	1	0.29	0.00	1.15	8.91	40	1	0.28	0.00	1.11
XYL2OL	10-99	8.61	121	10	1.00	0.57	1.45	8.55	38	6	2.01	0.91	3.22
ZANTBE	10-99	8.08	78	16	2.84	1.88	3.88	8.59	32	5	1.98	1.04	3.84
ZANTBE	≥100	8.30	72	12	2.20	1.34	3.12	8.93	28	6	2.70	1.25	4.37
ZANTP1	10-99	8.41	148	21	1.82	1.28	2.39	8.52	46	11	3.21	1.92	4.65
ZANTPR	10-99	8.40	129	21	2.12	1.49	2.78	8.69	47	10	2.75	1.59	4.04

APPENDIX 8

Recruitment Rates on Slope and Plateau Sites of the 50-ha FDP Plot in 1985

Comparison of recruitment into the 1-2 cm DBH size-class on the Slope versus on the Plateau of the 50-ha Forest Dynamics Project plot of Barro Colorado Island, Panamá during the 1985 census. The Recruits Ratio is the number of recruits on the Plateau per Plateau adult over the number of recruits on the Slope per Slope adult; where recruits per adult on the Slope is zero, the ratio is presented as X/0. All 156 50-ha FDP plot species are presented for which sufficient stems were present for a Chi-square comparison. * P<0.05; ** P<0.01.

	Plateau		Slope				
Species	Number of adults	Number of recruits	Number of adults	Number of recruits	Recruits Ratio	χ^2	P-value
ACALDI	428	78	271	24	2.06	9.98	* *
AEGIPA	45	9	13	4	0.65	0.52	
ALCHCO	44	2	30	2	0.68	0.15	
ALIBED	41	31	10	10	0.76	0.59	
ALLOPS	48	22	13	2	2.98	2.41	
ALSEBL	315	682	64	217	0.64	33.68	* *
ANAXPA	37	4	435	63	0.75	0.32	
ANDIIN	5	12	1	5	0.48	1.99	
ANNOAC	267	40	128	18	1.07	0.05	
ANNOSP	10	15	2	5	0.60	1.00	
ASPICR	10	27	7	15	1.26	0.52	
BEILPE	77	329	32	204	0.67	20.43	* *
BROSAL	40	38	17	13	1.24	0.46	
CALOLO	10	51	3	72	0.21	87.12	* *
CAPPFR	2130	214	935	111	0.85	2.04	
CASEAC	72	39	14	23	0.33	19.71	* *
CASEAR	57	9	10	1	1.58	0.19	
CASESY	29	10	20	3	2.30	1.69	
CASSEL	44	67	27	21	1.96	7.49	* *
CECRIN	69	40	22	10	1.28	0.48	
CECROB	12	5	6	0	0.42/0	2.50	
CESTME	106	14	99	14	0.93	0.03	
CHR1EC	110	7	164	18	0.58	1.53	
CHR2AR	9	52	3	14	1.24	0.51	
CHR2CA	9	7	2	2	0.78	0.10	
CLIDOC	5	5	1	1	1.00	0.00	
COCCCO	17	12	6	10	0.42	4.28	*
CONOCI	86	16	155	22	1.31	0.68	
CORDAL	27	6	5	3	0.37	2.14	
CORDBI	137	76	48	22	1.21	0.62	
CORDLA	263	79	124	55	0.68	4.99	*
COU2CU	588	185	31	22	0.44	13.74	* *
CROTBI	78	109	39	60	0.91	0.36	
CUPASY	126	98	28	35	0.62	5.92	*
DES2PA	2824	1159	667	427	0.64	62.70	* *
DRYPST	26	78	24	99	0.73	4.46	*
ERY1CO	78	4	55	1	2.82	0.94	
ERY2MA	48	17	8	11	0.26	14.29	* *
ERY2PA	55	2	25	3	0.30	1.92	
EUGECO	5	57	3	30	1.14	0.34	
EUGEGA	89	172	21	43	0.94	0.12	
EUGENE	34	38	7	16	0.49	6.01	*
EUGEOE	27	222	3	63	0.39	46.40	* *

Appendix 8 continued.

Species	Plateau Number of adults	Plateau Number of recruits	Slope Number of adults	Slope Number of recruits	Recruits Ratio	χ^2	P-value
FARAOC	5357	1859	914	468	0.68	57.29	* *
GAR2IN	54	361	14	108	0.87	1.71	
GUAPST	33	3	9	2	0.41	1.02	
GUARGR	2	2	1	4	0.25	3.00	
GUARGU	406	85	180	86	0.44	30.79	* *
GUARSP	78	93	41	45	1.09	0.21	
GUATDU	44	81	29	45	1.19	0.85	
GUETFO	52	12	9	6	0.35	4.94	*
GUSTSU	229	6	62	2	0.81	0.07	
HAMEAX	54	10	29	8	0.67	0.72	
HASSFL	193	16	81	15	0.45	5.28	*
HEISAC	20	6	15	4	1.13	0.03	
HEISCO	117	65	34	26	0.73	1.91	
HERRPU	331	36	133	21	0.69	1.86	
HIRTTR	407	406	243	269	0.90	1.76	
HYBAPR	27543	3676	8534	1466	0.78	67.12	* *
HYERAL	12	6	7	5	0.70	0.35	
INGACO	15	22	3	2	2.20	1.20	
INGAGO	4	18	2	10	0.90	0.07	
INGAMA	8	98	6	73	1.01	0.00	
INGAPE	1	13	2	18	1.44	1.03	
INGAQU	41	28	24	31	0.53	6.18	*
INGAS1	13	37	7	7	2.85	7.05	* *
INGASA	11	9	2	10	0.16	20.25	* *
INGAUM	37	82	6	25	0.53	7.89	* *
JAC1CO	95	4	21	2	0.44	0.94	
LACIAG	96	196	26	68	0.78	3.11	
LAETTH	36	45	2	6	0.42	4.32	*
LICAHY	18	6	3	2	0.50	0.75	
LICAPL	2	23	2	27	0.85	0.32	
LONCLA	29	74	10	24	1.06	0.07	
LUEHSE	30	17	8	4	1.13	0.05	
MACRGL	9	4	8	3	1.19	0.05	
MALMSP	70	33	23	11	0.99	0.00	
MALPRO	36	11	11	2	1.68	0.47	
MAQUCO	122	86	61	43	1.00	0.00	
MAR1LA	1	0	1	3	0.00	3.00	
MAYTSC	14	4	5	1	1.43	0.10	
MICOAF	99	53	10	2	2.68	2.02	
MICOAR	31	152	5	23	1.07	0.08	
MICONE	236	81	30	7	1.47	0.97	
MOURMY	1602	1105	362	181	1.38	16.24	* *
MYRCGA	2	7	2	2	3.50	2.78	
NECTCI	2	36	1	9	2.00	3.60	
NECTPU	5	4	1	2	0.40	1.20	
NEEAAM	46	16	16	4	1.39	0.35	
OCOTCE	65	36	13	13	0.55	3.43	
OCOTOB	10	19	4	16	0.48	5.04	*
OCOTWH	21	25	45	63	0.85	0.47	
OLMEAS	56	8	120	10	1.71	1.32	
OURALU	169	115	18	32	0.38	24.92	* *
PALIGU	489	255	89	50	0.93	0.23	
PENTMA	157	22	92	17	0.76	0.74	
PEREXA	19	25	3	1	3.95	2.12	
PHOECI	7	8	1	3	0.38	2.19	
PICRLA	159	64	97	51	0.77	2.04	
PIPEAE	52	9	83	12	1.20	0.17	
PIPECO	2837	879	659	213	0.96	0.31	
PIPEPE	33	13	82	24	1.35	0.75	
PIPERE	39	7	31	1	5.56	3.28	
PLA1PI	28	19	6	9	0.45	4.05	*
PLA2EL	22	6	4	3	0.36	2.23	

Appendix 8 continued.

	Plateau		Slope				
Species	Number of adults	Number of recruits	Number of adults	Number of recruits	Recruits Ratio	χ^2	P-value
POSOLA	8	3	3	2	0.56	0.41	
POULAR	20	51	42	29	3.69	36.31	* *
POUTRE	42	149	11	62	0.63	9.55	* *
PRI2CO	50	57	15	15	1.14	0.20	
PROTCO	16	48	7	28	0.75	1.47	
PROTPA	80	235	29	72	1.18	1.56	
PROTTE	110	252	51	135	0.87	1.84	
PSIDFR	2	2	1	2	0.50	0.50	
PSYCCH	10	5	6	1	3.00	1.11	
PSYCDE	68	23	5	0	0.34/0	1.69	
PSYCG2	3	1	2	2	0.33	0.89	
PSYCG3	6	8	11	5	2.93	3.92	*
PSYCHO	4089	774	1084	233	0.88	2.90	
PSYCLI	13	5	4	1	1.54	0.16	
PSYCMA	486	143	116	32	1.07	0.11	
PTERRO	8	156	3	61	0.96	0.08	
QUARAS	214	84	115	63	0.72	4.04	*
QUASAM	53	4	23	0	0.08/0	1.74	
RANDAR	317	65	59	19	0.64	3.05	
RINOSY	696	151	294	86	0.74	4.93	*
SENNDA	81	12	40	4	1.48	0.47	
SIMAAM	50	128	8	31	0.66	4.35	*
SIPAPA	81	15	52	8	1.20	0.18	
SLOATE	8	22	1	7	0.39	4.98	*
SOLAHA	30	10	21	4	1.75	0.92	
SOROAF	934	251	421	92	1.23	2.89	
SPONMO	2	4	1	0	2.00/0	2.00	
SPONRA	13	10	9	4	1.73	0.88	
STYLST	84	71	28	33	0.72	2.51	
SWARS1	197	174	38	40	0.84	1.00	
SWARS2	584	127	202	47	0.93	0.16	
SYMPGL	6	5	3	11	0.23	9.03	* *
TAB1RO	9	14	10	8	1.94	2.34	
TAB2AR	109	84	18	30	0.46	13.82	* *
TACHVE	5	238	2	110	0.87	1.57	
TALINE	233	34	104	8	1.90	2.75	
TALIPR	13	57	7	18	1.71	3.99	*
TET2PA	84	449	27	137	1.05	0.28	
TOCOPI	1	2	1	0	2.00/0	2.00	
TRI2PA	64	45	7	7	0.70	0.76	
TRI2TU	374	864	83	508	0.38	328.49	* *
TRIPCU	30	11	5	3	0.61	0.58	
TROPRA	33	15	15	14	0.49	3.91	*
UNONPI	112	47	56	35	0.67	3.23	
VIROSE	137	68	68	32	1.05	0.06	
VISMBA	33	7	15	0	0.21/0	3.18	
XYL1MA	50	53	48	80	0.64	6.64	* *
XYL2OL	58	5	20	4	0.43	1.67	
ZANTBE	38	43	17	11	1.75	2.81	
ZANTP1	7	11	5	1	7.86	5.49	*
ZANTPR	3	10	3	9	1.11	0.05	

APPENDIX 9

Recruitment Rates on Slope and Plateau Sites of the 50-ha FDP Plot in 1990

Comparison of recruitment into the 1-2 cm DBH size-class on Slope versus Plateau sites of the 50-ha Forest Dynamics Project plot of Barro Colorado Island, Panamá during the 1990 census. The Recruits Ratio is the number of recruits on the Plateau per Plateau adult over the number of recruits on the Slope per Slope adult; where recruits per adult on the Slope is zero, the ratio is presented as X/0. All 153 50-ha FDP plot species are presented for which sufficient stems were present for Chi-square analysis. * P<0.05; ** P<0.01.

	Plateau		Slope				
Species	Number of adults	Number of recruits	Number of adults	Number of recruits	Recruits ratio	χ^2	P-value
ACALDI	305	67	167	35	1.05	0.05	
ADE1TR	70	14	9	1	1.80	0.33	
ALCHOO	45	7	31	2	2.41	1.28	
ALIBED	41	37	9	10	0.81	0.34	
ALLOPS	42	12	12	3	1.14	0.04	
ALSEBL	334	734	73	286	0.56	70.73	**
ANAXPA	62	26	525	124	1.78	7.28	**
ANDIIN	4	13	1	6	0.54	1.59	
ANNOAC	276	47	127	11	1.97	4.23	*
ANNOSP	15	33	2	8	0.55	2.37	
ASPICR	11	24	8	13	1.34	0.74	
BEILPE	78	220	32	176	0.51	45.25	**
BROSAL	39	41	16	9	1.87	2.98	
CALOLO	10	85	3	124	0.21	154.74	**
CAPPFR	2055	123	897	72	0.75	3.94	*
CASEAC	65	47	17	17	0.72	1.32	
CASEAR	55	8	10	1	1.45	0.13	
CASESY	27	12	17	6	1.26	0.21	
CASSEL	50	75	24	27	1.33	1.65	
CECRIN	73	21	24	12	0.58	2.39	
CECROB	10	6	8	1	4.80	2.58	
CESTME	75	18	62	8	1.86	2.20	
CHR1EC	104	7	162	11	0.99	0.00	
CHR2AR	10	126	3	45	0.84	1.01	
CHR2CA	9	13	2	7	0.41	3.80	
CLIDDE	10	10	3	3	1.00	0.00	
CLIDOC	8	8	1	1	1.00	0.00	
COCCCO	19	14	5	6	0.61	1.02	
CONOCI	72	24	102	31	1.10	0.12	
CORDAL	31	10	5	1	1.61	0.21	
CORDBI	154	154	54	40	1.35	2.88	
CORDLA	263	105	131	44	1.19	0.93	
COU2CU	665	276	46	33	0.58	9.05	**
CROTBI	140	226	45	31	2.34	20.99	**
CUPASY	138	117	30	22	1.16	0.39	
DES2PA	2575	1261	627	441	0.70	43.30	**
DRYPST	32	84	28	83	0.89	0.62	
ERY2MA	51	32	9	18	0.31	17.29	**
ERY2PA	56	8	29	7	0.59	1.05	
EUGECO	4	65	2	27	1.20	0.66	
EUGEGA	96	240	25	45	1.39	4.13	*
EUGENE	37	42	8	11	0.83	0.32	
EUGEOE	27	282	6	74	0.85	1.62	

Appendix 9 continued.

	Plateau		Slope				
Species	Number of adults	Number of recruits	Number of adults	Number of recruits	Recruits ratio	χ^2	P-value
FARAOC	5981	2142	1041	502	0.74	36.26	* *
GAR2IN	57	349	14	99	0.87	1.60	
GUARGU	419	127	213	85	0.76	3.88	*
GUARSP	71	90	36	42	1.09	0.20	
GUATDU	39	55	32	38	1.19	0.67	
GUETFO	48	11	11	2	1.26	0.09	
GUSTSU	226	17	64	8	0.60	1.43	
HAMEAX	56	28	25	10	1.25	0.37	
HAMPAP	16	6	6	1	2.25	0.60	
HASSFL	186	8	83	4	0.89	0.03	
HEISAC	25	2	15	1	1.20	0.02	
HEISCO	117	55	37	16	1.09	0.09	
HERRPU	349	38	130	16	0.88	0.17	
HIRTTR	450	344	287	219	1.00	0.00	
HYBAPR	27031	3538	8647	1251	0.90	9.28	* *
HYERAL	12	4	7	4	0.58	0.60	
INGACO	22	33	2	3	1.00	0.00	
INGAGO	4	32	2	19	0.84	0.35	
INGAMA	8	115	7	66	1.52	7.57	* *
INGAQU	59	36	32	24	0.81	0.62	
INGAS1	18	41	10	15	1.52	1.94	
INGASA	13	28	2	2	2.15	1.15	
INGAUM	31	88	5	20	0.71	1.94	
LACIAG	93	179	34	77	0.85	1.43	
LAETTH	44	64	3	6	0.73	0.56	
LICAHY	20	7	3	8	0.13	21.47	* *
LICAPL	2	29	1	22	0.66	2.21	
LONCLA	22	94	7	31	0.96	0.03	
LUEHSE	32	28	9	7	1.13	0.08	
MACRGL	9	7	8	2	3.11	2.23	
MALMSP	80	32	27	14	0.77	0.66	
MALPRO	34	4	11	3	0.43	1.28	
MAQUCO	109	90	54	53	0.84	1.00	
MAYTSC	13	4	7	2	1.08	0.01	
MICOAF	119	67	8	4	1.13	0.05	
MICOAR	41	198	5	49	0.49	20.51	* *
MICONE	255	161	21	12	1.10	0.11	
MOURMY	1866	888	398	154	1.23	5.64	*
MYRCGA	3	4	3	1	4.00	1.80	
NECTGL	3	27	1	11	0.82	0.32	
NECTPU	6	10	1	1	1.67	0.24	
NEEAAM	49	16	14	3	1.52	0.45	
OCOTCE	60	49	12	18	0.54	5.02	*
OCOTOB	6	38	3	18	1.06	0.04	
OCOTWH	20	13	46	37	0.81	0.44	
OLMEAS	48	2	112	4	1.17	0.03	
OURALU	161	118	21	14	1.10	0.11	
PALIGU	1040	517	157	63	1.24	2.59	
PENTMA	169	16	86	17	0.48	4.67	*
PEREXA	22	32	3	3	1.45	0.39	
PHOECI	5	13	1	4	0.65	0.58	
PICRLA	152	100	98	48	1.34	2.84	
PIPEA1	12	3	7	0	0.25/0	1.75	
PIPEAE	26	7	42	4	2.83	3.01	
PIPECO	1330	181	329	47	0.95	0.09	
PIPECU	19	1	15	2	0.39	0.62	
PIPEPE	16	3	52	11	0.89	0.03	
PIPERE	40	5	34	1	4.25	2.07	
PLA1PI	25	37	6	6	1.48	0.80	
PLA2EL	20	12	4	7	0.34	5.57	*
POULAR	18	11	46	13	2.16	3.72	
POUTRE	43	191	12	71	0.75	4.28	*

Appendix 9 continued.

Species	Plateau Number of adults	Plateau Number of recruits	Slope Number of adults	Slope Number of recruits	Recruits ratio	χ^2	P-value
PRI2CO	53	49	14	15	0.86	0.25	
PROTCO	14	69	7	28	1.23	0.87	
PROTPA	82	290	26	88	1.04	0.13	
PROTTE	104	274	45	138	0.86	2.12	
PSE1SE	2	4	2	0	2.00/0	4.00	*
PSIDFR	2	6	1	0	3.00/0	3.00	
PSYCDE	54	26	2	2	0.48	1.04	
PSYCG3	6	8	8	7	1.52	0.67	
PSYCHO	3741	747	989	174	1.13	2.26	
PSYCLI	17	15	2	1	1.76	0.31	
PSYCMA	496	177	108	28	1.38	2.49	
PTERRO	4	185	2	52	1.78	13.84	* *
QUARAS	206	73	111	59	0.67	5.44	*
RANDAR	321	66	72	21	0.70	1.97	
RINOSY	722	181	296	73	1.02	0.01	
SAPIAU	4	3	3	0	0.75/0	2.25	
SENNDA	67	15	33	5	1.48	0.58	
SIMAAM	52	175	10	40	0.84	0.97	
SIPAPA	78	21	48	11	1.17	0.19	
SLOATE	7	9	2	6	0.43	2.74	
SOLAHA	21	10	13	8	0.77	0.29	
SOROAF	951	172	421	61	1.49	6.40	*
SPONMO	2	9	1	0	4.50/0	4.50	*
SPONRA	12	23	9	7	2.46	4.67	*
STERAP	7	3	3	1	1.29	0.05	
STYLST	81	89	23	26	0.97	0.02	
SWARS1	202	189	37	50	0.69	5.40	*
SWARS2	598	104	212	41	0.90	0.33	
SYMPGL	6	5	2	17	0.10	32.06	* *
TAB1RO	8	14	9	14	1.13	0.10	
TAB2AR	109	111	19	31	0.62	5.48	*
TACHVE	5	348	2	172	0.81	5.17	*
TALINE	236	24	102	6	1.73	1.47	
TALIPR	10	56	5	26	1.08	0.10	
TET2PA	85	479	26	138	1.06	0.38	
THEVAH	14	3	14	2	1.50	0.20	
TRI2PA	76	47	7	5	0.87	0.09	
TRI2TU	333	1017	72	516	0.43	264.53	* *
TRIPCU	33	7	5	4	0.27	5.18	*
TROPRA	29	16	10	14	0.39	6.96	* *
UNONPI	128	30	66	47	0.33	25.04	* *
URERBA	5	6	3	3	1.20	0.07	
VIROSE	156	31	76	12	1.26	0.46	
XYL1MA	63	57	62	88	0.64	7.13	* *
ZANTBE	39	15	17	6	1.09	0.03	
ZANTP1	6	22	6	4	5.50	12.46	* *
ZANTPR	7	6	3	1	2.57	0.82	
ZUELGU	3	3	1	1	1.00	0.00	

APPENDIX 10

Seed-trap Summaries by Species for the 50-ha FDP Plot

Seed-trap summaries by species for the 200 seed-traps on the 50-ha Forest Dynamics Project plot of Barro Colorado Island, Panamá during the period 1987 - 1994, inclusive. A trap was included as having received a seed if either ≥ 1 mature seed or ≥ 1 fruit containing a mature seed was found in the trap.

	Number of traps into which the following structures fell					
Species	≥ 1 seed	≥ 1 flower	≥ 1 flower and ≥ 1 seed	≥ 1 seed and 0 flowers	≥ 1 flower and 0 seeds	Neither flowers nor seeds
ACACME	0	0	0	0	0	200
ACALDI	0	7	0	0	7	193
ACALMA	0	0	0	0	0	200
ADE1TR	5	17	2	3	15	180
AEGIPA	0	1	0	0	1	199
ALCHCO	49	17	10	39	7	144
ALCHLA	0	0	0	0	0	200
ALIBED	1	0	0	1	0	199
ALLOPS	12	1	0	12	1	187
ALSEBL	169	70	69	100	1	30
AMAICO	1	0	0	1	0	199
ANACEX	23	23	15	8	8	169
ANAXPA	0	0	0	0	0	200
ANDIIN	1	1	1	0	0	199
ANNOAC	3	0	0	3	0	197
ANNOHA	0	0	0	0	0	200
ANNOSP	30	4	4	26	0	170
APEIME	36	38	15	21	23	141
APEITI	19	14	2	17	12	169
APEIHY	0	0	0	0	0	200
APHESI	0	0	0	0	0	200
APPUSE	0	0	0	0	0	200
ARDIBA	0	0	0	0	0	200
ARDIFE	0	0	0	0	0	200
ARDIGU	0	0	0	0	0	200
ASPICR	6	1	1	5	0	194
AST1ST	3	1	1	2	0	197
AST2GR	6	18	1	5	17	177
BACTBA	0	0	0	0	0	200
BACTC1	0	0	0	0	0	200
BACTC2	0	0	0	0	0	200
BACTMA	2	0	0	2	0	198
BANAGU	0	0	0	0	0	200
BEILPE	55	32	22	33	10	135
BERTGU	0	0	0	0	0	200
BROSAL	77	23	15	62	8	115
BROSGU	0	0	0	0	0	200
CALOLO	16	13	2	14	11	173
CAPPFR	10	14	6	4	8	182
CASEAC	4	2	2	2	0	196
CASEAR	11	14	9	2	5	184
CASECO	0	0	0	0	0	200
CASEGU	1	1	1	0	0	199
CASESY	5	9	5	0	4	191
CASSEL	13	16	11	2	5	182
CAVAPL	8	4	3	5	1	191
CECRIN	33	13	7	26	6	161
CECROB	3	6	1	2	5	192
CEDROD	4	0	0	4	0	196
CEIBPE	16	9	2	14	7	177
CELTSC	0	0	0	0	0	200

Appendix 10 continued.

Species	Number of traps into which the following structures fell					
	≥ 1 seed	≥ 1 flower	≥ 1 flower and ≥ 1 seed	≥ 1 seed and 0 flowers	≥ 1 flower and 0 seeds	Neither flowers nor seeds
CESPMA	0	0	0	0	0	200
CESTME	0	0	0	0	0	200
CHA1TE	0	0	0	0	0	200
CHA2SC	0	0	0	0	0	200
CHIMPA	0	0	0	0	0	200
CHR1EC	2	0	0	2	0	198
CHR2AR	7	8	1	6	7	186
CHR2CA	49	5	4	45	1	150
CLIDDE	0	0	0	0	0	200
CLIDOC	1	3	1	0	2	197
CLIDSE	0	0	0	0	0	200
CNEMPE	0	0	0	0	0	200
COCCCO	6	1	0	6	1	193
COCCMA	4	3	1	3	2	194
COLUGL	0	0	0	0	0	200
CONOBR	0	0	0	0	0	200
CONOCI	1	1	1	0	0	199
CORDAL	64	114	51	13	63	73
CORDBI	67	40	23	44	17	116
CORDLA	101	57	38	63	19	80
COU2CU	36	13	12	24	1	163
COUTHE	0	0	0	0	0	200
CROTBI	5	4	3	2	1	194
CUPACI	2	0	0	2	0	198
CUPALA	6	2	0	6	2	192
CUPARU	16	0	0	16	0	184
CUPASY	8	6	2	6	4	188
CYPHHA	3	0	0	3	0	197
DENDAR	108	11	10	98	1	91
DENDST	53	6	4	49	2	145
DES2PA	56	14	10	46	4	140
DIO2AR	1	1	0	1	1	198
DIPTPA	30	75	23	7	52	118
DRYPST	25	6	2	23	4	171
ELAEOL	0	0	0	0	0	200
ENTESC	0	0	0	0	0	200
ERY1CO	1	1	1	0	0	199
ERY2MA	0	0	0	0	0	200
ERY2PA	0	0	0	0	0	200
EUGECO	21	14	7	14	7	172
EUGEGA	1	0	0	1	0	199
EUGENE	4	4	0	4	4	192
EUGEOE	126	15	9	117	6	68
FARAOC	190	133	130	60	3	7
FICUBU	0	0	0	0	0	200
FICUCI	19	1	0	19	1	180
FICUC1	5	0	0	5	0	195
FICUC2	35	3	3	32	0	165
FICUIN	54	2	1	53	1	145
FICUMA	0	1	0	0	1	199
FICUOB	114	0	0	114	0	86
FICUPE	17	2	2	15	0	183
FICUPO	15	0	0	15	0	185
FICUTO	24	0	0	24	0	176
FICUTR	13	0	0	13	0	187
FICUYO	37	1	1	36	0	163
GAR2IN	13	3	1	12	2	185
GAR2MA	5	8	2	3	6	189
GENIAM	13	3	2	11	1	186
GEONIN	0	0	0	0	0	200
GUAPST	72	17	10	62	7	121
GUARGR	22	6	3	19	3	175

Appendix 10 continued.

Species	Number of traps into which the following structures fell					
	≥ 1 seed	≥ 1 flower	≥ 1 flower and ≥ 1 seed	≥ 1 seed and 0 flowers	≥ 1 flower and 0 seeds	Neither flowers nor seeds
GUARGU	72	22	15	57	7	121
GUARSP	8	0	0	8	0	192
GUATDU	98	26	19	79	7	95
GUAZUL	7	15	7	0	8	185
GUETFO	6	5	1	5	4	190
GUSTSU	20	21	11	9	10	170
HAMEAX	0	0	0	0	0	200
HAMEPA	0	0	0	0	0	200
HAMPAP	57	1	0	57	1	142
HASSFL	60	29	17	43	12	128
HEISAC	15	2	1	14	1	184
HEISCO	69	30	15	54	15	116
HERRPU	1	1	0	1	1	198
HIRTAM	0	26	0	0	26	174
HIRTTR	54	82	32	22	50	96
HURACR	5	20	5	0	15	180
HYBAPR	178	101	100	78	1	21
HYERAL	88	5	4	84	1	111
INGACO	17	8	1	16	7	176
INGAFA	18	9	2	16	7	175
INGAGO	1	0	0	1	0	199
INGAMA	0	2	0	0	2	198
INGAMI	0	0	0	0	0	200
INGAM1	7	3	1	6	2	191
INGAPE	0	1	0	0	1	199
INGAPU	0	2	0	0	2	198
INGAQU	4	3	0	4	3	193
INGARU	1	1	1	0	0	199
INGASA	8	4	1	7	3	189
INGASP	0	0	0	0	0	200
INGAUM	18	6	1	17	5	177
INGAS1	0	0	0	0	0	200
JAC1CO	200	73	73	127	0	0
KOANWE	1	0	0	1	0	199
LACIAG	5	0	0	5	0	195
LACMPA	24	4	3	21	1	175
LAETPR	16	6	6	10	0	184
LAETTH	5	6	3	2	3	192
LAFOPU	3	0	0	3	0	197
LEANDI	0	0	0	0	0	200
LICAHY	0	0	0	0	0	200
LICAPL	1	8	1	0	7	192
LINDLA	25	5	3	22	2	173
LONCLA	23	6	3	20	3	174
LOPIDA	0	0	0	0	0	200
LOZAPI	0	0	0	0	0	200
LUEHSE	199	55	55	144	0	1
LYCIMA	0	0	0	0	0	200
MACLTI	0	0	0	0	0	200
MACRGL	1	4	1	0	3	196
MALMSP	8	1	0	8	1	191
MALPRO	0	0	0	0	0	200
MAQUCO	0	2	0	0	2	198
MARGNO	0	0	0	0	0	200
MAR1LA	0	0	0	0	0	200
MAYTSC	0	0	0	0	0	200
MICOAF	5	3	3	2	0	195
MICOAR	6	4	4	2	0	194
MICOEL	0	0	0	0	0	200
MICOHO	0	0	0	0	0	200
MICOIM	4	1	1	3	0	196
MICONE	1	1	0	1	1	198

Appendix 10 continued.

Species	Number of traps into which the following structures fell					
	≥ 1 seed	≥ 1 flower	≥ 1 flower and ≥ 1 seed	≥1 seed and 0 flowers	≥ 1 flower and 0 seeds	Neither flowers nor seeds
MICOPR	1	0	0	1	0	199
MOURMY	73	29	17	56	12	115
MYRCGA	0	1	0	0	1	199
MYROFR	0	0	0	0	0	200
NECTCI	4	0	0	4	0	196
NECTGL	7	1	0	7	1	192
NECTPU	6	0	0	6	0	194
NECTS1	0	0	0	0	0	200
NECTS3	0	0	0	0	0	200
NEEAAM	8	0	0	8	0	192
OCHRPY	5	0	0	5	0	195
OCOTCE	11	3	0	11	3	186
OCOTOB	5	1	0	5	1	194
OCOTPU	17	2	0	17	2	181
OCOTWH	13	11	4	9	7	180
OENOMA	0	0	0	0	0	200
OLMEAS	1	3	0	1	3	196
ORMOAM	0	1	0	0	1	199
ORMOCR	1	1	0	1	1	198
ORMOMA	0	0	0	0	0	200
OURALU	25	10	7	18	3	172
PALIGU	63	5	5	58	0	137
PENTMA	1	0	0	1	0	199
PEREXA	0	0	0	0	0	200
PHOECI	8	0	0	8	0	192
PICRLA	5	1	0	5	1	194
PIPEAE	0	0	0	0	0	200
PIPEA1	0	0	0	0	0	200
PIPECA	0	0	0	0	0	200
PIPECO	0	0	0	0	0	200
PIPECU	0	0	0	0	0	200
PIPEIM	0	0	0	0	0	200
PIPEPE	0	0	0	0	0	200
PIPERE	0	1	0	0	1	199
PIT1MA	2	5	0	2	5	193
PIT1RU	0	0	0	0	0	200
PLA1PI	25	31	18	7	13	162
PLA2EL	40	52	27	13	25	135
POCHQU	1	1	0	1	1	198
POCHSE	1	1	0	1	1	198
POSOLA	3	1	0	3	1	196
POULAR	16	13	7	9	6	178
POURBI	6	1	0	6	1	193
POUTFO	0	0	0	0	0	200
POUTRE	51	25	8	43	17	132
POUTST	5	6	2	3	4	191
PRI2CO	10	49	10	0	39	151
PROTCO	0	5	0	0	5	195
PROTPA	6	19	2	4	17	177
PROTTE	56	22	12	44	10	134
PROTSP	0	0	0	0	0	200
PSE1SE	13	1	1	12	0	187
PSIDFR	0	0	0	0	0	200
PSYCAC	4	1	1	3	0	196
PSYCB1	0	0	0	0	0	200
PSYCCH	0	0	0	0	0	200
PSYCDE	3	0	0	3	0	197
PSYCFU	31	1	0	31	1	168
PSYCG1	0	0	0	0	0	200
PSYCG2	0	0	0	0	0	200
PSYCG3	0	0	0	0	0	200
PSYCHO	100	12	12	88	0	100

Appendix 10 continued.

	Number of traps into which the following structures fell					
Species	≥ 1 seed	≥ 1 flower	≥ 1 flower and ≥ 1 seed	≥ 1 seed and 0 flowers	≥ 1 flower and 0 seeds	Neither flowers nor seeds
PSYCLI	1	1	1	0	0	199
PSYCMA	2	1	0	2	1	197
PSYCPI	0	0	0	0	0	200
PSYCRA	2	1	0	2	1	197
PTERBE	0	0	0	0	0	200
PTERRO	12	9	3	9	6	182
QUARAS	154	91	80	74	11	35
QUASAM	5	17	2	3	15	180
RANDAR	114	10	7	107	3	83
RANDFO	0	0	0	0	0	200
RINOSY	15	15	7	8	8	177
SAPIAU	17	2	2	15	0	183
SAPISP	0	0	0	0	0	200
SCH1ZO	6	1	1	5	0	194
SCH2MO	44	0	0	44	0	156
SCHIPA	0	0	0	0	0	200
SENNDA	0	0	0	0	0	200
SIMAAM	65	38	19	46	19	116
SIPAGU	0	0	0	0	0	200
SIPAPA	0	3	0	0	3	197
SLOATE	15	10	5	10	5	180
SOCREX	0	0	0	0	0	200
SOLAAR	0	1	0	0	1	199
SOLAAS	0	0	0	0	0	200
SOLAHA	4	1	0	4	1	195
SOLAST	0	0	0	0	0	200
SOROAF	82	16	9	73	7	111
SPACME	3	0	0	3	0	197
SPONMO	30	26	5	25	21	149
SPONRA	33	21	8	25	13	154
STEMGR	0	2	0	0	2	198
STERAP	0	2	0	0	2	198
STYLST	15	1	0	15	1	184
SWARS1	1	13	0	1	13	186
SWARS2	6	15	2	4	13	181
SYMPGL	5	10	3	2	7	188
TAB1GU	46	25	18	28	7	147
TAB1RO	129	19	15	114	4	67
TAB2AR	35	53	24	11	29	136
TACHVE	8	4	1	7	3	189
TALINE	3	4	2	1	2	195
TALIPR	0	0	0	0	0	200
TERMAM	200	9	9	191	0	0
TERMOB	36	3	3	33	0	164
TERNTE	0	0	0	0	0	200
TET2PA	77	42	26	51	16	107
TET4JO	8	4	2	6	2	190
THEOCA	0	0	0	0	0	200
THEVAH	0	1	0	0	1	199
TOCOPI	6	1	0	6	1	193
TRATAS	71	6	2	69	4	125
TREMMI	5	8	2	3	6	189
TRI1GI	0	0	0	0	0	200
TRI2PA	16	3	2	14	1	183
TRI2TU	193	124	121	72	3	4
TRI4GA	10	5	3	7	2	188
TRIPCU	41	36	27	14	9	150
TROPRA	0	0	0	0	0	200
TURPOC	3	4	1	2	3	194
UNONPI	8	4	2	6	2	190
URERBA	0	0	0	0	0	200
VIROSE	84	53	27	57	26	90

Appendix 10 continued.

	Number of traps into which the following structures fell					
Species	≥ 1 seed	≥ 1 flower	≥ 1 flower and ≥ 1 seed	≥1 seed and 0 flowers	≥ 1 flower and 0 seeds	Neither flowers nor seeds
VIROSU	80	36	24	56	12	108
VIROSP	6	5	1	5	4	190
VISMBA	0	0	0	0	0	200
VISMBI	0	0	0	0	0	200
VISMMA	0	0	0	0	0	200
VOCHPE	3	10	3	0	7	190
XYL1MA	8	4	1	7	3	189
XYL2CH	0	0	0	0	0	200
XYL2OL	1	0	0	1	0	199
ZANTBE	37	35	5	32	30	133
ZANTP1	3	16	2	1	14	183
ZANTPR	14	15	4	10	11	175
ZANTSE	0	0	0	0	0	200
ZUELGU	7	3	1	6	2	191