PATTERNS AND PROCESSES OF SEED DISPERSAL AND FECUNDITY IN THE NEOTROPICAL TREE, JACARANDA COPAIA.

by

FRANK ANDREW JONES

(Under the Direction of Stephen P. Hubbell)

ABSTRACT

Seed dispersal is a critical life history stage of plants, yet its causes and consequences in tropical forest ecosystems remain poorly understood. I used a novel genetic technique, genotyping maternal tissue attached to dispersed seeds, to measure dispersal distance in a large natural tree population on Barro Colorado Island (BCI), Panama. I developed 10 microsatellite markers for *Jacaranda copaia* and used these markers to genotype seeds caught within seed traps in the 50 ha Forest Dynamics Plot on BCI. I found that a mixture model consisting of two different dispersal distributions, a Gaussian distribution describing local dispersal and an exponential distribution describing dispersal at longer distances, best-fit the observed distribution of seeds across two years in this species. Genetically measured distances showed that > 20% of seeds in each year moved distances > 100 m. Dispersal kernels differed between the years presumably due to differences in wind profiles between the years. Greater numbers of seeds were observed moving in one year due to greater seed production. Dispersal distances measured using the genetic markers were compared to estimates made using inverse models of seed shadows. I show that inverse modeling underpredicts the proportion of seeds moving distances >

100 m compared to the genetically determined dispersal distances. Finally, I examined the causes and patterns of individual variation in seed production and fecundity for three years in *J. copaia*. I found evidence in each year for a positive effect of individual canopy area and the fecundity of neighboring trees on seed production and differing effects of habitat associations on seed production.

The study reveals that some species may be capable of moving a large fraction of their seeds to distances > 100 m. The implications of this finding are that sources of dispersal limitation in forest communities in some species may not solely be due to limited dispersal ability, but rather limited numbers of propagules, or variable numbers of propagules, available to be dispersed. The results further suggest caution in interpreting previous findings using inverse techniques, namely that as currently formulated, they may not adequately characterize the tail of the dispersal curve.

INDEX WORDS: wind dispersal, fecundity, microsatellite DNA, Barro Colorado Island, Panama, maximum likelihood estimation, model selection, dispersal kernel, directed dispersal, inverse modeling

PATTERNS AND MECHANISMS OF SEED DISPERSAL AND FECUNDITY IN THE NEOTROPICAL TREE, JACARANDA COPAIA.

by

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INTRODUCTION

Understanding spatial processes is critical to understanding plant population and community dynamics (Tilman and Kareiva 1997, Epperson 2003). Seed dispersal is the foremost spatial process in plants (Nathan and Muller-Landau 2000) and is a central process in a number of the major mechanisms proposed to explain the local maintenance of high tree species diversity in tropical moist forests. Seed dispersal plays a central role in the enemies hypothesis (Janzen 1970, Connell 1971), the dispersal limitation hypothesis (Tilman 1994, Hurrtt and Pacala 1995, Hubbell et al. 1999, Wright et al. 1999), competition/colonization tradeoffs (Tilman 1994, Knietel and Chase 2004), a theory of the importance of historical processes in determining community diversity (Dick et al. 2003, Ricklefs 2004), and a neutral theory of relative species abundance (Hubbell 2001, Volkov et al. 2002). Recent arguments about the maintenance of diversity state that regional processes are critical in determining local species richness and that the main process that integrates populations within regions is dispersal (Ricklefs 2004).

Dispersal influences the growth, persistence, and evolution of populations. It carries seeds to safe sites that potentially are rare in space and time (Harper 1977, Wenny and Levey 1998); determines spread and colonization rates (Skellam 1951); structures and defines metapopulations (Hanski 2000); determines local and regional spatial genetic structure (Epperson 2003); and together with pollen movement is major component of gene flow among populations (Hamrick and Nason 1996, Slatkin 1985). Species' dispersal ability can explain historical and biogeographic changes in vegetation (Petit, et al. 1997, Dick and Bermighham 2003) and influence future population and community responses to habitat fragmentation and global climate change

(Clark 1998, Cain et. al. 2000, Malanson and Armstrong 1996). Although dispersal is widely acknowledged as one of the most critical processes in plant ecology and evolution, it remains one of the least well-understood (Turchin 1998).

Due to the increased recognition of the importance of seed dispersal to understanding ecological and evolutionary dynamics of plant populations, there has been increased interest in developing methods to estimate, measure, and predict spatially explicit dispersal patterns within forest communities (Nathan and Muller-Landau 2000). Several indirect approaches, including inverse modeling, mechanistic modeling, and hierarchical genetic analyses, have been used to study dispersal patterns within and among populations. Two of these approaches, inverse modeling and directly measuring dispersal using genetic markers, are explored in this dissertation.

The inverse modeling approach parameterizes or fits any one of a variety of flexibly shaped functions (normal, lognormal, Weibull distributions, etc.) using maximum likelihood techniques to predict the density of seed rain caught in seed traps across a landscape (Ribbens, et al. 1994, Clark et al. 1998, Clark et al. 1999). The total number of seeds or seedlings expected at any given location is the integration of all estimated dispersal curves of all trees at that point. Inverse modeling of dispersal has become an important component in a variety of spatially explicit forest simulators, such as SORTIE (Ribbens, et al. 1994). Inverse modeling has revealed significant dispersal limitation in tropical tree species on BCI (Dalling et al. 2002).

Most curve-fitting exercises and models of dispersal are indirect measures and their results are dependent upon often overly simplistic assumptions of the mechanisms of dispersal in closed communities (Clark et al. 1998, Clark et al. 1999, Higgins and Richards 1999). Despite these innovative, indirect approaches, there remains a considerable void of empirical data on the actual frequency, patterns, and mechanisms of dispersal within and among natural plant populations. (Higgins and Richardson 1999, Cain et al. 2000, Bullock and Clarke 2000, Nathan et al. 2003).

The direct empirical measurement of seed dispersal in natural populations has lagged far behind its theoretical and indirect exploration (Wang and Smith 2002). This is likely because “The direct measurement of dispersal for most organisms and systems is a logistical nightmare” (Kneitel and Chase 2004). However, the recent description of a simple genetic approach for assigning maternal parentage to single dispersed seeds (Godoy and Jordano 2001) makes tractable the direct measurement of dispersal distances and detailed inquiries into the patterns and processes of dispersal within populations.

Seed coat tissues (endocarp, samaras, seed wings, etc) are mitotically derived tissue from plant ovaries. Therefore recombination has not occurred in this tissue. Therefore, maternally derived seed tissue has the identical diploid genotype of the mother. Therefore, with knowledge of the exact locations of maternal plants and with unique multilocus genotypes of putative mothers in a population, one can genotype maternal tissue of dispersed seed and match it to the parent in the population. This approach enables one to assign parentage and thereby identify dispersal distance with extremely high precision, particularly when using hyperdiverse microsatellite markers. Furthermore, through exclusion of adults in the study population, the technique allows for the identification of seeds that have immigrated from trees outside the boundaries of the study population and therefore provides an estimate of seed-mediated gene flow.

I employed the above technique to study spatially explicit patterns of seed dispersal in the wind-dispersed neotropical tree across two years on Barro Colorado Island, Panama. The overarching goals of the work were to directly measure 2) dispersal distances within a large natural tropical tree population to document the frequency of long distance dispersal, 2) the differential deposition of seeds to areas suitable for the species growth and establishment (tree fall gaps), and 3) compare predictions made by inverse modeling approaches to patterns of seed dispersal directly measured in the field.

The first chapter of this dissertation, entitled "Isolation and characterization of microsatellite loci in the tropical tree *Jacaranda copaia* (Bignoniaceae)" describes the development of ten variable microsatellite loci for the study species. The paper, published in the journal Molecular Ecology Notes (Jones and Hubbell 2003), provides the technical details behind the development of the markers, extraction protocols for the species, primer sequences, and PCR conditions. The initial survey of genetic diversity showed that *Jacaranda copaia* shows extremely high levels of genetic diversity as measured by levels of heterozygosity and the number of alleles observed per locus. The loci described in this paper are then used in the next paper to examine patterns of dispersal distances in *Jacaranda copaia.*

The second chapter of the dissertation, "Direct genetic measurement of seed dispersal and fecundity in a tropical tree, *Jacaranda copaia*" describes the study of genetic measurement of dispersal patterns in *Jacaranda copaia* across two years, 2000 and 2002, in the Forest Dynamics Plot on Barro Colorado Island, Panama. I examined patterns of seed fall to 300 ½ m^2 seed traps across an 84 ha area on BCI in Panama. We used four genetic markers to identify the maternal seed source for two years of seed fall on the plot. We found that greater than 20 % of seeds moved distances greater than 100m in both years. When a probability density function, hereafter refered to as a seed dispersal kernel, was fit to the observed distribution of dispersal distances, we found that a mixture distribution consisting of a local Gaussian curve with a negative exponential tail best-fit the observed data. This implies that separate mechanisms may govern dispersal at local and at distances > 100 m. I suggest that local dispersal is a diffusion process described by a Gaussian-shaped curve, while long distance dispersal in this species is determined by the proportion of seeds that are uplifted above the canopy and carried in wind currents to longer distances.

We also measured individual-level patterns of fecundity across the plot and found greater levels of fecundity in 2002 than in 2000 primarily due to the increased loss of seeds in 2000 to predispersal insect seed predators. Wind profiles in 2000 and 2002 show greater amount of wind in 2002, which is consistent with higher measured dispersal distances in that year. Increased fecundity also increased the absolute number of seeds moving long distances in this year. We found no evidence of increased seed fall or movement of seeds to tree fall gaps.

The third paper examines predictions made by inverse modeling approaches that have been used to study spatially explicit patterns of seed dispersal within forests. I compared fractions of seeds dispersed to different distances to predictions made by fitting dispersal kernels to data using inverse modeling methods. I also explored how different measures of individual fecundity, aside from tree basal area, can improve fits to data using inverse methods. Individually measured fecundity can drastically improve the fit of models to data. This is due to the failure of inverse techniques to adequately model process error in the relationship of tree basal area to measures of fecundity. I found that inverse models provide biased overestimates of fractions of seeds dispersed distances < 100m while underestimating the fraction of seeds that move distances > 100 m.

The fourth and final chapter of this dissertation, "Individual and neighborhood determinants of fecundity in *Jacaranda copaia*", examines the importance of local neighborhood factors in determining variation in fecundity in *Jacaranda copaia*. We measured individual fecundity in the field for the majority of reproductive-sized *Jacaranda copaia* individuals for three years on the BCI 50 ha plot. Using non-linear regression models and model selection techniques, we found that conspecific fecundity and density, habitat variables, and individual crown area all contributed to explaining some of the variation in fecundity in *Jacaranda* across the plot. The finding that increased density of *Jacaranda* led to increased fecundity implies that positive density dependence may be operating at the adult level in *Jacaranda* populations. This result provides an addition mechanism, along with dispersal limitation and habitat specialization, that could potentially explain the aggregated nature of tropical tree individuals within tropical forests (Condit et al. 2000).

The studies contained in this dissertation are among the first studies to directly examine patterns of seed dispersal and fecundity in any tropical tree population for multiple years. Both dispersal and fecundity are difficult to measure in the field. However, due to the unique nature of *Jacaranda* fruit capsules and to the unique use of genetic techniques described here, the study represents one of the most in depth studies to date on the spatial factors that determine fecundity and dispersal patterns in any tree population.

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CHAPTER 1

ISOLATION AND CHARACTERIZATION OF MICROSATELLITE LOCI IN THE TROPICAL TREE *JACARANDA COPAIA* (BIGNONIACEAE).[1]

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[1] Jones, F.A and S.P. Hubbell. To be submitted to *Molecular Ecology Notes*

ABSTRACT

We isolated ten microsatellite loci for *Jacaranda copaia* for the purpose of directly measuring seed and pollen movement within the 50 ha Forest Dynamics Plot on Barro Colorado Island, Panama and for studies of population genetic structure and gene flow across the Isthmus of Panama. Enriched repeat libraries were screened for microsatellite repeats and polymorphic primer pairs were developed. 110 adult individuals were screened for allelic diversity and loci showed high levels of heterozygosity. These loci show both high maternal and paternal exclusion probabilities.

Direct studies of gene flow via seed in plants have been hampered by the lack of a straightforward method of unambiguously identifying the maternal parent in hermaphroditic species. However, this problem can be overcome by genotyping maternal tissue that usually surrounds seeds including seed endocarp, seed wings, or samaras (Godoy and Jordano 2000, Wang & Smith 2002). Because seed coat tissue is maternal tissue and an exact diploid match to the maternal parent in the population, seed maternal parentage can be assigned to dispersed seeds with knowledge of adult genotypes in the population. With this goal in mind, we developed microsatellite markers to directly study seed and pollen movement of *Jacaranda copaia* within the 50 ha Forest Dynamics Plot (FDP) on Barro Colorado Island (BCI), Panama and to investigate the population genetic structure of this species across the Isthmus of Panama.

Jacaranda copaia is a large, wind-dispersed pioneer tree that colonizes large tree- fall gaps (Brokaw 1985). *Jacaranda copaia* ranges from Bolivia Belize and is a common pioneer within the FDP. Previous work has shown that the wind-dispersed seeds of *Jacaranda copaia* are among the most well-dispersed seeds within the FDP (Dalling *et al*. 2002). Mating system studies have shown that *Jacaranda copaia* is a predominantly outcrossed species (James *et al.* 1998).

We used a hybridization selection method (Kandpal, *et al.*1994 and Kijas *et al.* 1994) to create an enriched CA repeat library. Genomic DNA was restricted using *Sau3AI* and size fractionation done using ChromaSpin columns (Clontech Laboratories Palo Alto, CA) to isolate fragments larger than 400 bp. *Sau3AI* linkers were ligated to the fragments, run through the ChromaSpin column to remove excess linker, and amplified to create a whole genome PCR library using the following PCR reaction: 1x PCR buffer, 1.5 mM $MgCl_2$, 15 µl of purified ligation reaction, 100 μM each dNTP, 0.5 μM *Sau*3A I primer, and 2.5 units of *Taq* polymerase (Sigma) in a total reaction volume of 100 μl. Cycle conditions consisted of 3 m at 94º, followed by 25 cycles for 1 m at 94º, 1 m at 68º, 2 m at 72º and a final elongation step of 10 m.

Selective hybridization was carried out using Vectrex Avidin D (Vector Laboratories, Burlingame, CA) and a biotinylated probe (5'-$(CA)_{15}$TATAAGATA-Biotin). A second PCR reaction was carried out after this step to increase the number of genomic fragments enriched for CA repeats. One μl of the PCR product was ligated into TOPO TA plasmid vector (Invitrogen, Carlsbad, CA) and transformed into *E. coli* according to manufacturer's protocol.

Colony lifts were screened using the CA_{15} probe and the Phototope chemiluminescent detection system (New England Biolabs, Cambridge MA). Thirty colonies that showed strong hybridization signals were sequenced using the BigDye Terminator Kit (Applied Biosystems, Foster City, CA) according to manufacturers protocol with the T7 primer and electrophoresed on a ABI 3700 capillary electrophoresis sequencer (Applied Biosystems, Foster City, CA). Sequences were aligned and contigs created using SEQUENCHER (GeneCodes, Ann Arbor, MI).

Primers were designed for 15 repeat regions using Primer3 web-based software (http://www-genome.wi.mit.edu/cgi-bin/primer/primer3_www.cgi) and synthesized (IDT Technologies). Total genomic DNA was isolated from adult tissue using a standard CTAB method (Doyle and Doyle 1990) and resultant samples were further diluted 1:4 with deionized water. PCR reactions contained 1 μl of template DNA, 1x GeneAmp buffer II, 2.5 mM of $MgCl_2$, 200 μM of each dNTP, 125 μM of forward and reverse primers each, 0.5 units of AmpliTaq Gold DNA polymerase (Applied Biosystems, Foster City, California) for a total volume of 10 μl per reaction. After experimentation with annealing temperatures, levels of polymorphism of all primer pairs were checked on a sample of 10 randomly selected adult individuals by adding 0.01 µl of fluorescently labeled [F]dCTP (Applied Biosystems, Foster City, California) to the PCR cocktail. Cycling conditions consisted of 7 m at 95º, followed by 30 s at 95º, 30 s at annealing temperature (Table 1), a 72º extension for 30 s, and a final extension at 72º for 5 m on an Eppendorf Master Cycler (Eppendorf, Hamburg, Germany).

For the ten loci that showed allelic variation, fluorescently labeled primers (6-FAM, HEX, IDT Technolgies) and (NED, Applied Biosystems, Foster City, CA) were synthesized. Genotypic data were collected from 110 randomly selected adult individuals from the FDP population. After amplification, 1 µl of PCR product was mixed with 1.1 µl of loading solution (0.7 µl deionized formamide, 0.25 µl of ROX, and 0.15 µl of loading dye (Applied Biosystems, Foster City CA). Samples were electrophoresed on 4.75% acrylamide gels and an ABI 377 using GENESCAN. These markers can also be successfully amplified from maternal tissue taken from seed wings of this species.

Allele frequencies were examined first in CERVUS 2.0 (Mashall *et al.* 1998) (Table 1). Deviations from Hardy-Weinberg equilibrium were further explored in the GENEPOP version 3.3 (http://wbiomed.curtin.edu.au/genepop/; Raymond and Rousset 1995) using the probability test with default values. F_{IS} values are reported according to the method of Weir and Cockerham (1984). Loci showed high levels of observed and expected heterozygosity. Allelic richness ranged from 5 to 24 alleles per locus and the average of 13.5 alleles per locus. The expected heterozygosity ranged between 0.567 and 0.916 and the average expected heterozygosity was 0.778. Locus JACC4 and JACC11 showed showed significant deviations from Hardy-Weinberg equilibrium, specifically heterozygote deficit consistent with the presence of null alleles. All loci yield high exclusion probabilities. For example, collectively, these loci show total exclusionary power of the first parent to be 0.998. These markers will be of great use in directly measuring the movement of seeds and pollen within this population and in estimating population structure across the Isthmus of Panama and elsewhere in the tropics.

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Locus	Primer sequences	T	Repeat	Size	N	k	H_O	H_E	F_{IS}	Accession number
JACC 1	F: CGGCTCATGGGCAGTACC *R: GGCTTCATACCACTGATTGC	63	$(CA)_{15}$	185 – 207	110	5	0.800	0.585	- 0.370†	AY257038
JACC 2	F: ACGATAAATGGGCGAGAGAG *R: GGTGACTTGGGTTGATGTTCTTT	63	$(CT)_{19}(CA)_{10}$	207-233	110	15	0.836	0.819	- 0.022	AY257039
JACC 4	F: TCCCTAATCTTGCCTGCTTG *R: ACTCACTGGGCGCTCGAC	60	$(GT)_{14}(GA)_{8}$	207 -267	110	24	0.764	0.916	+ 0.106†	AY257040
JACC 11	F: GGACATGCACTTTCCTTTTATG *R:TGATGGAGAATATCTAAAGCACTCC	63	$(CA)_{16}$	145 – 153	110	5	0.636	0.660	+ 0.036	AY257041
JACC 18	F: TGGGACATCTACAGCCAAGTC *R: AGACAATGAGAAACGCCACTC	63	$(GT)_{2}GA(GT)_{11}$	268 - 300	110	15	0.964	0.899	- 0.072†	AY257042
JACC 21	F: ATCTCCTCAAACACCCACAT *R: TCATTGCCTCCAACACACTT	63	$(GT)_{9}$	230 - 250	110	10	0.745	0.567	- 0.317†	AY257043
JACC 22	F: TTGACAGCTCTTTGTTTGAACC *R: AAGATTCCTTTTGACAGCTTCG	58	$(GT)_{27}$	164 - 217	110	24	0.945	0.880	- 0.075	AY257044
JACC 1.1	F: CTCCTGACGAAGTCAAAAAG *R: ATCAAGTTTCAGAAGACAGG	54	$(GT)_{12}$	110 - 144	110	16	0.864	0.823	- 0.050	AY257045
JACC 9	F:AATAATTAACTCAACTGGCCACTCC *R:TTTAGTTGTCTCCCTGTTTGAGATG	61	$(GT)_{15}$	173-197	110	11	0.936	0.844	- 0.110†	AY257046
JACC 31	F:TCCTTAGCTTTGAAATGAATAAAAGAG *R:ACGTAGAGGGGATTTGTAATTTCTC	63	$(CA)_{16}$	176 – 194	110	10	0.918	0.792	- 0.160†	AY257047
Average						13.5		0.778		

Table 1.1. Locus name, primer sequences, repeat motif, allele size range, number of individuals genotyped (N), number of alleles observed (k),observed (H_O) and expected (H_E) heterozygosity, and GenBank accession number. * refers to the fluorescently labeled primer in the reaction. † refres to significant departure from HW equilibrium ($P < 0.05$)

CHAPTER 2

DIRECT GENETIC MEASUREMENT OF SEED DISPERSAL AND FECUNDITY IN A TROPICAL TREE, *JACARANDA COPAIA*.[1]

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[1] Jones, F.A and S.P. Hubbell. To be submitted to *American Naturalist*

ABSTRACT

Seed dispersal is a critical life history stage of plants. Due to the complexity of the dispersal process, its' short duration, the great numbers of seeds often produced, and the inability to simultaneously track multiple seeds, surprisingly little empirical data exists on actual patterns of seed dispersal in natural populations, particularly at distances > 100 m. We determined patterns of seed dispersal via wind in the gap-dependent tropical tree *Jacaranda copaia* by genotyping maternal tissue attached to dispersed seeds. We captured seeds in a large seed trap array for two years across 84 ha of tropical forest on Barro Colorado Island, Panama. Genetic analysis revealed that a large proportion of seeds, greater than 20% in each year, moved distances greater than 100m. Mean dispersal distances differ between years due to differences in wind profiles. The number of seeds moving long distances increased due to increases in seed production in 2002.

We fit a variety of dispersal kernels to our directly measured data and found that a mixture distribution, consisting of a Gaussian shaped curve with a negative exponential tail, best fit the observed number of dispersed seeds locally and at distances > 100m. That the mixture model best fit the data suggests that different physical mechanisms govern local and long distance dispersal in *J. copaia*, probably because a proportion of seeds are uplifted above the forest canopy and are moved long distances by wind currents. We also test the hypothesis of directed dispersal to tree fall gaps by wind-dispersed species by determining whether more seeds land in gap sites than expected compared to understory sites.

Keywords: fecundity, microsatellite DNA, Barro Colorado Island, maximum likelihood estimation, model selection, dispersal kernel, directed dispersal.

INTRODUCTION

The role of seed dispersal in understanding historical, contemporary, and future ecological dynamics and in shaping patterns of species diversity and abundance on local and regional scales has been the focus of much recent attention (Petit et al., 1998, Higgins et al, 2003, Clark et al. 1999, Levine and Murrell 2003, Hubbell 2001, Levin et al. 2003). Theoretical studies have demonstrated that dispersal limitation is important for the maintenance of species diversity in ecological communities (Tilman 1994, Hurtt and Pacala 1995, Hubbell 2001) and strong dispersal limitation has been found in hyperdiverse tropical forest ecosystems (Dalling et al. 2001, Wright 2002, Hubbell et al. 1999). The high abundance of seed predators, herbivores and pathogens near parent plants (Janzen 1970, Connell 1971, Gilbert, et al 1994, Clark and Clark 1984, Mueller-Landau et al. 2003), the rarity of regeneration sites suitable for seedling establishment and recruitment, and negative density dependence during the seed to seedling transition and at later life stages (Webb and Peart 1999, Harms et al 2001, Hubbell et al. 2001) suggests that dispersal may be particularly beneficial in tropical forests.

Tropical trees that require high light environments for regeneration face the problem of rarity of regeneration sites in closed canopy forest (Hubbell and Foster 1986), pest-pressure near the parent plant, (Howe, et al. 1985, Dalling et al. 1997), and potentially high levels of negative density dependence (Hubbell, et al 2001). Two dispersal strategies, long distance dispersal (LDD) and directed dispersal, may have evolved under strong selection from pest pressure, density-dependent effects, and a shortage of nearby regeneration sites. By spreading seeds widely across the landscape, LDD would be advantageous in escaping enemies, reducing competition with kin, reducing asymmetric effect of the maternal plant on seeds and seedlings

(Wright 2002), and increasing the colonization of rare sites suitable for regeneration (Webb and Peart 1999, Hovestadt et al. 2001, Howe and Smallwood 1982).

Directed dispersal is the disproportionate arrival of seeds to sites favorable for seedling and adult recruitment (Howe and Smallwood 1982). Directed dispersal can be viewed as a strategy to increase the probability of encountering unpredictable or rare conditions necessary for regeneration in time and space (Wenny 2001). To the extent that a dispersal agent carries seeds to sites especially suitable for establishment and growth, directed dispersal may partially compensate for the absolute shortage of suitable sites. Although most examples of directed dispersal involve animal-dispersed seeds, several studies of wind-dispersed tropical trees have shown that wind-dispersed seeds are dispersed disproportionately to new and regenerating tree fall gaps relative to paired sites in the understory (Schupp et al. 1989).

Despite hypotheses regarding the advantages of LDD and directed dispersal in tropical forest species, empirical data on the frequency, patterns, and mechanisms of dispersal within natural tree populations are sparse (Higgins and Richardson 1999, Cain et al. 2000, Bullock and Clarke 2000, Nathan et al 2003). Seed dispersal studies have often used curve-fitting techniques to estimate dispersal kernels based on seed collections made at known locations in the field (Wilson 1993, Portnoy and Wilson 1993, Nathan and Muller-Landau 2000). One problem with curve- fitting techniques, including inverse modeling methods (Ribbens et al. 1994, Clark et al 1998, Clark et al. 1999, Dalling et al. 2002), is that low frequency LDD can be masked by high frequency of short distance dispersal events (Turchin 1998). Failure to detect LDD events may underestimate the tail of the dispersal distribution and therefore underestimate the frequency of long distance dispersal. A solution to this problem is to use genetic markers to identify the maternal source of dispersed seeds within a mapped population and determine the actual distances that seeds move (Wang and Smith 2002). From the known dispersal distances one can then determine the dispersal kernel describing the distances that seeds move within the population.

Direct genetic studies of seed dispersal, akin to paternity studies undertaken to study pollen movement, have just begun (Godoy and Jordano 2001). Such studies have been hindered in the past by a lack of effective maternally inherited genetic markers for unambiguous parentage assignment for dispersed seeds and seedlings (Turchin 1998, Ouburg et al. 1999). Most genetic studies of seed movement have actually examined the parentage of established seedlings and therefore cannot distinguish between post dispersal recruitment processes and original patterns of dispersal (Meagher and Thompson 1987, Schnabel et al 1998, Aldrich and Hamrick 1998, Dow and Ashley 1996). Many post-dispersal processes, such as density and distant dependent mortality or absence of suitable recruitment sites, can alter the recruitment curve significantly from the dispersal curve (Janzen 1970, Connell 1971). Genetic studies of established seedlings for hermaphroditic species may also have difficulty in distinguishing which of the two presumptive parents was the seed source and which was the pollen source without a maternally inherited marker.

We studied dispersal and fecundity patterns in a common Neotropical wind-dispersed tree, *Jacaranda copaia* (Bignoniaceae), within an 84 ha area that includes the 50 ha Forest Dynamics Plot (FDP) on Barro Colorado Island (BCI), Panama. We developed microsatellite markers for *J. copaia* and genotyped all potential mothers at mapped locations throughout the 84 ha. We genotyped samples of dispersed seeds collected in large arrays of seed traps placed in understory and tree fall gap sites throughout the plot. We then determined the exact distances that seeds moved within the plot by matching seed genotypes to genotypes of the potential mothers at known locations within the plot (*sensu* Godoy and Jordano, 2001). We also examined population-wide fecundity patterns and wind speeds during the time period of seed dispersal to examine two potential mechanisms governing dispersal patterns across the study area.

Having measured seed dispersal distances in this manner, we address the following questions regarding the levels and patterns of seed dispersal in a large natural tree population: (1) How frequent is LDD (here defined as dispersal at distances greater than 100m) relative to short-distance dispersal in *J. copaia*? (2) Which models of dispersal best fit observed dispersal distances and what mechanisms may be responsible for observed data? (3) What is the relationship between measured dispersal distances, wind profiles, and fecundity? (4) How does LDD vary among years? and (5) Are *J. copaia* seeds disproportionately deposited in tree fall gaps relative to understory sites?

METHODS

Study Site

Our study was conducted in and near the 50-ha forest dynamics plot (FDP) on BCI, Panama. Detailed descriptions of the flora, fauna, and climate of BCI can be found in Croat (1978) and Leigh *et al*. (1982). The BCI FDP, was established in 1980 and consists of a standing number of approximately 240,000 mapped stems > 1 cm diameter at breast height (dbh) of approximately 300 species (Hubbell and Foster 1983). The FDP has been recensused 4 times since 1980, with the most recent census completed in 2000. For each year, 1985-1996 and 2000-2002, a census of canopy height at every 5x5 m grid point has been taken from which we can identify the location of low canopy height light gaps within the plot.

Study Species

Jacaranda copaia (Bignoniaceae) is a large canopy tree (up to 45 m tall) and is a characteristic species of Neotropical moist forests from Belize to Brazil and Bolivia (Croat 1978). The small wind dispersed seeds (< 2 mg) are produced in large woody capsules in the canopy of adult trees (≥ 20cm dbh) and on BCI are dispersed August through November, with a peak in September. The population of *J. copaia* on the BCI FDP has 286 individuals ≥ 1 cm dbh. *Jacaranda copaia* is a pioneer tree that requires large tree-fall gaps to regenerate (Brokaw 1985). A study of realized vital rates and size distributions for 70 of the most common species in the FDP found that *J. copaia* is at the extreme of shade-intolerant species. It shows a skewed size distribution with many large adults and an extreme tail of a few small individuals. Such distributions typically occur in species that are extremely shade-intolerant (Wright et al. 2003). Seeds of *J. copaia* are non-dormant (Gonzalez 1991) and do not form a persistent seed bank in the soil (Dalling et al. 1997). Its small seeds, lack of a seed bank, and high light requirement suggest that seed germination, seedling establishment, and recruitment in *J. copaia* depend on dispersal to recently created gap sites and on high levels of irradiance found within in these sites (Pearson et al. 2002).

Seed Traps and Gap Identification

A long- term study of seed rain into 200 permanent 0.5 m^2 seed traps in the plot has continued uninterrupted since 1986 (Wright, et al. 1999, Dalling, et al 2001, Harms et al. 2000). Seed traps are censused weekly and all reproductive parts of all species are counted and identified. Because the existing 200-trap network poorly sampled tree fall gaps, we placed an additional 98 traps within 51 new tree fall gaps of varying size across the FDP in 2000, with up to three seed traps placed within the largest gaps. Forty-four gap traps were placed within 30 m of the existing seed traps to allow for comparisons between gap and understory sites. An additional 21 traps in the pre-existing trap network were located in gap areas. We quantified the extent of canopy openness directly above each trap using hemispherical photography and analyzed images using Hemiview (Delta-T Devices, Ltd. Cambridge, UK).

Wind passage and fecundity

We examined patterns of wind passage on BCI as well as fecundity of *J. copaia* within the FDP to explore two potential mechanisms that affect dispersal patterns. We used total daily wind passage (km) collected from an analog cup anemometer at a 40 m height on the Lutz Ravine tower on BCI. Data collected from August 1st through December 31st were used to compare total wind passage profiles in 2000 and 2002. Data is courtesy of the Terrestrial Environmental Sciences Program of the Smithsonian Tropical Research Institute (http://www.stri.org/tesp/).

One can estimate the total capsule production for individual trees because *J. copaia* has woody capsules that persist on the forest floor following seed release. We established a transect in each cardinal direction (North, South, East, and West) beneath the canopy of a majority of the adult *J. copaia* individuals (N=188) within the 50 ha plot in November and December of 2000 and 2002. In 2001, seed production was low, only 184 seeds were collected in the 200 seed traps across the entire plot. Therefore fecundity, estimates were only made in 2000 and 2002 (Figure 2).

Each sampling transect for capsules extended to the edge of each tree's canopy in each of the four directions. At 1m intervals along each transect, we placed a ½-m2 PVC frame on the ground and within the frame counted the total number of mature dehisced capsules, immature capsules, and galled capsules infected with one of two types of predispersal insect seed predators (either a wasp or a beetle).

Tissue Collection

We collected leaf tissue from the canopies of all individual *J. copaia* trees present on the FDP in 2000 (N=286). We mapped and collected tissue from an additional 101 trees > 20 cm dbh from a 100m wide strip surrounding the FDP. We included these individuals outside the plot because they are potential sources of seeds caught in traps inside the 50 ha plot. The leaf tissue was flash frozen in liquid nitrogen and transported frozen to the University of Georgia (UGA)for DNA extraction and genetic analysis.

We collected all *J. copaia* seeds weekly from seed traps across the FDP in 2000. The following year, 2001, was a low seed production year so we did not collect seeds that year. Since 2002 was a high seed production year, we randomly sampled up to five seeds per week per trap and then randomly choose 1200 seeds for genotyping from this sample. Maternal tissue of seeds was removed, packaged individually, lyophilized, and stored on Drierite for transport to UGA. Seeds were chosen for genotyping by randomized selection from each year's sample.

DNA Extraction

We used a modified CTAB extraction protocol for both adult and seed wing tissue (Doyle and Doyle 2000). 100 to 200 mg of leaf tissue was homogenized in 2ml centrifuge tubes in 800 uL CTAB buffer solution for three minutes at maximum speed in a MixerMill 300 (Qiagen) with a single tungsten carbide bead. Tubes were incubated for at least one hour at 65ºC and inverted several times during incubation. 400 μL of chloroform:isoamyl alcohol mixture (24:1) was added to each tube. Tubes were inverted 200 times and centrifuged for 10 minutes at 6000 rpm. 400 µL of the supernatant was transferred to a new tube, and 40 µL of 3M sodium acetate (pH 5.2) was added. The mixture was allowed to incubate for 10 min, followed by the addition of 1ml of 100% EtOH and placed in a -20ºC freezer for at least 30 min. DNA was pelleted by centrifuging the tubes for 10 minutes at 14,000 rpm at 4ºC. EtOH was decanted and the pellet was washed twice with 500 µL of 70% ice-cold EtOH and allowed to sit for 5 minutes. DNA pellets were air dried in a sterile hood for two hours before resuspension in 100 µL (50 µL for seed wing DNA) of ultrapure H_2O. Tubes were lightly vortexed and incubated at 55ºC for 1h to hydrate the DNA before storage at -20ºC.

Genotyping Reactions

Details of microsatellite library construction and primer development for *J. copaia* are given in Jones and Hubbell (2003). We genotyped adult trees > 20 cm dbh at four microsatellite loci (n = 305). Because of high heterozygosity, large number of alleles per locus, and low probability of individual genetic identity, four loci were sufficient for our analysis of maternal seed parentage (Table 1). Details of genotyping reactions including PCR recipe, thermocycling conditions, and optimal primer annealing temperatures for adult and juvenile leaf tissue are given in Jones and Hubbell (2003). Modifications to this protocol for the genotyping of seed wing tissue included increasing the template amount in the reaction to 2-3 µL, adding bovine serum albumin (BSA) at a concentration of 0.7% to each reaction, and increasing the number of PCR cycles from 30 to 35. Each locus was amplified in a separate reaction and all four loci were pooled for genotyping runs. Genotyping runs were carried out in 96 well plates on an ABI 3700 capillary electrophoresis automated sequencer using ROX 400HD size standard (Applied Biosystems). Electropherograms were scored using Genescan 3.1 and Genotyper 3.7 (Applied Biosystems).

Matching Seed wings to Trees

Matching of multilocus genotypes of seeds to maternal parents was conducted using the "identity check" option in CERVUS 2.0 (Marshall, et al. 1999). Ambiguity in parentage assignment can arise when multiple adults share the same multilocus genotype. For the seeds that matched multiple trees in the population, we assigned parentage to the nearest adult source. For the most common occurrence of this ambiguity, the difference between the distances to the two closest matching individuals is < 4m. In each case, the overall effect of maternal ambiguity on determination of dispersal distances is therefore conservatively biased towards shorter dispersal distances.

Dispersal kernel estimation

A common goal of seed dispersal research is to find and fit a dispersal curve that accurately describes the relationship between seed density and the distance away from the maternal plant. To determine the dispersal kernel that best describe the observed distribution of genotyped seeds away from maternal plants, we binned identified seeds into 10-m intervals based upon their genetically determined dispersal distances. We fit four single component distributions (1-4 below) and a two-component mixture distribution (5) to the data using maximum likelihood techniques. Because of the discrete nature of our data collected over a continuous area, we assumed Poisson errors (Hilborn and Mangel 1997):

Gaussian: $$seeds = \alpha e^{-\frac{1}{2}\left(\frac{x}{\beta}\right)^2} \tag{1}$$

negative exponential: $$seeds = \alpha e^{-\beta x} \tag{2}$$

2DT model: $$seeds = \alpha \frac{\gamma}{2\alpha\Gamma(1/\gamma)} e^{-\left|\frac{x}{\alpha}\right|^{\gamma}} \tag{3}$$

lognormal: $$seeds = \alpha e^{\frac{-\frac{1}{2}\ln\left(\frac{x}{\beta}\right)^2}{\gamma}} \frac{1}{x} \tag{4}$$

mixture model $$seeds = \alpha e^{-\frac{1}{2}\left(\frac{x}{\beta}\right)^2} + \gamma e^{-\delta x} \tag{5}$$

where x is the distance from the maternal tree, α, β, γ, and δ are free parameters, and Γ is the gamma function. We report the parameters with the greatest likelihood value for each model, Akaike's Information Criterion (Burnham and Anderson 1998, Hilborn and Mangel 1997), AIC differences (Δ_i), Akaike weights (w_i), total R^2 of observed vs. predicted seeds, and separate R^2 for local (< 100m) and long distance (>100m) dispersal distances. AIC is formulated as:

$$AIC = -2\log(L(\hat{\theta} \mid y)) + 2K \tag{6}$$

Where $\log(L(\hat{\theta} \mid y)$ is the log-likelihood of the estimated parameters given the data and K is the number of estimated free parameters in the model. AIC differences (Burnham and Anderson 1998) are calculated as

$$\Delta_i = AIC_i - AIC_{min} \tag{7}$$

Where AIC_i is the AIC value for model i, and AIC_{min} is the minimum AIC value in the set of R candidate models. To interpret relative differences among model likelihoods and their resultant AIC values, likelihoods are normalized to be a set of positive Akaike weights:

$$w_i = \frac{\exp(-\frac{1}{2}\Delta_i)}{\sum_{r=1}^{R}\exp(-\frac{1}{2}\Delta_i)} \tag{8}$$

w_i is considered as the relative weight of evidence in favor of model i being the best model given the set of R models that includes the best model (Burnham and Anderson 1997, Johnson and Oldham 2004). The greater the Akaike weight (w_i), the more support for model i as the best model given the data. Furthermore, the ratio between Akaike weights for two models is interpreted as an evidence ratio for support for one model over the other. Ratios > 0.90 are considered strong support of one model over another (Burnham and Anderson 1998).

RESULTS

Genotypic data

We genotyped 305 adult *J. copaia* (<20 cm dbh) in the FDP and buffer area population representing 100% of the potential adults > 20 cm dbh in the 84 ha area. *Jacaranda copaia* exhibits high heterozygosity at the four loci examined within the BCI population (Table 1). Observed heterozygosity ranged from 0.70 to 0.86, and the number of alleles per locus ranged from 10 to 15, with an average number of alleles per locus of 14.8 and a total of 47 alleles across all loci (Table 1). The four markers in the adult population of *J. copaia* for the maternal parentage analysis have a collective probability of identity ($\mathrm{PI}_{\mathrm{ID}\mathit{unbiased}}$) of < $1\text{x}10^{-5}$ (Waits et al. 2001). The $\mathrm{PI}_{\mathrm{ID}\mathit{unbiased}}$ is an estimate of the probability that two individuals in the population will share the exact same genotype, adjusted for sample size. For our purposes, this probability allows us to estimate the probability of erroneously assigning the parentage of a seed to a tree on the plot when in fact it dispersed from a non-sampled individual outside our study area.

Therefore, it is also an estimate of the probability that an individually determined dispersal distance for a given genotyped seed is an underestimate.

Seed assignment and dispersal distances

A total of 1190 seeds were captured in 298 seed traps in 2000 and 4138 in 2002 (Figure 2). We extracted DNA from a 384 and 480 seed wings in 2000 and 2002, respectively. We obtained sufficient genetic information from 279 seeds (23% of total trap captures) in 2000 and 447 seeds in 2002 (11% of all seeds captured) to positively identify the maternal source of seeds or exclude all potential adults within the population as parents. The maternal source of the remainder of individual seeds remained ambiguous because of incomplete genetic information due to extraction or PCR failure and are not included in the below analysis. Successful identification of maternal parents was made for 235 seeds in 2000 and 373 seeds in 2002. Forty-four and 74 seeds were not assigned a parent from within the 84-ha study area in 2000 and 2002, respectively, and therefore are considered to have moved the minimum distance from the closest border of the mapped area to traps within the plot.

Distribution of seed dispersal distances to understory and gap sites are given in Figure 1. Seed dispersal distances ranged from 2.7 m to 421.8 m in 2000 and 2.9 to 710.50 m in 2002. The median seed movement was 20.5 m and 27.0 m in 2000 and 2002, respectively, and the modal distance was 9.73 m in each year. Seeds, on average, moved greater distances in 2002 than in 2000. Mean dispersal distances were 40.11 m ±65.9 (mean ± SD) in 2000 and 58.8 m ± 101.28 in 2002 (X^2 = 15. 85, df=1, P< 0.0001, Kruskal-Wallis rank sum test).

A total of 44 seeds could not be assigned a maternal parent in 2000 and 74 in 2002. Collectively, these represent 15.8% and 16.6% of the resolved sample in each year, respectively.

Because all potential mother trees were sampled within 100 m of the edge of the existing plot, this implies that each excluded seed has moved at minimum distance of 100 m into the plot. However, because we can not definitively source these individual seeds and directly determine the distance they have moved, they are not included in the fitting exercises below.

Gap vs. understory patterns

We examined the total number of seeds, the distance that genetically identified seeds moved from adults trees to understory and gap sites, and the number of genetically excluded seeds present in gap vs. understory sites (Figure 1). Hemispherical photos reveal that gap and understory traps differed in mean canopy openness (t=12.15, df=54, $P<0.00001$). Gap and understory traps within 30m of each other were compared for differences in the mean number of seeds captured in 2000 and 2002. However, paired gap and understory traps did not differ in the mean number of all seeds captured in 2000 or 2002 (t=-0.359, df=87, $P > 0.05$, t=1.21, df=118, P >0.05). Traps in gaps and understory also did not differ in the distances that genotyped seeds moved, considering only traps in which both paired understory and gap traps contained at least one genotyped seed ($X^2 = 21.96$, df=20, P>0.05, $X^2 = 21.56$, df=22, P>0.05, Kruskal-Wallis Rank sum test). Traps in understory sites had and 29 and 38 excluded seeds in 2000 and 2002, respectively, whereas traps in gaps sites had 10 and 33 excluded seeds in 2000 and 2002, respectively.

Dispersal kernel fits

Maximum likelihood parameter estimates and goodness of fit statistics for directly measured data are shown in Table 2 and the fitted dispersal kernels are depicted in Figure 2.

AIC values and Akaike weights clearly indicate that the two- component mixture model (5) best describes the data in each year. The evidence ratio of Akaike weights of the compound model to its closest competitor, the lognormal model, was high (2.49E+6 and 3.20E+8 in 2000 and 2002, respectively) in 2000 and 2002, respectively, implying strong support for the mixture model over all other models examined. Other commonly fit models, Gaussian and negative exponential (Okubo and Levin 1989) and 2DT model (Clark 1998, Clark et al. 1998, Clark et al 1999), showed poor fits to the data, particularly at distances greater than 100m (Table 2).

A total of 21 seeds moved distances ≥ 100m, in 2000, and 46 seeds in 2002, not including genetically excluded seeds. When excluded seeds are included, 65 (23% of total seeds examined) and 112 (25%) moved distances greater than 100 m in 2000 and 2002, respectively. All single component dispersal models were outperformed by the compound model both in terms of likelihood values as well as the goodness-of-fit of observed to expected data (R^2) at distances ≥ 100m (Table 2).

Annual variation in wind and fecundity

Wind passage ranged from 42.4 to 221.1 km day^{-1}, with a mean passage rate of 78.66 km day^{-1} ± 28.11 in 2000, and ranged from 32.5 to 271.4 km day^{-1} with a mean rate of 87.32 km day^{-1} ± 56.09 in 2002 (Figure 4). Mean rate of passage was greater in 2002 than in 2000 (t=-1.728, df=305, $P < 0.05$). Mean wind speed per day was 0.9 m sec^{-1} and 1.1 m sec^{-1} in 2000 and 2002, respectively. Maximum daily mean wind speeds were 2.55 and 3.14 m sec^{-1} in 2000 and 2002.

Total seed capsule production was higher in 2000 than in 2002. However, because of greater seed predation in 2000, the total number of mature seed-producing capsules produced, and therefore the number of seeds, was lower in 2000 than in 2002 (Figure 3). Estimated capsule fecundity (all capsules regardless of predation or maturity status) ranged from 0 to 773 capsules tree^{-1} (mean = 47.62 ± 95.10) in 2000 and from 0 to 451 capsules tree^{-1} (mean=35.89 ± 68.62) in 2002.

DISCUSSION

This study is among the first to use maternally derived tissue from dispersed seeds to determine dispersal distances in a tropical tree. We have shown that the maternal parents of seeds can be positively identified by genotyping maternally derived tissue attached to wind dispersed seeds of the tropical tree, *J. copaia.* With this genetic technique, we determined dispersal patterns with greater resolution than was previously possible with non-genetic methods.

Model comparison

Of the five dispersal models considered, we found that a mixture distribution, consisting of a local Gaussian dispersal kernel and a long- distance, negative exponential tail best predicted the measured seed dispersal distances. The best fit of the mixture model was despite the increased penalty given to the mixture models because of the greater number of free parameters (equation 6). Our result is consistent with several non-genetic studies that have also found that mixture distributions best -fit observed dispersal data (Higgins and Richardson 1999, Bullock and Clarke 2000, Higgins et al. 2003, Clark 1998, Giladi 2004)

We suggest that the better fit to the data given by the mixture model is due to separate physical processes that govern dispersal at local and long distances (Greene and Johnson 1995, Higgins et al 2003). The local Gaussian shaped dispersal kernel is likely to be due to seeds that fail to be uplifted and fall within 100m of the tree (Horn et al. 2001). Recent simulations of wind-dispersed seeds have shown that uplift can create distinct dispersal patterns near and far from the tree in wind dispersed plants (Nathan et al. 2002). We observed *J. copaia* seeds uplifted to heights > 20m above the tree from a canopy crane at a separate forest site in Panama (F. A. Jones, personal observation).

Therefore, we suspect that the negative exponential tail of the dispersal curve in *J. copaia* is due to the uplift of seeds above the canopy of the tree and subsequent transport of these seeds long distances (Nathan et al. 2002). In both years of the study, we find that a significant proportion of the seeds move distances >100m (23% in 2000, 25% in 2002), suggesting that seed uplift may be a common occurrence in this species. However, because of the total number of seeds in the tail is relatively small and our scale of measurement is ultimately limited by the dimensions of our study area, the nature of the tail still remains relatively poorly defined.

Fecundity and wind profiles

Wind passage and fecundity have an effect on the shape and scale parameters of the dispersal kernels, respectively. The shape parameters in the models correspond to the expected mean and variance in the distribution of dispersal distances. Increases in the amount and speed of wind should increase mean dispersal distance, and thus affect the values of the shape parameters in fitted models. The scale parameter governs the value of f(x) at 0, so increases in fecundity would increase the absolute number of seeds that arrive at a given distance away from the parent plant.

Long distance dispersal can be achieved by increasing the absolute number of seeds that reach the tail through increases in fecundity (Willson 1993). *Jacaranda copaia* shows marked differences in seed production both among individuals within size classes within years and within and among individuals among years within the BCI population (F. A. Jones, unpublished data).

At the population level, mature capsule production and resultant seed trap captures were on the order of three times greater in 2002 than in 2000.

Although greater numbers seed capsules were produced in 2000, trees in that year suffered an estimated loss of 56% of mature seeds due to predispersal insect predators. Predispersal seed predation rates were much lower in 2002 (< 7%), resulting in a larger number of mature seeds in 2002 despite the higher capsule production in 2000 (Figure 3). That predispersal seed predation reduced the scale parameters of the dispersal curve (i.e. total number of seeds produced as defined by the parameter α in each year) is consistent with one of the original predictions made by Janzen (1970) that high levels of predispersal seed predation reduces the number of seeds that disperse away from the parent plant. Recent studies have shown that variable reproductive output greatly alters migration rates (Clark 1998, Clark, et al. 2001), obscures tradeoffs between competition and colonization ability (Clark et al. 2004), and can affect seedling recruitment within local tree neighborhoods (De Steven and Wright 2002). Thus the observed variation in fecundity may have lasting impacts on population dynamics of *J. copaia*.

Mean dispersal distance was higher in 2002 than in 2000. Although we genotyped a greater number of seeds in 2002 than in 2000, we genotyped a smaller proportion of the total seed captures in 2002 than in 2000 (11 vs. 23%). Therefore, we do not believe that the greater observed dispersal distances in 2002 were due to the greater number of genotyped seeds. Wind passage was greater in 2002 than in 2000, suggesting that increased wind or increased wind speed during the time when seeds were released is responsible for the differences in the dispersal distances and dispersal kernels observed between the years.

Augspurger (1986) determined that the descent rate of *J. copaia* in still air was 39.2 cm sec^{-1}. Using her predicted height of a tree of 30m and the average daily wind speed measured on the

Lutz tower, we determined the average daily dispersal distance for *J. copaia* for each year using the equation, $D = V_w(H/V_f)$ where D is the horizontal displacement away from the point of release, V_w is the wind velocity, H is the height of release, and V_f is rate of descent. The mean dispersal distance calculated in this way, based on each day's average wind velocity in August – December, was 46.31m ± 24.82 in 2000 and 51.56m ± 49.52 in 2002. Each of these estimates are well within 1 standard deviation of the mean of our directly measured dispersal distances of (40.11 m ± 65.90 in 2000 and 58.82 m ± 101.28 in 2002), although the standard deviations in the directly measured dispersal distances are twice what they are in the estimated dispersal distances. This may indicate that short periods of increased wind speed or uplifting events can carry seeds greater distances than mean daily wind profiles can predict.

Directed Dispersal

The mechanisms proposed in the past to account for more wind-dispersed seeds in gaps include downdrafts or other microenvironmental conditions (eddies, turbulence, temperature differences) above tree fall gaps, which capture wind-borne seeds and force them to drop out of the air column and into the gap (Schupp et al. 1986). We found no evidence for increased seed number or increased seed dispersal distance to traps in tree fall gaps for the two years of this study. Previous studies have found that wind dispersed tree, liana, and shrub seeds were more abundant in seed traps placed in tree fall gaps than those paired in the understory in two Neotropical forests (Augspurger and Franson 1988, Denslow and Gomez-Diaz 1990). In the BCI forest, Augspurger and Franson (1988) found evidence for increased abundance of seeds in tree fall gaps relative to understory sites, but because their study examined seeds that are dispersed at the beginning of the wet season in May, *J. copaia* was not included in their study.

Jacaranda copaia is unique among wind- dispersed trees on BCI in that it releases its' seeds well into the wet season in August and September, whereas most wind dispersed trees on BCI release their seeds at the beginning of the wet season (S. J. Wright, unpublished data;, Foster 1982). The timing of new gap creation on BCI is non-random across years. Brokaw (1985) found that the greatest creation of new gaps occurred in August and September during periods of heavy rainstorms. September and October in Panama are often punctuated by a short period of dry, windy conditions ("veranillo" or little summer) characterized by low precipitation and high sunlight. That we found no evidence of greater numbers of seeds or greater distances that seeds moved to gap or understory sites suggests that *J. copaia*'s dispersal strategy is to spread seeds as wide and far as possible through LDD perhaps to encounter gaps that are rare in space and time. However, its seeds dispersal phenology may be timed to take advantage of new gap creation during the period of high sunlight and winds in the short dry period in September and October.

CONCLUSION

Through the use of a novel genetic technique to examine patterns of seed movement, we have found that long distance dispersal is relatively common in the tropical wind-dispersed species *J. copaia*. We found strong evidence in both years for separate dispersal kernels describing local and long distance seed dispersal. In addition, we have shown that increases in wind speed and fecundity can alter the dispersal kernel and increase the total number of *J. copaia* seeds moving long distances, respectively. Comparisons of the directly determined dispersal distances presented here with those calculated using non-genetic curve fitting techniques reveal that the conventional techniques underestimate the frequency of LDD events, and thus fail to capture the tail of the dispersal kernel (Jones and Hubbell, in preparation). Thus genetic techniques can effectively elucidate both the patterns of and mechanisms governing long distance seed dispersal in wind-dispersed species.

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Table 2.1. Genetic diversity statistics for four microsatellite loci used in the maternal parentage analysis of *Jacaranda copaia* recruits on Barro Colorado Island, Panama. H_e and H_o are expected and observed heterozygosity, respectively.

Locus	**No. alleles**	**H_e**	**H_o**	**$P_{ID\textit{unbiased}}$**
JACC9	11	0.86	0.85	0.034
JACC18	15	0.86	0.86	0.029
JACC21	10	0.67	0.70	0.15
JACC31	11	0.80	0.81	0.055
Average	14.83	0.82	0.82	9.04e-06

Table 2.2. Maximum likelihood parameter estimates and goodness of fit measures for two years of genetically determined seed dispersal distances and distance from nearest possible parent to recruit from 1983-2000 for *Jacaranda copaia* within the Forest Dynamics Plot on Barro Colorado Island. AIC is Akaike's an Information Criterion, $\mathbf{\Delta_i}$ is the relative difference between the best model and model *i,* and w_i are Akaike weights. R^2 values were determined across the entire distance as well as for distances < 100m ≥ 100 m.

Distribution	**Year**	**Parameters**				**AIC**	$\mathbf{\Delta_i}$	w_i	**<100m**	**≥100m**	**Total**
		α	β	γ	δ				$\mathbf{R^2}$	$\mathbf{R^2}$	$\mathbf{R^2}$
1)Gaussian	2000	25.29	78.11	-	-	379.25	258.68	6.73E-57	0.822	0.118	0.662
2)Exponential	2000	67.34	0.025	-	-	203.03	82.46	1.24E-18	0.951	0.120	0.944
3)2DT	2000	6275.34	4.93	0.488	-	161.00	40.43	1.66E-09	0.810	0.175	0.890
4)Lognormal	2000	998.31	0.9831	24.90	-	149.64	24.07	4.87E-07	0.932	0.162	0.962
5)Compound	**2000**	**63.80**	**29.46**	**2.06**	**0.006**	**120.57**	**0**	**0.999**	**0.983**	**0.293**	**0.991**
1)Gaussian	2002	26.08	117.78	-	-	643.99	437.84	8.39E-96	0.740	0.609	0.541
2)Exponential	2002	68.91	0.017	-	-	345.06	138.91	6.85E-31	0.719	0.605	0.835
3)2DT	2002	9245.13	9.24	0.50	-	274.70	68.55	1.30E-15	0.501	0.629	0.760
4)Lognormal	2002	1473.25	1.04	30.52	-	245.32	39.17	2.12E-09	0.679	0.616	0.854
5)Compound	**2002**	**74.74**	**35.51**	**4.28**	**0.005**	**206.15**	**0**	**0.999**	**0.599**	**0.800**	**0.910**

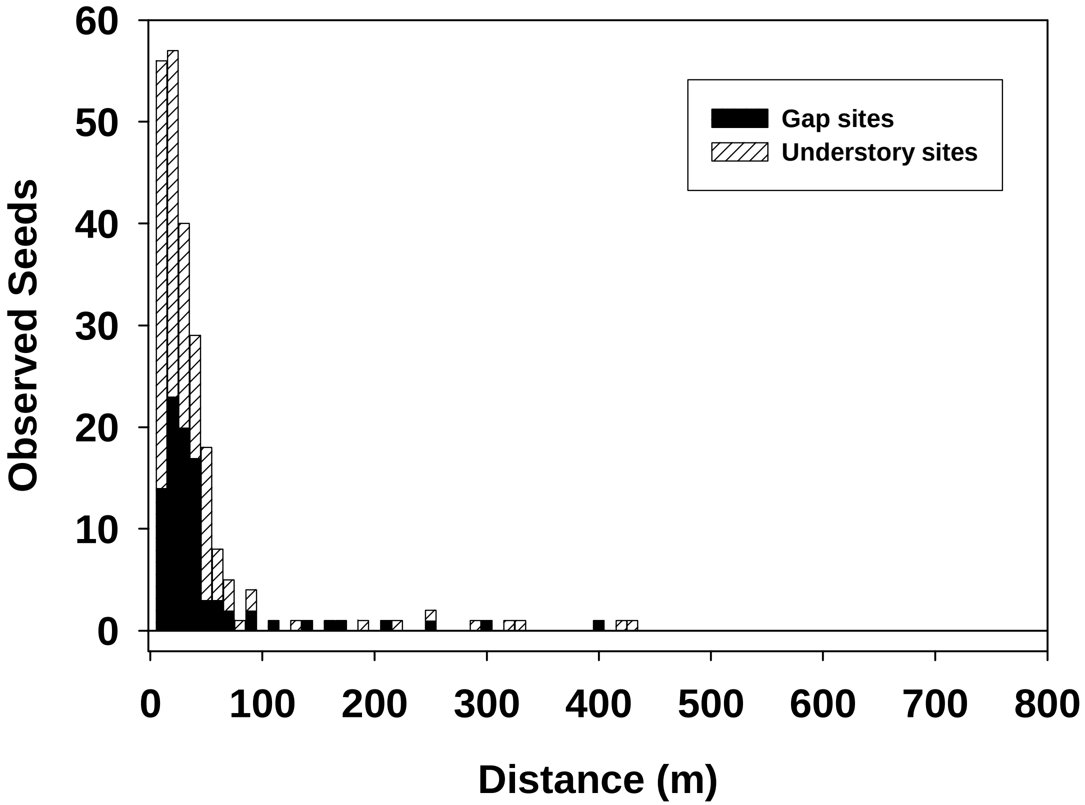

Figure 2.1a. Observed and expected *Jacaranda* seed numbers at different distances away from the maternal tree for 2000 on Barro Colorado Island Panama.

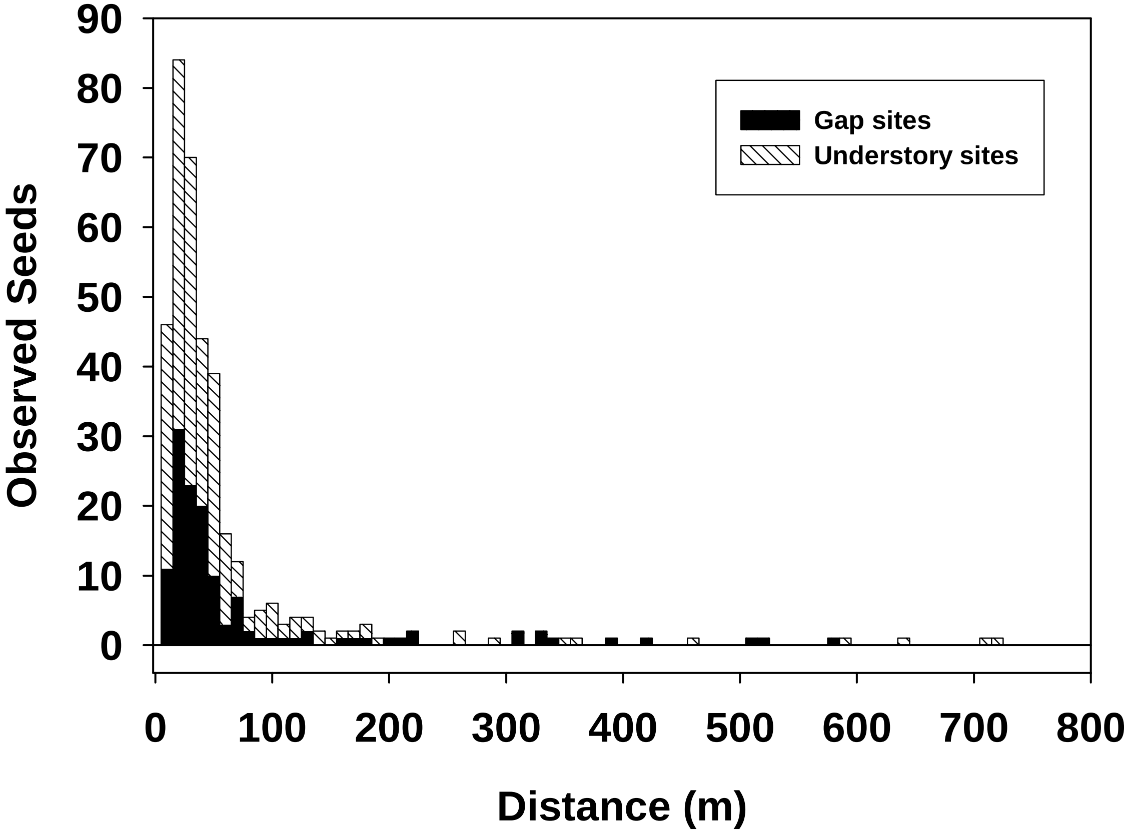

Figure 2.1b. Observed and expected *Jacaranda* seed numbers at different distances away from the maternal tree for two years 2002 (b), on Barro Colorado Island Panama.

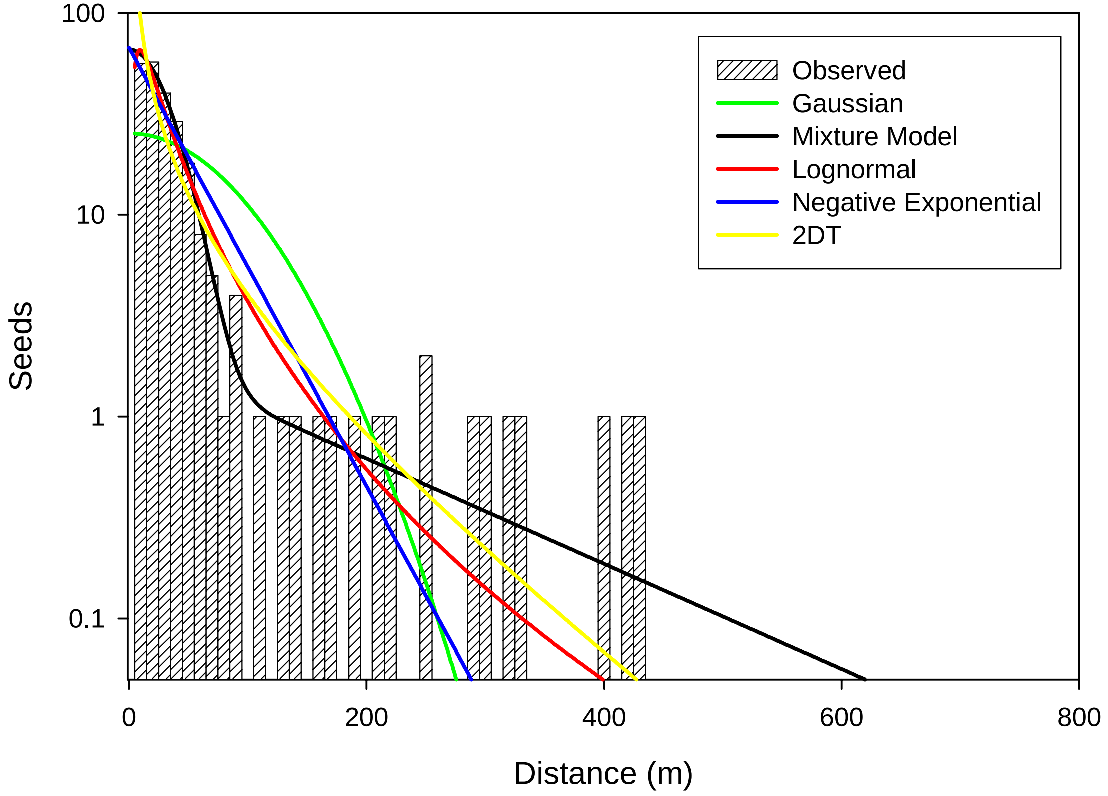

Figure 2.2a. Maximum likelihood fit dispersal kernels to observed dispersal distance data for *Jacaranda copaia* for 2000 on Barro Colorado Island, Panama. Lines are different expected numbers of seeds as a function of distance to parent tree under different dispersal kernels.

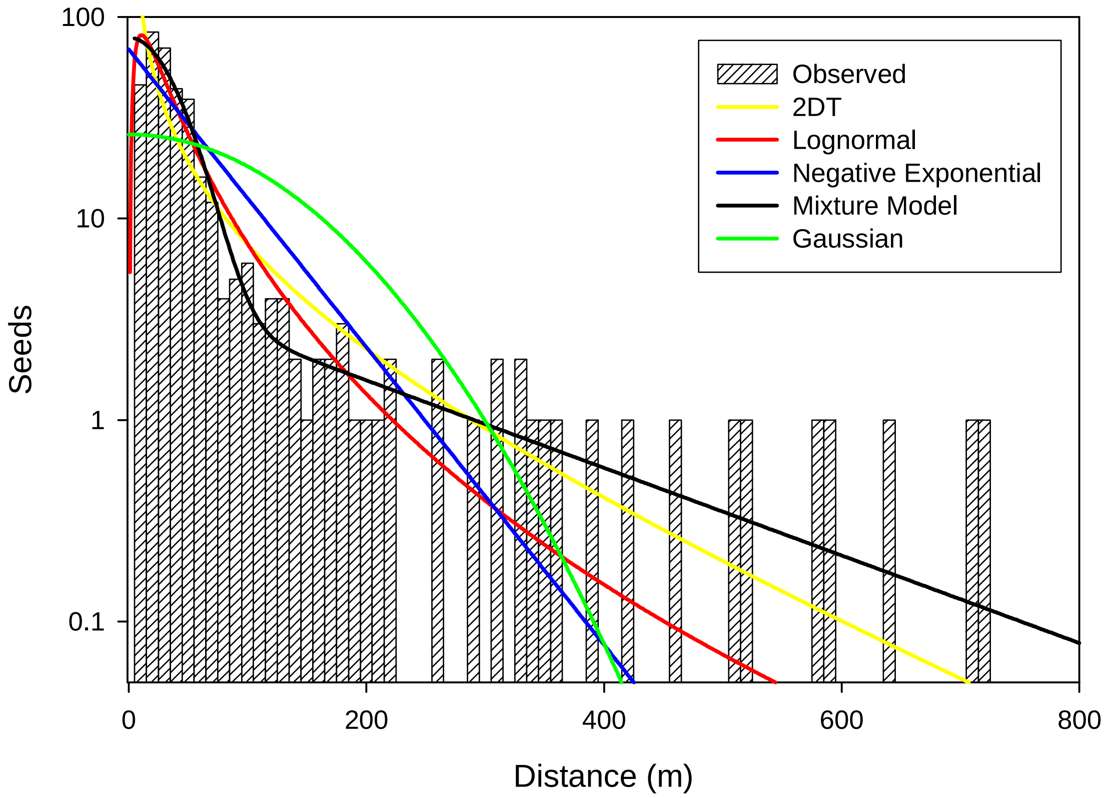

Figure 2.2. Maximum likelihood fit dispersal kernels to observed dispersal distance data for *Jacaranda copaia* for two years, 2002 on Barro Colorado Island, Panama. Lines are different expected numbers of seeds as a function of distance to parent tree under different dispersal kernels.

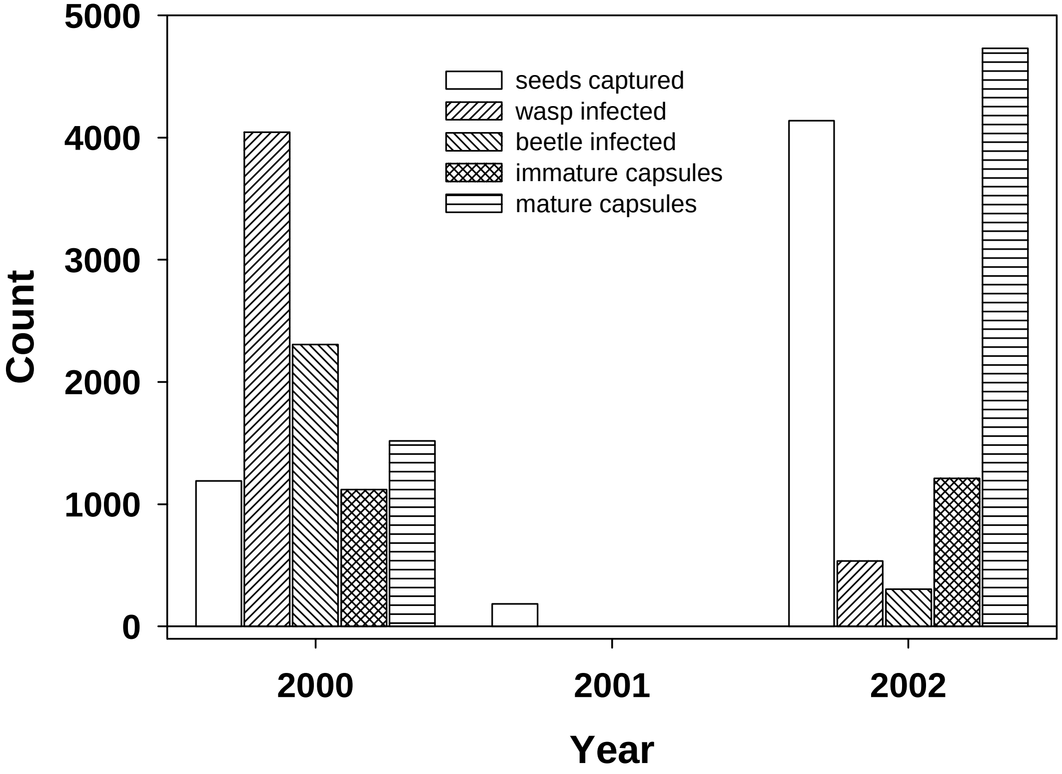

Figure 2.3. Total seed captures, seed predation by wasp and beetles, immature, and mature capsule production for *Jacaranda copaia* across two years on Barro Colorado Island, Panama.

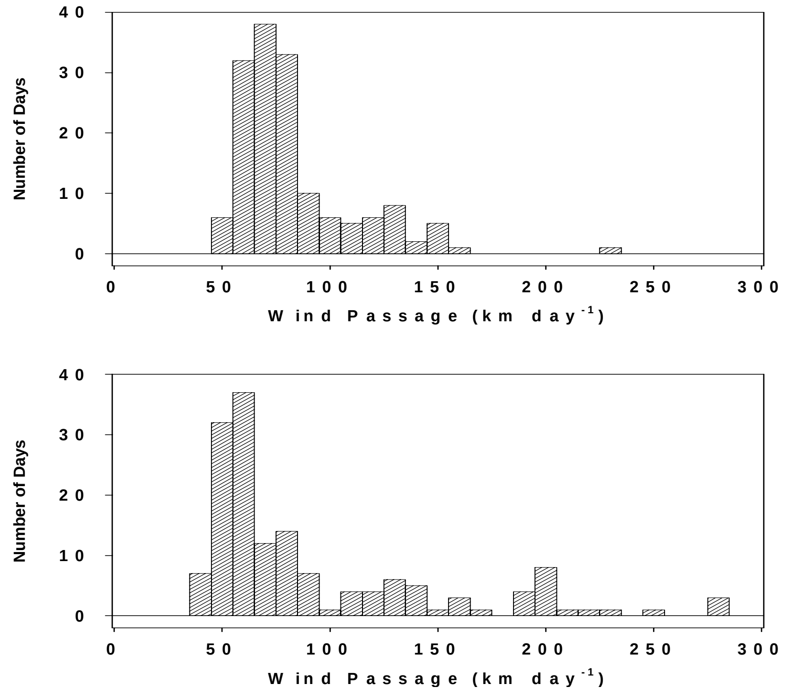

Figure 2.4. Frequency histogram for total daily wind passage (km) for August 1st through December 31st for 2000 (a) and 2002 (b) as measured from an analog cup anemometer from the Lutz ravine tower on Barro Colorado Island, Panama.

CHAPTER 3

LONG DISTANCE SEED DISPERSAL IN A TROPICAL TREE: A COMPARISON OF GENETICALLY DETERMINED AND INVERSELY MODELED DISPERSAL IN *JACARANDA COPAIA*.[1]

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[1] Jones, F.A and S.P. Hubbell. To be submitted to *Diversity and Distributions*

ABSTRACT

Direct measures of seed dispersal and tree fecundity are difficult to obtain in closed canopy forests. We compared direct genetically measured patterns of seed dispersal and individually estimated tree fecundities in the Neotropical tree, *Jacaranda copaia*, to estimates made by inverse modeling methods. Dispersal distances for *J. copaia* were determined by genotyping seeds caught in two years in a large array of seed traps within the 50 ha Forest Dynamics Plot on Barro Colorado Island, Panama. We estimated individual tree fecundity in the field by counting reproductive structures that had fallen to the ground beneath the tree. We found that a lognormal inverse model best fit seed rain data for both years and outperformed other commonly used dispersal kernels. Fecundity of individual trees was found to be poorly predicted by tree basal area. As a result, we achieved better fits in the inverse models when other variables for tree fecundity besides basal area, such as crown area and total capsule number, were used in our analyses. Previous genetic analyses have shown that > 20% seeds in *Jacaranda copaia* move distances greater than 100m. Inverse models, however, poorly described distances that seeds moved when compared to our direct genetic estimates, particularly at distances > 100 m. Results have implications not only for studies of long distance dispersal but for studies focused on assessing the degree of dispersal limitation present within populations across space and time.

Keywords: inverse models, dispersal kernel, dispersal limitation, fecundity, microsatellite DNA, Barro Colorado Island, maximum likelihood estimation, model selection.

INTRODUCTION

Recent empirical studies have focused on the role and importance of dispersal and recruitment limitation within tropical tree communities (Hubbell et al. 1999, Dalling et al. 2001). Although limited dispersal ability may maintain species diversity at the community level, it can have detrimental population-level consequences within species. Most seeds are dispersed short distances, usually within one or two tree heights, and land near the parent plant. Although high seed density might be numerically advantageous in terms of the seedlings produced, seeds and seedlings may suffer disproportionate mortality due to density, distance, and species-dependent predators and pathogens (Janzen 1970, Connell 1971, Harms et al, 2001). Furthermore, asymmetric competition with the parent plant (Howe and Smallwood 1982, Wright 2002) and a general rarity of suitable recruitment sites near the parent plant (Wenny and Levey 1998) may disfavor local dispersal. Dispersal limitation, in concert with negative distance and density dependent agents, is a potentially strong selective force favoring the evolution of long distance dispersal in tropical trees (Muller-Landau et al. 2003). The role of long distance dispersal in these systems is difficult to evaluate, however, as few empirical studies of the frequency of long distance dispersal exist in any tropical plant (Higgins et al. 2003, Ouburg 1999, Nathan et al. 2003).

Long-distance dispersal is notoriously difficult to quantify. This has prompted a discussion in the literature of the best way to estimate and predict dispersal patterns, particularly for seeds that move large distances (Cain et al 2001, Higgins and Richards 1999, Nathan et al. 2003). Recent attention has been given to inverse modeling techniques to analyze patterns of seed rain to seed traps (Ribbens et al. 1994, Clark et al. 1998, Clark et al. 1999, Clark et al 2001). These modeling methods are called *inverse* because one “backs out” the best fit parameters by maximum likelihood from the data, fitting a flexible mathematical function (the dispersal kernel) to counts of seeds recorded within seed traps in combination with a parameter (the fecundity or scale parameter) that predicts the strength or number of seeds each individual produces. Fecundity is usually assumed to be a function of absolute plant size. These methods incorporate an error probability density function appropriate for ordinal count data, such as the Poisson or negative binomial distributions, which is used to maximize the likelihood of parameters, given counts of seeds in traps, tree sizes, and distances of trees to traps (Ribbens, et al 1994, Clark et al. 1998, Clark et al. 1999). The result is a seed shadow that predicts the expected density of seeds at a seed trap as a function of the input of seeds from all potential parents to that point:

$$\frac{seeds}{m^2} = \alpha \sum_{i=1}^{n} (dbh_i) f(x) + \varepsilon_i \tag{1}$$

The predicted density of seeds at any location is the sum of the contribution all trees *i* in the population as a function of distance *x* from tree *i*. The dispersal kernel (*f*(x)) is scaled to predict the number of seeds at distance *x* by some measure of the fecundity of the tree (dbh above) and the scale parameter α.

Dispersal kernels can be any of a variety of flexibly shaped probability density functions. Estimated parameters of the function include those that describe the shape of the distribution (e.g. mean and variance). Choosing an appropriate functional form of the dispersal kernel that accurately describes the pattern of seeds around trees is a critical step (Willson 1993). Recent work has demonstrated improved fits to data using fat tailed probability density functions whose shapes permit greater long distance dispersal but that have a reasonable shape (e.g. Gaussian-like), near the parent tree (Clark et al. 1998, Clark et al. 1999, Hovestadt et al. 2001). Fat-tailed distributions are those that have a greater area under the curve in the extreme values than a negative exponential distribution fit to the same data.

Inverse modeling techniques have been used to parameterize spatially realistic simulations of forest dynamics (e.g. SORTIE, Ribbens et al. 1994), predict the strength of dispersal limitation in tropical forests (Dalling et al. 2001), reconstruct mechanisms responsible for post-glacial tree migration (Clark 1998, Clark et al. 2001), and forecast the response of vegetation to current global environmental change (Clark et al, 1998, Higgins et al. 2003). However, we know of no field-based tests of inverse modeling techniques performed to assess the degree to which they accurately describe actual dispersal patterns within closed canopy forest systems, particularly at large distances from the parent tree.

We used nuclear microsatellite genetic markers to determine the distances that seeds move in the wind-dispersed Neotropical tree, *Jacaranda copaia* (Bignoniaceae), within the 50 ha Forest Dynamics Plot (FDP) on Barro Colorado Island, (BCI), Panama. We determined the distances that seeds moved by genotyping maternal wing tissue present on dispersed seeds that were collected in a large seed trap array in the FDP. Dispersed seed maternal genotypes were matched to adult genotypes in the population. Here, we compare the results of these direct genetic measurements of seed dispersal patterns in *Jacaranda copaia* (Jones and Hubbell, Chapter 2) to results obtained using inverse modeling techniques applied to seed rain data recorded in the same years. Our goal is to determine the degree to which inverse modeling methods accurately describe dispersal and fecundity patterns in a natural population, and if they do not, when and how they fail.

Specifically, we ask: 1) How do directly measured dispersal distances and densities compare to those obtained by inverse modeling methods? 2) How well do inverse model predictions describe patterns of seed movement at large distances, i.e., in the tail of the distribution? 3) How does variation in fecundity at the individual tree level affect inverse model fits? Our hypothesis is that inverse methods significantly underestimate the tail of the dispersal curve because they cannot accurately distinguish between local and long distance seed dispersal.

METHODS

Study Site

The 50-ha forest dynamics plot (FDP) on BCI was established in 1980 (Hubbell and Foster 1983). It consists of a standing number of approximately 215,000 mapped stems > 1 cm diameter at breast height (dbh) of approximately 300 species tree and shrub. The FDP has been recensused 4 times since 1980, with the most recent census completed in 2000. The FDP is also the site of an 18-year study of seed rain into a set of 200 permanent ½ m^2 seed traps. Traps are censused weekly and all seeds are counted and identified to the species level. We placed an additional 98 traps within more than 50 new tree fall gaps of varying size across the FDP. We added these traps because gap microsites were not well represented in the pre-existing trap network (Jones and Hubbell, Chapter 2).

Study Species

Jacaranda copaia (Bignoniaceae) is a large emergent canopy tree (up to 45 m tall) characteristic of Neotropical moist forests, ranges from Belize to Brazil and Bolivia (Croat 1978). It is a light demanding colonizer of large tree fall gaps (Brokaw 1985). Seeds are non-dormant (Gonzalez 1991) which suggests that seedling establishment depends upon current dispersal into existing gaps. There were 205 reproductive-sized *Jacaranda copaia* within the BCI FDP and an additional 100 reproductive-sized individuals within 100m of the FDP in the years of this study, 2000 and 2002.

Genetic information used in direct estimation

Details of microsatellite library construction and primer development are outlined in Jones and Hubbell (2003). Procedures for adult and seed wing DNA extraction, loci used in genotyping reactions, and distance determination are given elsewhere (Jones and Hubbell unpublished manuscript). Briefly, we used four microsatellite loci developed specifically for *Jacaranda copaia* (Jones and Hubbell 2003) to genotype all adults within the FDP and a 100m buffer area surrounding the plot (N=305). *Jacaranda copaia* seeds were collected from the seed traps described above, maternal wing tissue was removed, DNA was extracted, and they were genotyped using the four loci. Given complete genetic information at all four loci, we were able to definitively source and determine the distance moved by 279 and 477 seeds in 2000 and 2002, respectively.

We previously reported that a mixed model consisting of two component distributions best fit the directly measured dispersal data (Jones and Hubbell, Chapter 2). However, because of difficulties due to parameter tradeoffs, mixed models themselves are not amenable to inverse modeling and direct parameter estimates of the long distance component are not possible unless constraints are applied to the parameter values (Clark 1998, Clark et al. 1999). Therefore, fat-tailed probability density functions that can account for realistic local and long distance movement of seeds have been used instead (Clark et al. 1998).

Fecundity Estimation

Individual tree fecundity estimates in closed forest tree canopies are rare (Clark et al. 2004). Visual estimates of tree fecundity from crown observations have been shown to be inaccurate in tropical trees (Chapman et al. 1992). However, individual fecundity estimation is possible in *Jacaranda copaia* because this species produces seeds in large woody capsules that are dropped from the crown after seeds are released. These capsules persist in the soil for months after falling from the canopy. Individual tree fecundities were estimated by establishing transects beneath the majority of reproductive sized (≥ 20 cm dbh, N=188) *Jacaranda copaia* individuals and counting the number of seed capsules produced by each tree for both years of the study (details are provided in Jones and Comita, Chapter 3). Numbers of seeds produced per mature capsule are on the order of approximately 500 and are relatively constant (S. J. Wright, personal communication).

Inverse modeling

Inverse modeling simultaneously estimates fecundity and dispersal patterns without the direct observation of individual tree seed production and measurement of the distances that individual seeds move. (Ribbens, et al. 1994, Clark et al. 1998, 1999, 2004, Dalling et al. 2001). These models use tree locations, tree diameters, seed trap locations, and seed trap counts to parameterize spatially explicit models of seed dispersal. The models estimate annual seed deposition to any location within the study area as a function of a structural dispersal kernel scaled to the fecundity of individual trees. In these models fecundity is assumed to scale linearly with basal area.

We used inverse modeling methods to estimate seed shadows for *Jacaranda copaia* using counts of all seeds falling into seed traps in 2000 and 2002. We performed the modeling using a program, FITSHADOW (available from H. Muller-Landau), which runs in the R operating environment (www.cran.r-project.org). The functions used for the dispersal kernel are given below:

Gaussian : $$f(x)=e^{-\frac{1}{2}\left(\frac{x}{\beta}\right)^2} \qquad (2)$$

exponential: $$f(x)=e^{-\beta x} \qquad (3)$$

2DT model (Clark 1998): $$f(x)=\frac{1}{2\pi\beta x}e^{\frac{-x}{\beta}} \qquad (4)$$

lognormal: $$f(x)=e^{\frac{-\frac{1}{2}\ln\left(\frac{x}{\beta}\right)^2}{\gamma}}\frac{1}{x} \qquad (5)$$

β and γ and are free parameters. Shape and scale parameters were fit assuming negative binomially distributed error, where k is the over-dispersion parameter. To examine the effect that variation in fecundity has on inverse model fits, we estimated crown area and fecundity (total capsules produced) for individual trees in the field and compared the inverse model fits using these estimates to fits done using basal area.

Model Selection

The best-fit inverse model for each year was selected based upon information theoretic methods using Akaike's Information Criterion (AIC):

$$AIC=-2\log(L(\hat{\theta}\mid y))+2K \qquad (6)$$

Where $\log(L(\hat{\theta}\mid y)$ is the log-likelihood of the estimated parameters given the data and K is the number of estimated free parameters in the model. AIC differences (Burnham and Anderson 1998) are calculated as

$$\Delta_i=\mathrm{AIC}_i-\mathrm{AIC}_{min} \qquad (7)$$

Where AIC_i is the AIC value for model i, and AIC_{min} is the minimum AIC value in the set of R candidate models. To interpret relative differences among model likelihoods and their resultant AIC values, likelihoods are normalized to be a set of positive Akaike weights:

$$w_i = \frac{\exp(-\frac{1}{2}\Delta_i)}{\sum_{r=1}^{R}\exp(-\frac{1}{2}\Delta_i)} \tag{8}$$

w_i is the relative weight of support in favor of model i as the best model among the set of R models evaluated (Burnham and Anderson 1997, Johnson and Oldham 2004). Weights > 0.90 are considered strong support of the model (Burnham and Anderson 1998). The ratio between Akaike weights for two models can be interpreted as an evidence ratio for support for one model over the other.

We compared the distance of a genotyped seed to the nearest potential seed parent to determine the degree of seed shadow overlap and examine the effect that the nearest tree can have on inverse modeling results and fits. We also directly compared dbh to total capsules to examine the relationship between dbh and fecundity.

Comparing genetically determined distances and fits to inverse model predictions

We compared the proportion of seeds observed at each 10 m interval determined using the genetic method to the proportion of seeds predicted by fitted inverse models to fall within each 10 m interval up to a distance of 1000 m. We also contrasted observed and expected seeds distances ≤ 100m and > 100 m. The finite integrals of each dispersal kernel within 10 m intervals (normalized across 1000m) were compared to the directly measured fraction of seeds in each distance class. We calculated two goodness-of-fit statistics based upon observed and expected data: the slope of the relationship between predicted finite integral between 10 m distances classes and observed fraction of seeds at each 10m distance interval, and a weighted R^2:

$$R^2 = 1 - \frac{\sum_{i=1}^{N}(obs_i - \exp_i)^2}{\sum_{i=1}^{N}(obs_i - o\bar{b}s)^2}$$

where obs_i is the observed proportional of genetically measured seed rain in distance class i, exp_i is the model prediction at distance class i, $\overline{obs_i}$ is the mean observed seed rain across all i distance classes, and N is the number of distance intervals. This is an index of the proportion of variance explained by the model relative to that explained by the mean. The index describes the level of agreement between the model and data in both trend and location, in that it relates the degree of scatter about a line with slope = 1. Unlike the squared correlation coefficient, r^2, this index is not bounded between 0 and 1. The index can be negative when the mean of the observed data better describes the seed rain data than the model, indicating a poor model fit to the data (Clark et al. 1998). Slopes of the predicted vs. observed relationship < 1 indicate that the model produces a biased overestimate, while slopes > 1 indicate a biased underestimate.

RESULTS

Inverse model fits and model selection

Among the inverse models fitted to seed trap data, the best fits for both years were obtained from lognormal distributions (Table 1). Gaussian and exponential models, two models commonly used to fit seed dispersal curves, performed markedly worse than the lognormal. A commonly used model with a fat-tail, the 2DT model, (Clark et al. 1999) fit the data better than the Gaussian and exponential models, but did not perform as well as did the lognormal distribution. The evidence ratios in favor of the lognormal compared to the next best fit model, the 2DT model, were 39.25 in 2000 and 5.63E+5 in 2002, indicating strong support for the lognormal in both years.

Comparison of inverse model fits to observed dispersal patterns

We compared the proportion of seeds deposited in 10 m distance intervals predicted by the best-fit inverse model (lognormal) to the observed proportion of seeds in the same interval as measured genetically in each year. The observed proportion of seeds at each distance interval was different from the inverse model predictions in both years (D=0.75, $P < 0.00001$ in 2000 and D=0.61, $P < 0.00001$ in 2002, Kolmogorov-Smirnov test). Slopes of the relationship between observed and expected seeds show that certain portions of the inversely modeled curve, namely local and long distance dispersal, show different patterns of bias (Table 3). The proportions of seeds arriving at all dispersal distances < 100m were overestimated and the fits were poor (Table 3). For distances > 100 m the fits were better in 2000, but not in 2002. In both years the inverse model produced an underestimate of the fraction of seeds moving distance > 100 m as evidenced by slopes > 1. These patterns held even when more realistic estimates of fecundity (crown area, number of capsules) were used in the inverse model fits (Table 3.)

Role of fecundity variation in inverse modeling

The choice of the independent variable on which to base the scale parameter in the inverse model had a large effect on the fit of the inverse models to the data. When we used the lognormal distribution, the fits to data were best when we used individual tree estimates of fecundity, such as the total number of capsules produced, rather than basal area (Table 2).

Crown area of individual trees also improved the fit of the model to data. In all cases, using estimates of crown area or capsule production in place of basal area greatly improved the fit. For example, in 2002 the fit improved from an r^2 of 0.14 to an r^2 of 0.73 for the lognormal model when capsule production was used in place of basal area (Table 2).

Because most inverse models use basal area of individual trees to estimate reproductive output, we regressed capsule production on basal area (Figure 3). A weak correlation exists between these two variables (total capsules = 11.49+0.01(basal area), $r^2 = 0.07$; total capsules = 21.98+0.006(basal area), $r^2 = 0.02$ in 2000 and 2002, respectively). Correlations between crown area and capsule production are stronger (total capsules = -0.29+ 0.98(crown area m^2), $r^2 = 0.55$; and total capsules= 10.53 + 0.12(crown area m^2) $r^2 = 0.10$ in 2000 and 2002, data not shown). Thus, individual variation in capsule production in this species is less related to basal area of individual trees than it is to crown area. We explore several other causes of this variation, including the impact of neighborhood conspecific relatedness and heterospecific size and crowding on individual fecundity in another study (Jones and Hubbell, unpublished ms).

DISCUSSION

When inverse modeling results in *Jacaranda* were compared to direct measures of dispersal, we found that predictions made by inverse modeling were systematically biased and fit our directly measured dispersal data poorly. The best-fit dispersal kernel, the lognormal, predicts that on average, less than 0.08% and 0.13% of *Jacaranda copaia* seeds in 2000 and 2002, respectively, would move distances > 100 m. However, our genetic study of wind-dispersed seeds revealed that > 20% of seeds moved distances > 100m in both years (Hubbell and Jones, unpublished ms). Inverse models were biased toward overestimating levels of local dispersal at the expense of underestimating the frequency of dispersal at distances > 100 m (Table 3). A major reason that inverse methods fail to describe the tail of the curve may be their inability to distinguish lower frequency long distance dispersal events from high frequency local dispersal events (Figure 2).

Without the use of unique markers (genetic or not), long distance dispersal events can be partially masked if seeds moving long distances happen to fall close to other reproductive individuals. *Jacaranda* has relatively low density on the FDP (< 5 reproductive-sized individuals ha^{-1}). Most tropical species exist in low densities, compared to their temperate counterparts. Our results suggest that the assessment of long distance dispersal, at least using inverse modeling techniques, will be even more difficult in high density tropical species or in temperate populations (where densities are typically higher than in the tropics) due to greater seed shadow overlap in such species.

Mean wind speeds may be lognormally distributed (Greene and Johnson 1995). Therefore, from a deterministic perspective, there is a biological reason to expect that the lognormal may fit the data better than other pdfs. In a separate analysis, we found that a mixed model, consisting of a local Gaussain curve and a long distance, negative exponential tail, fit the directly measured dispersal distances in *J. copaia* much better than any other single distribution model (Jones and Hubbell, Chapter 2). We interpreted this result as potential evidence of two or more distinct physical processes that can govern local and long distance dispersal. Seeds that are uplifted by thermals rising over the canopy can carry seeds long distances and as a result, seed densities at long distances are better fit by a flatter negative exponential distribution. In contrast, seeds that fail to be uplifted may remain relatively close to the tree and follow a Guassian curve comparable to diffusion equations (Jones and Hubbell, Chapter 2, Nathan et al. 2003). Thus, inverse modeling techniques may not be able to accurately predict both short and long distance dispersal of individual trees since a single-dispersal kernel may not adequately describe different underlying physical mechanisms responsible for the different curves.

Several lines of evidence suggest that the potential for long distance dispersal in *Jacaranda copaia* is great. The maximum average wind speed during the period when seeds are dispersed in *Jacaranda* (August-December) is half the maximum average wind speed of the period when all other wind-dispersed tree seeds on the FDP are released (February-May) (Muller-Landau 2001). Nevertheless, *Jacaranda* is one of the most effective dispersers on the FDP. It is one of only two species on the FDP that has successfully dispersed seeds to each of the 200 seed traps over a 15 year period (S. J. Wright, personal communication). This suggests that other mechanisms besides maximum wind speed, such as the vertical movement of seeds in thermals, may play an important role in determining dispersal distances. Hundreds of seeds were observed rising vertically in conditions of relatively little horizontal wind to heights > 25 m above the canopy before moving horizontally (F. A. Jones, personal observation).

Fecundity variation

We found that a failure to incorporate within-size class variation in fecundity in the inverse models resulted in poorer fits than when direct estimates of fecundity were incorporated into the model. The determination and estimation of total plant fecundity can be problematic for large trees in closed canopy forests (Clark, et al. 2004). Thus, a variety of variables have been used as predictors for the realized seed output for individual plants. Greene and Johnson (1994) found that seed production is inversely correlated with the mean seed mass as a power law function and that tree size, as measured by basal area, is directly proportional to seed production in trees. Itoh et al. (2003) found that the fruiting probability of *Dryobalanops aromatica* in a Bornean forest plot increased with DBH. Most models of individual plant fecundity and critical reproductive size are allometric models (Thomas 1996, Wright et al. 2004) with some measure of tree size predicting annual seed and fruit production. Inverse modeling makes this assumption as well. The scale parameter, α (equation 1) scales the probability density function to obtain the seed density at the source ($x=0$). Parameter α is multiplied by basal area in most inverse models to estimate the total expected number of seeds produced by each individual tree (i.e. individual fecundity). (Ribbens et al. 1994, Clark et al. 1998, Clark et al. 1999).

Fecundity and reproductive status can vary greatly among trees and the assumption that fecundity is linearly related to basal area is not generally true. Moreover, variation in fecundity within size classes is not captured by the error probability term in equation 1. Rather, the negative binomial error term is conditioned on seed trap count data alone. Fecundity in this model is treated as a strictly deterministic process described exactly by the parameter relationship in equation 1. It is not. Typically, as it is easily obtained in the field, the measure of tree size used is diameter at breast height (DBH) then converted to basal area (BA). Although basal area may be a good predictor of fecundity for some species, we found a poor relationship between basal area and fecundity in *Jacaranda copaia*. In addition, we found that crown area was a better predictor of seed production than basal area. Our results suggest that the assumed linear relationship between basal area and fecundity may need to be examined on a species by species basis. Furthermore, failure to recognize this variation may result in poor predictions of dispersal patterns.

Clark et al. (2004) found that inverse modeling tends to overestimate fecundity due to the inflexibility of applying a single linear fecundity parameter across all sizes of trees. Uncertainty is introduced at the level of the population rather than at the individual tree level. This results in high levels of process error in the model. Clark et al. (2004) have found, consistent with our findings, that incorporating the reproductive status of individual trees in addition to seed trap data can provide more realistic estimates of individual fecundity and better fits to data (Clark et al. 2004).

Variation in fecundity has important implications for seed dispersal research and for examining the role of dispersal limitation in tropical forest ecosystems. In some species, such as *Jacaranda*, fecund individuals may disperse a larger absolute number of seeds to long distances. However, population level dispersal limitation may be increased by limited and variable numbers of seeds produced within and among size classes of individuals within and among years. Individual fecundity variation increases the degree of dispersal limitation at the population level, but it also means that dispersal limitation can vary across space and time. Thus, the degree of dispersal limitation affecting individuals and populations is not a constant but is variable. Theoretical models have explained the role of variable reproduction of species within communities in relation to the maintenance of diversity (Chesson and Warner 1981). However, little attention has been paid to individual variation in reproductive output within populations of species and its potential role in the maintenance of species diversity. This variation also has important evolutionary implications, as increased variation in reproductive output and status directly lowers effective population size (Silverton and Lovett Doust 1991). That we found a large fraction of reproductive sized individuals were in fact not reproductive in each year, suggests that the effective population size of *Jacaranda* may be much lower than the census size.

Jacaranda is one of the most effective dispersers on BCI. Therefore, at first glance, one might expect *Jacaranda* to be among the least dispersal-limited species within the FDP.

Dispersal limitation on the population level, however, can be overcome when dispersal capacity increases, when individual tree fecundity increases, or when the density of reproductive trees increases (Nathan and Muller-Landau 2000, Wright 2002). In *Jacaranda,* high variation in fecundity lowers the effective numbers of adults in the population and therefore may increase dispersal limitation. As we have shown, individual seeds are capable of moving large distances. However, because of variation in fecundity and the effective number of reproductive trees, variation in fecundity may play a greater role in dispersal limitation in this species than limited dispersability of seeds.

Despite the limitations of inverse modeling methods, these techniques are at the moment more tractable than our genetic analyses, which are more costly in time and money to accomplish. However, for studies where the long distance dispersal is of particular importance, inverse methods may not accurately describe the magnitude and frequency of these events. The combination of inverse modeling techniques or Bayesian hierarchical approaches (Clark et al. 2003, Clark et al. 2004) and the direct genetic approach deserves further development. Such an approach can utilize multiple sources of information better than we have. For example, the number of seeds captured in a trap but that were not genotyped is potentially useful information that was not fully used in this study. Also, environmental variation (humidity, wind speed and direction, etc) could also be incorporated, in an analogous way to mechanistic models, into such an analysis. The application of Bayesian methods that incorporate additional information on seed dispersal patterns to these questions should be very fruitful avenue for future research and could potentially resolve some of the drawbacks of each method. Collectively, a combination of techniques could potentially shed a great deal of insight into the demographic role of long distance dispersal events within populations their contributions to the origin and maintenance of biological diversity.

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Table 3.1. Parameter estimates for four different dispersal kernels fit to two years of data for *Jacaranda copaia* in the 50 Forest Dynamics Plot on Barro Colorado Island, Panama. AIC is Akaike's information criterion statistic, Δ_i relative difference between model i and the best-fit model, w_i is the Akaike weight, and R^2 goodness-of-fit statistic.

Model	Year	α	β	γ	k	AIC	Δ_i	w_i	R^2
Gaussian	2000	1.07E-05	49.81	-	0.39	1403.44	94.94	2.36E-21	0.04
Exponential	2000	7.72E-05	0.050	-	0.67	1331.44	22.94	1.01E-05	0.16
2DT	2000	0.1599	33.01	-	0.71	1315.84	7.34	0.024	0.25
Lognormal	**2000**	**1.51E-3**	**1.57**	**2.35**	**0.73**	**1308.5**	**0**	**0.975**	**0.29**
Gaussian	2002	4.94E-5	35.43	-	0.55	1818.54	58.04	2.49E-13	0.02
Exponential	2002	1.50E-4	0.05	-	0.63	1786.86	26.36	1.88E-06	0.07
2DT	2002	0.434	40.94	-	0.63	1782.38	21.88	1.77E-05	0.20
Lognormal	**2002**	**3.86E-3**	**1.57**	**2.58**	**0.69**	**1760.5**	**0**	**0.999**	**0.17**

Table 3.2. Inverse model parameters for two years of seed rain data for *Jacaranda copaia* with different measures of seed production from a population on the Forest Dynamics Plot on Barro Colorado Island. *β* and *γ* are the parameters in equation 5 and *k* is the dispersion parameter of the negative binomial distribution.

Year	**Fecundity**	**α**	*β*	*γ*	***k***	**-log likelihood**	**R^2**
2000	Basal area	1.51E-3	1.57	2.35	0.73	651.25	0.29
2000	Crown area	1.56	7.68	1.20	0.83	639.86	0.38
2000	**Total Capsules**	**12.27**	**0.856**	**2.71**	**0.93**	**631.50**	**0.53**
2002	Basal area	3.86E-3	1.57	2.58	0.65	877.25	0.14
2002	Crown area	3.14	2.08	2.37	0.68	879.61	0.15
2002	**Total Capsules**	**93.20**	**0.053**	**5.56**	**1.26**	**816.11**	**0.72**

Table 3.3. The slope of the relationship between predicted in parentheses and observed and weighted R^2 goodness-of-fit measures for observed proportion of distances that genetically determined seed and predictions made by fitting lognormal curve to the genetic data

	Total 2000	**Total 2002**	**≤100 2000**	**≤100 2002**	**>100 2000**	**>100 2002**
Basal area	0.2849 (0.202)	0.1480 (0.114)	0.2024 (-5.050)	0.0585 (-11.89)	7.4818 (0.3746)	21.113 (-0.252)
Crown area	0.5144 (0.072)	0.1706 (-3.893)	0.3969 (-0.791)	0.0714 (-10.07)	2.080 (0.4235)	11.662 (-0.196)
Total capsules	0.2613 (-2.60)	0.1186 (-6.086)	0.1845 (-5.972)	0.0420 (-15.04)	13.419 (0.3614)	121.23 (-0.310)

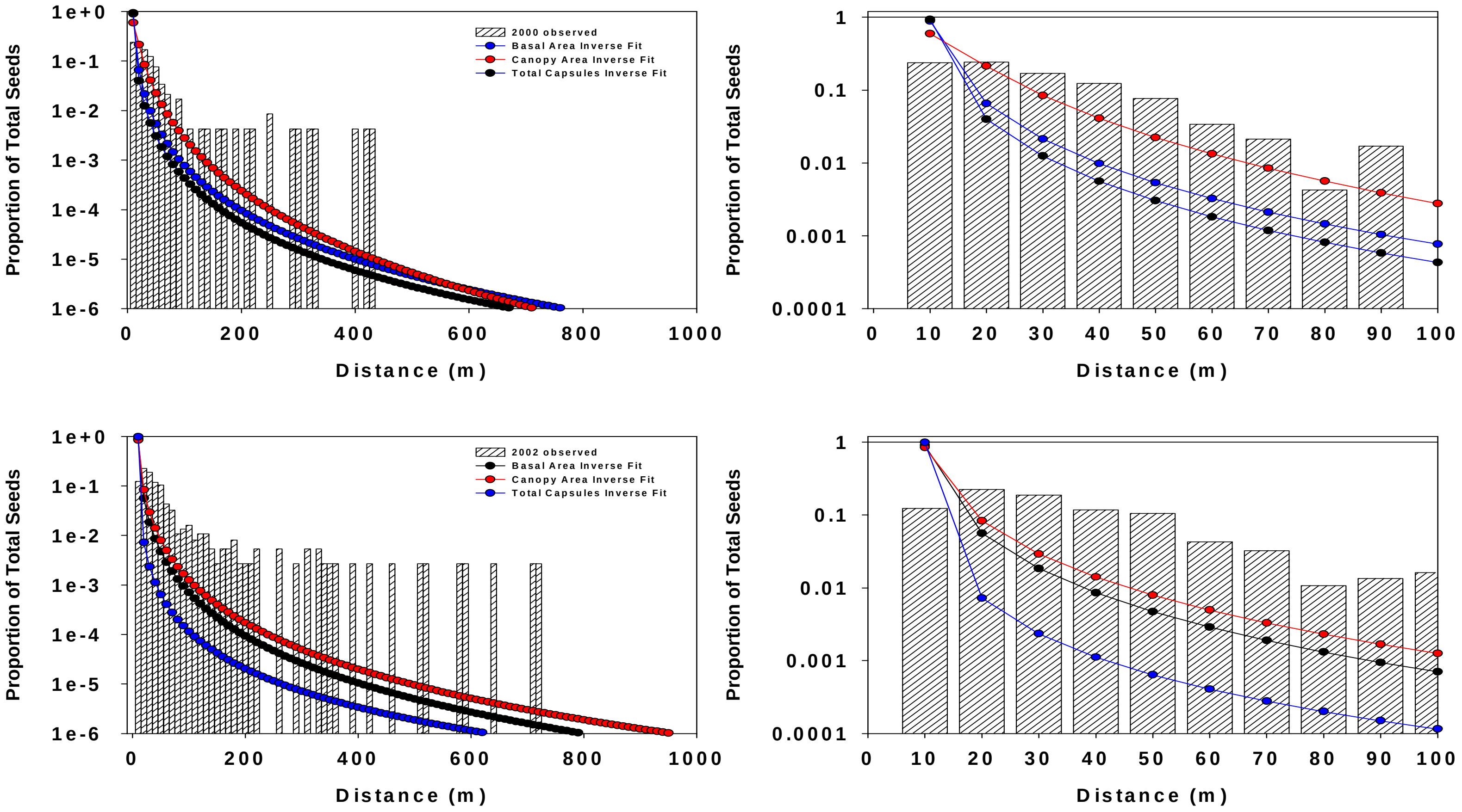

Figure 3.1 Local and long distance inverse model fits with observed data and best-fit single component models for direct curve for 2000 and 2002 seed fall data.

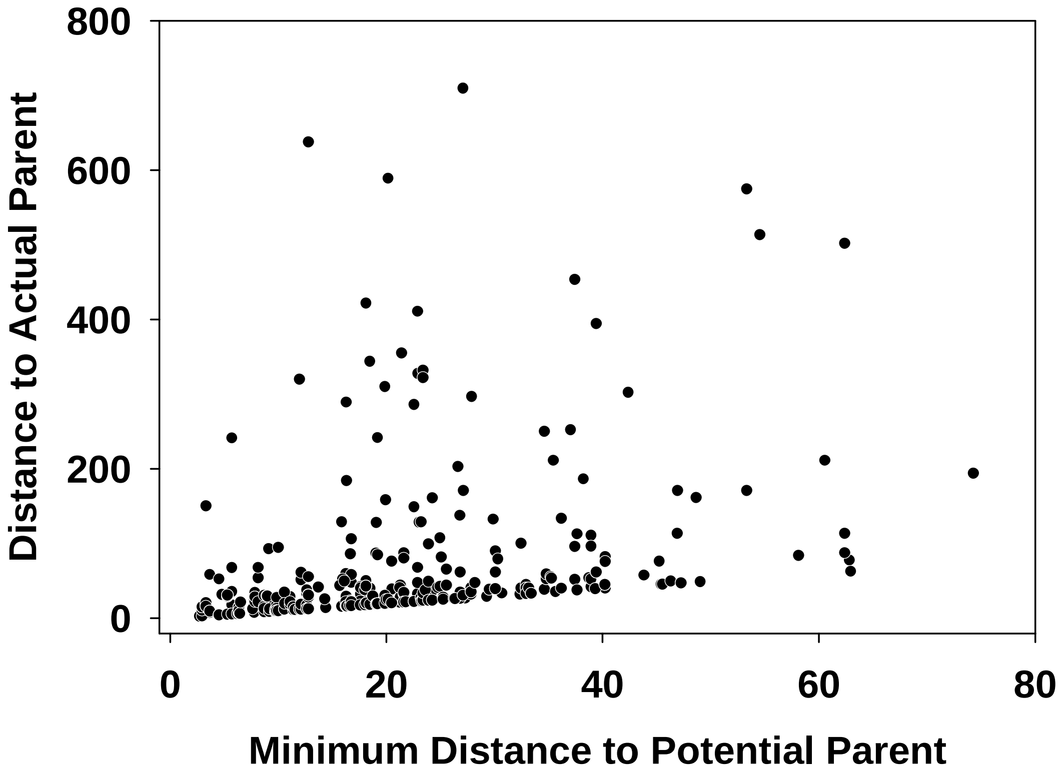

Figure 3.2. The relationship between minimum distance from potential parent to captured seed and the genetically determined distance for that seed for two years of *Jacaranda copaia* seed fall on the 50-ha Forest Dynamics Plot, Barro Colorado Island, Panama.

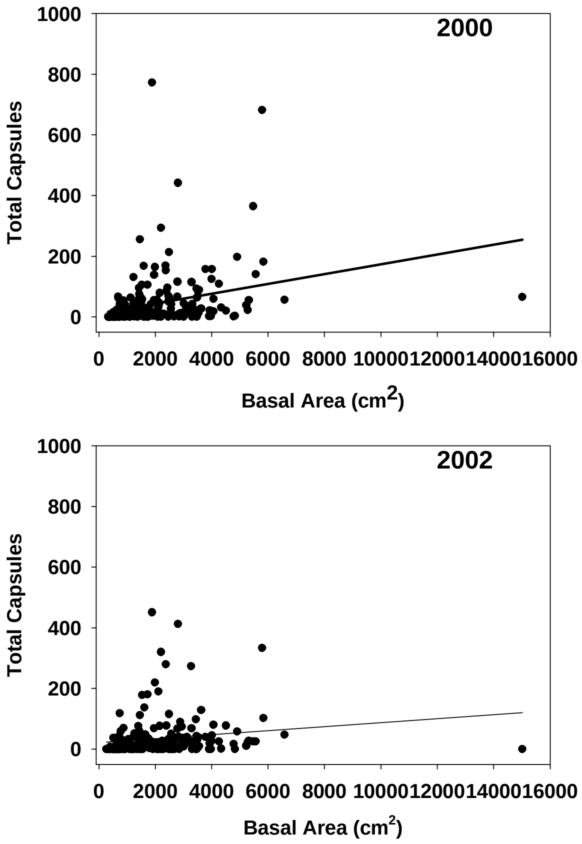

Figure 3.3. Relationship between diameter and breast height and total capsule production for *Jacaranda copaia* measured in two years from the 50 ha Forest Dynamics Plot, Barro Colorado Island.

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CHAPTER 4

INDIVIDUAL AND NEIGHBORHOOD DETERMINANTS OF FECUNDITY IN A NEOTROPICAL TREE, *JACARANDA COPAIA* (BIGNONIACEAE)[1]

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[1] Jones, F.A and L.S. Comita. To be submitted to *Journal of Ecology*

ABSTRACT

We examined individual and neighborhood factors determining focal plant fecundity in a population of the Neotropical tree *Jacaranda copaia* within the 50 ha forest dynamics plot on Barro Colorado Island, Panama. Fecundity estimates were made for the majority of reproductive-sized trees within the plot across three years. We used non-linear regression and model selection techniques to evaluate hypotheses related to individual, conspecific neighborhood, heterospecific neighborhood, and habitat variables that determine reproductive output in *J. copaia*. We found that canopy area, crown area, conspecific density and fecundity, and habitat variables influence fecundity in all three years of the study. Other variables, including heterospecific density, liana presence in the crown, and neighborhood species richness had effects in at least one year, but the effects were not sufficiently strong in other years to be included in the most parsimonious models. Genetic relatedness, as measured using microsatellite genetic markers, did not exert a negative effect on reproductive patterns. Our results suggest that increased canopy area, density of reproductive conspecific trees, and habitat associations can increase reproductive output in this species. However, negative density dependence at other life history stages may mitigate the positive effect of conspecific density on increased reproductive output.

Keywords: neighborhood effects, density dependence, genetic relatedness, model selection, maximum likelihood parameter estimation, spatial aggregation, tropical forest, habitat effects.

INTRODUCTION

Recent studies of the mechanisms maintaining tropical forest diversity have focused on the effects of the local biotic neighborhood on focal plant fitness, specifically how the densities of conspecific and heterospecific neighbors influence the survival and growth of saplings and adult trees (Hubbell et al 2001, Peters 2003, Uriarte et al. 2004). These studies have found that focal individuals that are surrounded by a high density of conspecific neighbors tend to exhibit lower growth in diameter and higher mortality compared to individuals surrounded by heterospecific species, consistent with previous studies that have found evidence of negative density dependence at various life stages (Webb and Peart 1999, Harms et al. 2001, Uriarte et al. 2004, Hubbell et al. 2001, Hille-Ris Lambers, et al. 2003, Brundell and Peart 2004). Thus, negative density dependence has been proposed to be a strong regulator of species diversity in tropical communities (Wright 2002), and it is frequently assumed that plants growing at high conspecific densities have lowered fitness.

However, individual fecundity is also a key component of fitness, and density of conspecific neighbors can positively affect an individual's fecundity. Fruit set is frequently pollen limited in many animal pollinated species. Isolated individuals may show reduced fecundity relative to individuals growing in higher densities, and seed set can be negatively correlated with distance to nearest conspecific adult, particularly when pollinators may not move long distances (Ghazoul et al .1998). Pollen limitation may be a primary cause of low fecundity in self-incompatible perennial plants (Burd 1994, Morales and Galetto 2003). Many tropical trees are self-incompatible, and therefore their fecundity may be increased by the presence of conspecific neighbors. However, if neighbors are too closely related in species with self-incompatibility mechanisms, successful seed set may be lowered if mating occurs with related individuals (Wilcock and Neiland 2002). Thus, both the overall density of conspecific neighbors and the genetic relatedness of neighbors could have opposing effects on individual fecundity.

In a previous study, we found high levels of individual variation in reproductive output in the tropical tree species, *J. copaia* within the 50 Forest Dynamics Plot (FDP) on Barro Colorado Island (BCI). (Jones and Hubbell, unpublished ms). In the present study, we ask whether individual tree characteristics, along with the local biotic and abiotic neighborhood, can explain the observed within population variation in fecundity in *J. copaia* on the FDP. Specifically, we examine how *J. copaia* crown size, fecundity of neighboring conspecifics, genetic relatedness of neighboring conspecifics, diversity of neighboring heterospecifics, size of neighboring heterospecifics, local neighborhood diversity, liana presence, and habitat associations may affect reproductive output of seeds in *J. copaia* individuals.

Hypotheses

We predicted that individual fruit production would increase as a function of 1) increasing crown area of trees; 2) liana absence in the tree crown; 3) increased density and fecundity of neighboring *J. copaia* trees; 4) decreased genetic relatedness within a neighborhood; 5) decreased density and size of heterospecific neighbors; and 6) habitat associations. We further hypothesized that population-wide fruit production would be correlated with photosynthetically active radiation within a year. We adopted a multiple working hypothesis approach and used maximum likelihood parameter estimation in concert with model selection and information theoretic methods to evaluate hypotheses of individual and neighborhood patterns of fecundity within and among the *J. copaia* population on the FDP on BCI (Hilborn and Mangel 1997, Burnham and Anderson 1998, Johnson and Omland 2003).

METHODS

Site Description

We conducted our research within the 50-ha Forest Dynamics Plot (FDP) of Barro Colorado Island, Panama (BCI) (Hubbell and Foster 1983). The 50-ha FDP on BCI was established in 1980 and consists of a standing number of approximately 215,000 explicitly mapped stems > 1 cm diameter at breast height (DBH) of approximately 300 species. The FDP has been recensused 4 times since 1980, with the most recent census completed in 2000. We used information from the 2000 census to locate reproductive *J. copaia* adults within the 50-ha FDP.

Species Description

Jacaranda copaia is a large, wind-dispersed tree that colonizes large tree- fall gaps (Brokaw 1985) and is among the most light demanding species within the FDP (Wright et al. 2003). *Jacaranda copaia* ranges from Bolivia to Belize and is a common pioneer on BCI and across Panama. *Jacaranda copaia* produces large numbers of blue/violet flowers. Pollination of *J. copaia* likely occurs via large bees, and a paternity analysis has shown that pollen can regularly move distances greater than 500m (FAJ, unpublished data). *Jacaranda copaia* shows a tendency to flower and fruit synchronously in alternate years (Figure 1) with alternating periods of low and high seed production. Mating system studies using genetic markers have shown that *J. copaia* is a predominantly outcrossed species and likely self-incompatible (James *et al.* 1998).

Foster (1982) lists the minimum reproductive size of *J. copaia* as 20 cm dbh. Wright et al. (2003) found that the critical reproductive size threshold in *J. copaia* was 36.7 cm dbh (the inflection point of a logistic regression of reproductive/non reproductive individuals and dbh). In 2000, 205 potentially reproductive adult *J. copaia* (>20 cm dbh) were present in the BCI FDP.

The overall density of reproductive *J. copaia* adults across the plot was 4.1 individuals ha^{-1}. Individuals tend to be highly clumped at most scales, potentially due to the fact that the *J. copaia* requires high light environments found only within the largest gaps, which are rare within the BCI forest (Hubbell and Foster 1986).

Jacaranda copaia flowers at the peak of the dry season on BCI. Seeds of *J. copaia* are produced in large woody capsules with two locules. Each locule produces approximately 250 seeds (S. J. Wright, personal communication). Seed dispersal occurs in late August and September on BCI when capsules dehisce and seeds are released (Figure 2). After capsule senescence, dehiscence, and seed release, the dry woody capsules fall to the ground beneath the tree.

Seeds of *J. copaia* are wind-dispersed. Previous work has shown that the wind-dispersed seeds of *J. copaia* are among the most well dispersed seeds within the FDP (Dalling *et al*. 2002). A study of seed movement distances using genetic markers developed for this species (Jones and Hubbell 2003) has shown > 20% of seeds analyzed moved distances greater than 100m (Jones and Hubbell, Chapter 2).

Fecundity Estimation

The dehiscence of mature, immature, and predated woody capsules and the persistence of these capsules on the forest floor following seed release makes tractable the direct estimation of total capsule production for individual *J. copaia* trees. We established transects in each cardinal direction (North, South, East, and West) beneath the canopy each of 188 adult *J. copaia* individuals in November and December of 2000, 2002 and 2003 Seed production in 2001 was low, with only 184 seeds found in 200 seed traps in the FDP. Therefore fecundity estimates were not collected in 2001 (Figure 2).

For each tree, a transect extended from the base of the trunk to the edge of the tree's canopy in each direction. We calculated crown area of each tree by using the length of each transect to determine the area of an ellipse along the two main axes. At 1m intervals along each transect, a 0.5-m^2 PVC frame was laid on the ground and the total number of mature dehisced capsules, immature non-dehisced capsules, galled capsules infected with wasp seed predators, and capsules infected with bruchid beetle larvae were counted within the frame. Total capsule production was determined from the number of mature, immature, and predated capsules counted beneath each tree. Neighborhood analyses of seed predation and immature capsule production are presented in a separate paper (Jones et. al, in preparation). Because lianas shade portions of the canopy and can reduce tree fecundity (Wright et. al 2004), we also recorded presence or absence of large lianas in the crown of each tree.

PAR

Photosynthetically active radiation (PAR) is measured hourly, maximum, and minimum from a 40m meterological tower on BCI. PAR is measured every 15 minutes using a LiCor 190SB PAR sensor. We used the mean of the maximum daily PAR reading across the months of January to August, the period of flowering and fruit development in *J. copaia* to examine the effect of maximum yearly PAR on capsule and seed production among years. Data is available from the Smithsonian Tropical Research Institute's Terrestrial Environmental Sciences Program (www.stri.org/tesp).

Genetic Relatedness

We determined pairwise genetic relatedness among reproductive sized adults at six microsatellite loci developed for *J. copaia* (JACC2, JACC9, JACC 18, JACC21, JACC22, and JACC31, Jones and Hubbell 2003, Jones and Hubbell, unpublished ms.). Technical details on microsatellite development, primers, DNA extraction, thermocycling conditions, genotyping, and genetic diversity are given in Jones and Hubbell (2003) and Jones and Hubbell (unpublished ms). Genetic relatedness between pairs of individual adult trees was calculated according to the pairwise genetic relatedness measure of Queller and Goodnight (1989) using the KINSHIP 2.0 program (Queller and Goodnight 2001). Pair wise relatedness values are bounded by -1.0 and 1.0. Positive relatedness values approaching 1.0 indicate two individuals are more related than expected at random (relatedness = 0.0), while negative values approaching -1.0 mean that individuals are less related than expected at random.

Neighborhood indices

We examined the effect of the demographic neighborhood (Hubbell 1979) on fecundity and total capsule production across three years in *J. copaia*. We calculated conspecific neighborhood indices for focal plants (*sensu* Uriarte et al. 2004) for heterospecific size and density, conspecific fecundity, and conspecific genetic relatedness. We used a neighborhood index of conspecific fecundity (Fecundity Neighborhood Index, FNI) for all focal reproductive sized trees $i = 1 \ldots S$ surrounded by $j = 1 \ldots n$, neighborhood reproductive-sized *J. copaia* trees within a 100m radius:

$$FNI_i = \beta_{NFI} \sum_{j=1}^{n_i} \frac{totalcaps_j^a}{dist_{ij}^b} \qquad (1)$$

where *totalcaps*$_j$ is the total capsule production for tree *j*, *distance*$_{ij}$ is the Euclidean distance between focal tree *i* and neighborhood tree *j*. β_{NFI} ,*a* and *b* are fitted parameters.

A genetic relatedness neighborhood index (GNI) around each focal tree *i* was determined from an analysis of pair wise genetic relatedness, r_{ij} between tree *i* and neighboring *J. copaia* tree *j* using Queller and Goodnight's (1989) index of relatedness. We calculated a genetic neighborhood index, *GNI*,:

$$GNI_i = \beta_{GNI} \sum_{j=1}^{n_i} \frac{(r_{ij}+1)^c}{dist_{ij}^d} \tag{2}$$

for all trees within a 100m radius of focal tree *i*. β_{GNI}, *c,* and *d* are fitted parameters. The index of relatedness was adjusted to be a positive number (r_{ij}+1) to allow for exponents < 1.

Heterospecific species neighborhood variables were also included in the analysis. Species diversity was calculated as the number of species within a 50 m radius of the focal tree, *i*. The effect of the size of neighboring heterospecific plants and their distance was calculated as

$$HNI_i = \beta_{HNI} \sum_{j=1}^{n_i} \frac{basalarea_{ij}^e}{dist_{ij}^f} \tag{3}$$

where *basalarea*$_j$ is the basal area of neighborhood tree *j*, *dist*$_{ij}$ is the distance from neighbor to focal tree and β_{HNI} ,*e* and *f* are fitted parameters.

Habitat variables

Harms (et al. 2001) identified seven microhabitats within the BCI plot: high plateau, low plateau, mixed forest, stream, swamp, young forest, and slope. Each 20x20m area of the plot was designated as one of the six identified habitats. Areas containing more than one habitat type were assigned to a mixed forest category. Species may show associations within specific habitats due to the differences in the levels of resources, pathogens, or predators or other reasons.

Jacaranda copaia shows a positive habitat associations with "low plateau" sites and a negative association with "high plateau" sites (Harms et al. 2001). This habitat association is reflected in the fact that most *J. copaia* individuals (130) are found at higher densities in low plateau sites (5.2 trees ha^{-1}), the most common habitat type on the plot, while 30 individuals were found in high plateau sites (4.4 trees ha^{-1}). We include the habitats in which individual *J. copaia* are found in the BCI population as categorical factors in our analyses below.

Model parameterization

We used a non-linear regression approach and assumed normally distributed error:

$$n\left[\log(\sigma)+\frac{1}{2}\log(2\pi)\right]+\sum_{i=1}^{n}\frac{(Observed_i-Expected_i)^2}{2\sigma^2} \qquad (4)$$

to calculate the likelihood of the data given the model. In each of the analyses, we first examined individual tree factors (canopy crown area, liana presence), conspecific neighborhood indices, heterospecific neighborhood indices, and habitat variables. All analyses were conducted within the R operating environment (cran.r-project.org). We used Nelder-Mead optimization iteratively until the values that maximized the likelihood converged upon global maxima.

Model Selection

We first parameterized the global model using all the candidate submodels. These included crown area, liana presence/absence, neighborhood fecundity index, genetic neighborhood relatedness, heterospecific relatedness, heterospecific diversity, and habitat classification. To evaluate goodness-of-fit of data for the subsets of submodels, while controlling for model complexity, we used a small sample AIC$_c$:

$$AIC_c = -2\log(L(\hat{\theta})) + 2K\left(\frac{n}{n-K-1}\right) \tag{5}$$

where n is the sample size and K is the number of free parameters (+1 for σ^2). AIC_c is the recommended index when the ratio of sample size to K parameters is < 40 (Burnham and Anderson 2002). Each variable was successively added to the model in the order they are listed above to achieve the full model. If addition of the variable did not improve the AIC_c, the variable was excluded from the model and the next variable was added. We normalized likelihood values according to Akaike weights, w_i.

$$w_i = \frac{\exp(-0.5\Delta_i)}{\sum_{r=1}^{R}\exp(-0.5\Delta_i)} \tag{6}$$

where Δ_i is the difference between the minimum AIC_c of R models considered and model i. Akaike weights provide a relative weight of evidence for each model. Akaike weights are interpreted as the probability that model i is the best model given the observed data and the set of candidate models (Burnham and Anderson 2002, Johnson and Omland 2004): Goodness-of-fit was further determined by r^2 of observed vs. predicted values to determine the measure of fit to relative trend of the data.

RESULTS

Fecundity variation among years

Total fecundity, as measured by total capsule production, was higher in 2000 than in 2002 or 2003. However because of increased seed predation in 2000, the total number of mature capsules produced in 2000 was lower than in 2002 (Figure 2) (Jones and Comita, unpublished ms). Total capsule production in each year was positively correlated with the average daily maximum PAR in each year (Figure 3).

The total number of trees that produced capsules was also highest in 2000, with 86% of trees producing at least one capsule. The percentage of reproductive trees was less in 2002 and 2003 with 68% and 69% of trees producing at least one capsule in each year, respectively. Sixty five percent of the trees that were reproductive in 2000 were also reproductive in 2002, 55% of those reproductive in 2002 were also reproductive in 2003. Twenty-three percent were reproductive in 2000 but not in 2002, 26% were reproductive in 2002 but not in 2003. Two percent that were reproductive in 2002 we re not reproductive in 2000 and 13 percent that were not reproductive in 2002 were reproductive in 2003. Ten percent were not reproductive in either 2000 or 2002 and 17% were not reproductive in 2002 or 2003. Fifty four percent of all trees were reproductive all years, while 6% were not reproductive in any year. Therefore, 40% of trees were periodically reproductive, i.e. they were not reproductive in at least one of the three years we examined.

Total capsule production ranged from 0 to 773 capsules tree^{-1} (47.62 tree^{-1} ± 95.10, mean ± SD) in 2000, 0 to 451 capsules tree^{-1} (35.89 ± 68.62) in 2002, and 0 to-566 capsules tree^{-1} in 2003 (21.97 ± 57.03). Overall capsule production was highest in 2000, when daily average maximum PAR was greatest and capsule production was lowest in 2002 when daily average maximum PAR was lowest (Figure 3).

Model Results

In each year of our study, canopy area had the strongest positive effect on capsule production and was included in the year's best-fit model. (Table 1-3, Table 4-6). Canopy area was strongly selected over the null model in each year of the study. Canopy area explained 55%, 9%, and 20% of the variation in fecundity in 2000, 2002, and 2003, respectively.

The effect of liana presence was included in the most parsimonious model in 2000, but not in 2002 and 2003. Liana presence had a negative effect on total capsule in all years, but the effect was only strong enough to be included in the final model only in 2000 (Tables 4-6).

Neighborhood fecundity had a strong effect in each year of our study and was included in the best-fit models for 2000, 2002, and 2003. The increased fecundity of conspecific neighbors had a positive effect on fecundity of the focal reproductive *J. copaia* in each year. Heterospecific neighborhood, as determined by the size and distance of neighboring trees, had an overall negative effect on capsule production each year as predicted. The effect was only strong enough in 2000 to be included in the most parsimonious model for that year. Species diversity in the neighborhood had a positive effect on total capsule fecundity in 2000.

Habitat effects were strong enough in each year to be included in the model for each year, although differences among habitat types were present among years in terms of their effect on reproduction.

DISCUSSION

High interannual variability in seed production is the rule, rather than the exception in woody plants (Herrera 1998). However, different forces may influence levels of reproduction within and among years. We found a pattern of increased capsule production with increased mean maximum daily PAR across the entire population of *J. copaia* (Figure 4). However, the relationship between capsule production and PAR is likely complex because of periodic reproduction in *J. copaia* (Figure 1). Light limitation due to increased cloud cover can decrease growth and reproduction in tropical trees (Graham et al. 2003, Wright and VanSchaik 1994, Wright et al. 1999). The degree to which fecundity in the previous year determines present year fecundity was not explored in this study, but aperiodic reproduction of *J. copaia* both across the population and within individual trees could be due to light limitation, water and nutrient limitation, or both.

Canopy area

We found strong evidence for the role of crown area in determining patterns of reproduction in *J. copaia* in each year of our study. Estimating individual fecundity and seed production in tree populations can be difficult. For most forest communities, the canopy is largely inaccessible (Clark et al. 2004) and visual estimates of fruit production from crown observations have been shown to be inaccurate, at least in tropical trees (Chapman et al. 1992). Most estimators of tree fruit and seed production have therefore been based upon allometric models (Thomas 1996, Wright et al. 2004) that assume a correlation between some measure of tree size, usually DBH or basal area and annual seed or fruit production or reproductive status. However, our results suggest that other factors, particularly the size of individual canopies, may be more important in determining reproductive output than basal area of the tree.

Liana load

We found a negative effect of liana presence on fecundity in each year of our study, but this variable was strong enough only in 2000 to be included in the final parsimonious model. Our results suggest that liana presence in the canopy can potentially reduce fecundity, but the degree of liana infestation may be more important in determining the strength of the effect than the presence or absence of lianas. However, quantifying the extent of liana infestation in the crown of a tree is nearly impossible from the ground, and therefore we were limited to recording only presence/absence data. The presence of lianas in the canopy has been previously shown to negatively affect the reproductive status of trees within the BCI forest, including *J. copaia* (Wright, et al. 2004b). Lianas can limit seed production primarily by the shading and reducing the amount of canopy area exposed to sunlight. Liana leaves can replace the leaves of the host plant on a one to one basis (Kira and Ogawaw 1971). Liana abundance has been hypothesized to be increasing in Neotropical forests due to increased concentrations in atmospheric CO_2 (Phillips, et al. 2002). Evidence from leaf production data collected over seventeen years suggests that liana abundance may be increasing on the BCI plot (Wright, et al. 2004a). However, decreased fecundity due to increased liana abundance in the canopy could be offset by increased tree fecundities, also due to increased CO_2 in the atmosphere (LaDeau and Clark 2001).

Habitat effects

We found an effect of habitat in each year that was strong enough to be included in all of our most parsimonious models. Plants may show differential fecundities in different habitats because of differing resources. Janzen (1975) found significant differences among habitats in reproductive output and of *Guazuma ulmifolia* in Guanacaste province, Costa Rica, where habitats were separated by as little as a few hundred meters. Itoh et al. (2003) in a study of fruiting in Malaysian forests showed significant association of fruiting in *Dryobalanops aromatica* with habitat variables such as elevation, slope and soil type. Although we also found significant effects of habitat types on fecundity, the effects of a given habitat was not consistent among years, suggesting that the habitat-fecundity relationship is more complex than originally predicted.

Neighborhood Effects

We found evidence for increased fecundity due to increases in neighborhood conspecific density and fecundity in all years of our study. Our results suggest that fruit production is spatially aggregated in *J. copaia* and that this effect is present and strong even when we controlled for the effects of habitat, neighborhood heterospecific density, liana presence, and neighborhood genetic relatedness. Itoh et al. (2003) found that fruiting was spatially aggregated above the level of individual spatial aggregation in *Dryobalanops aromatica* and that the probability of fruiting increased with conspecific density, perhaps due to a site or habitat effect. However, the role of pollinator limitation was not discussed and they did not control for the effects of habitat within their model as we have here.

We found a negative effect of heterospecific neighborhood density in each year of our study, however the effect was only strong enough in 2000 to be included in our final model. *Jacaranda copaia* has been shown to be an extremely light demanding species; juveniles require high light and large tree fall gaps to recruit into the understory. Our results suggest that this sensitivity to low light conditions may extend to adult stages. In their survey of adult *J. copaia* in 1996, Wright, et al. (2004) found no shaded, adult reproductive *J. copaia* adults indicating an extreme sensitivity of reproduction in *J. copaia* to shading. Analyses of aerial photographs of the canopy of the plot also indicate that *J. copaia*'s tree crowns are rarely shaded (S. Bohlman, personal communication).

Contrary to expectations, we did not find strong evidence that genetic relatedness within a neighborhood strongly influences reproductive patterns in *J. copaia*. Although the effect was not strong enough to be included in the final model, increasing genetic relatedness did show a negative trend in its effect on capsule production in each year. Although related *J. copaia* tend to occur within 100m of one another (FAJ, unpublished data), potentially negative effect of high densities of related individuals could be over come if pollinators regularly move pollen at larger scales than the scale of relatedness. In another study, we found that pollen movement at scales > 200 m from the parent plant was common (FAJ, unpublished data). Therefore, high densities of *J. copaia* in flower may, as a group, attract more pollinators to the group, thereby enhancing individual fitness.

Our results have implications for the spatial aggregation of species. Janzen-Connell theory predicts regularly spaced individuals in tropical forest systems (Janzen 1970, Connell 1971), yet the majority of studies have shown that most species in tropical forest systems are clumped at most spatial scales (Hubbell 1979, Condit, et al 2000). Several mechanisms have been proposed to be responsible for observed under-dispersion of rainforest species, including dispersal limitation (Tilman 1994, Hurtt and Pacala 1995), and habitat and resource specialization for soil, water, and light resources (Harms et al. 2001). Condit, et al. (2000) in an examination of spatial patterns of trees in four 25-52 ha forest dynamics plots in Panama, Malaysia, Ecuador, and India found that most species in these diverse forests show strikingly similar spatial patterns of spatial aggregation. Although these patterns could be explained by limited dispersal, an examination of dispersal syndrome of the species showed little correlation between levels of clumping and dispersal mechanisms. Our results suggest that an additional cause of spatial aggregation in tropical forest species could be due to positive density dependence of in fruit and seed production.

Plants growing in higher conspecific densities may have a larger number of potential mates and thus may produce greater numbers of offspring. The potential benefits of high adult densities in terms of fecundity, however, may be outweighed by negative effects at later stages. Even though more seeds may be produced in high-density areas, seeds, seedlings, and juveniles may suffer disproportionate mortality and decreased growth in areas of high adult density (Brundell and Peart 2004). However, our study dispels the notion that the effects of high conspecific density in tropical trees communities are only negative.

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Table 4.1. Model fits AIC_c values, AIC_c weights (w_i), number of parameters (K) and r^2 of observed vs. expected for the fecundity model for *Jacaranda copaia* capsule production in 2000 on Barro Colorado Island, Panama. See Table 4 for parameter values and model information

Model	**Variable added**	K	AIC_c	Δ_i	w_i	r^2
1	Null	2	2227.1	174.5677	1.1E-38	-
2	Can area	3	2077.75	25.21323	3.1E-06	0.554
3	Liana	4	2075.27	22.73201	1.1E-05	0.565
4	FNI	7	2066.82	14.28375	0.00073	0.598
5	GNI	10	2072.8	20.26044	3.7E-05	0.600
6	HNI	13	2067.48	14.94646	0.00052	0.625
7	Spp. Richness	14	2069.61	17.06923	0.00018	0.625
8	Habitat	21	2057.48	4.94164	0.07781	0.680
9	**Best**	**17**	**2052.54**	**0**	**0.9207**	**0.673**

Table 4.2. Model fits AIC_c values, AIC_c weights (w_i), number of parameters (K) and r^2 of observed vs. expected for the fecundity model for *Jacaranda copaia* capsule production in 2002 on Barro Colorado Island, Panama. See Table 5 for parameter values and model information

Model	**Variable added**	K	AIC_c	Δ_i	w_i	r^2
1	Null	2	2042	44.584	1.81E-10	-
2	Can area	3	2024.1	26.738	1.36E-06	0.099
3	Liana	4	2024.6	27.174	1.09E-06	0.102
4	FNI	7	2003.3	5.8819	0.045936	0.129
5	GNI	10	2005.4	8.0007	0.015924	0.131
6	HNI	13	2009.7	12.307	0.001849	0.136
7	Spp. Richness	14	2002.8	5.431	0.057551	0.137
8	Habitat	21	2006.5	9.142	0.009	0.155
9	**Best**	**14**	**1997.4**	**0**	**0.869737**	**0.326**

Table 4.3. Model fits AIC$_c$ values, AIC$_c$ weights (w_i), number of parameters (K) and r^2 of observed vs. expected for the fecundity model for *Jacaranda copaia* capsule production in 2003 on Barro Colorado Island, Panama. See Table 6 for parameter values and model information.

Model	**Variable added**	$\boldsymbol{K}$	**AIC$_c$**	$\boldsymbol{\Delta_i}$	$\boldsymbol{w_i}$	$\mathbf{r^2}$
1	Null	1	2088.8	54.914	9E-13	-
2	Can area	2	2045.1	11.256	0.0027	0.209
3	Liana	3	2046.1	12.174	0.0017	0.213
4	FNI	6	2036.4	2.4673	0.2203	0.214
5	GNI	9	2041.4	7.5624	0.0172	0.199
6	HNI	12	2047.6	13.668	0.0008	0.220
7	Spp. Richness	13	2049	15.091	0.0004	0.223
8	Habitat	20	2048.6	14.712	0.0005	0.171
9	**Best**	**13**	**2033.9**	**0**	**0.7564**	**0.347**

Table 4.4. Maximum likelihood parameter values for fecundity models fit to individual *Jacaranda copaia* seed production in 2000 on the 50 ha forest dynamics plot, Barro Colorado Island.

Model	intercept	crown area	Liana presence	β_{FNI}	a	b	B_{GNI}	c	d	B_{HNI}	e	f	Spp. Div.	Hi plat	Low plat	mixed	slope	stream	swamp	young
1	48.3125	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
2	-33.7891	1.021	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
3	-28.0554	1.019	-23.073	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
4	-39.1638	1.040	-21.993	3.348	0.953	1.654	-	-	-	-	-	-	-	-	-	-	-	-	-	-
5	-38.1108	1.037	-22.197	4.527	0.9634	1.848	-14.772	0.0670	2.99	-	-	-	-	-	-	-	-	-	-	-
6	-28.0596	1.048	-23.915	2.424	1.067	1.707	-16.695	0.0015	2.98	-6.61E-10	1.995	1.94	-	-	-	-	-	-	-	-
7	-42.3828	1.048	-24.184	2.445	1.0639	1.714	-16.416	0.0010	3	-6.72E-10	1.995	1.93	0.309	-	-	-	-	-	-	-
8	-17.2571	1.086	-23.331	4.059	1.064	2.185	-24.402	4.68E-05	2.85	-7.13E-10	1.995	1.90	-0.338	63.39	6.611	36.41	-10.75	1.758	7.158	-84.88
9	-42.6779	1.059	-14.8	5.468	0.953	2.201	-	-	-	-4.24E-09	1.855	1.757	-	70.2	20.76	72.24	9.218	-2.976	-58.04	-81.37

Table 4.5. Maximum likelihood parameter values for fecundity models fit to individual *Jacaranda copaia* seed production in 2002 on the 50 ha forest dynamics plot, Barro Colorado Island.

model	intercept	crown area	Liana presence	β_{FNI}	a	b	B_{GNI}	c	d	B_{HNI}	e	f	Spp. Div.	Hi plat	Low plat	mixed	slope	stream	swamp	young
1	37.6562	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
2	11.8944	0.124	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
3	15.6250	0.123	-14.895	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
4	-0.05365	0.134	-10.006	0.536	1.21841	1.203	-	-	-	-	-	-	-	-	-	-	-	-	-	-
5	4.78002	0.125	-9.1595	0.536	1.35146	1.528	-21.326	1.472	2.999	-	-	-	-	-	-	-	-	-	-	-
6	12.0741	0.122	-9.3414	0.623	1.33627	1.560	-58.541	0.0001	3	-7.32E-11	2.094	1.835	-	-	-	-	-	-	-	-
7	-60.9321	0.135	-12.265	0.239	1.33627	1.061	-2.993	4.94E-06	0.219	-9.16E-11	2.094	1.612	1.967	-	-	-	-	-	-	-
8	-45.4607	0.141	-9.4564	0.301	1.33627	1.384	-0.391	1.644	3.33E-06	-6.94E-11	2.094	1.507	1.649	25.11	-14.4	63.01	-15.1	-7.72	-20.8	-32.1
9	-61.5981	0.144	-	0.854	1.13532	1.328	-	-	-	-	-	-	1.040	48.48	3.548	82.95	0.549	14.84	9.3754	-1.449

Table 4.6. Maximum likelihood parameter values for fecundity models fit to individual *Jacaranda copaia* seed production in 2003 on the 50 ha forest dynamics plot, Barro Colorado Island.

Model	intercept	crown area	Liana presence	β_{FNI}	a	b	B_{GNI}	c	d	B_{HNI}	e	f	Spp. Div.	Hi plat	Low plat	mixed	slope	stream	swamp	young
1	23.75	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
2	-13.156	0.363	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
3	-11.366	0.362	-11.74	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
4	-34.751	0.410	-6.377	0.644	0.5402	0.220	-	-	-	-	-	-	-	-	-	-	-	-	-	-
5	-29.654	0.400	-4.971	1.588	0.4821	0.325	-0.8177	2.99993	0.251	-	-	-	-	-	-	-	-	-	-	-
6	-23.26	0.396	-5.783	1.771	0.392	0.267	-1.1506	2.98372	0.305	-6.21E-09	1.670	1.488	-	-	-	-	-	-	-	-
7	-81.997	0.396	-6.813	2.205	0.3378	0.306	-0.9989	2.99998	0.330	-6.57E-09	1.670	1.353	0.306	-	-	-	-	-	-	-
8	-55.714	0.439	-9.03	1.406	0.3378	0.357	-0.0923	2.96813	2.916	-1.23E-10	1.670	0.0002	0.176	-22.59	2.051	55.05	-6.027	-4.91	31.94	-87.93
9	-42.147	0.454	-	1.267	0.511	0.414	-	-	-	-	-	-	-	-21.41	6.472	56.16	-1.81	1.795	36.277	-82.33

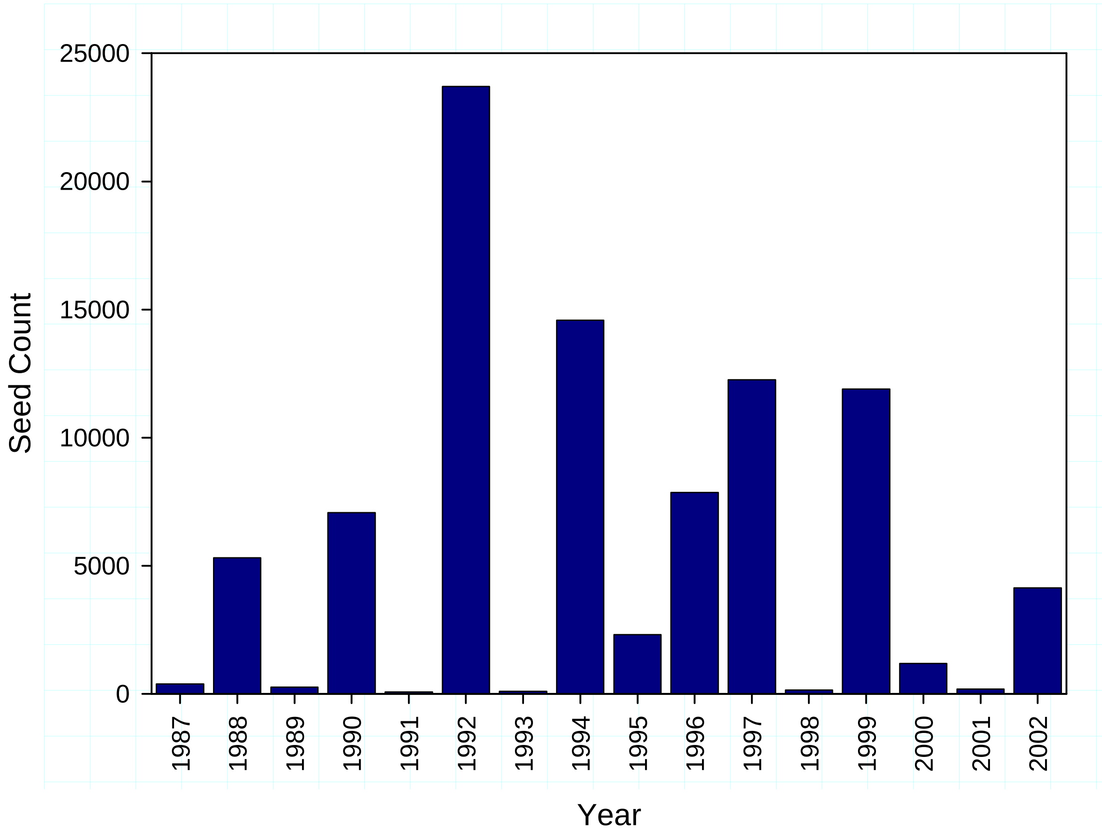

Figure 4.1. Historical seed trap captures for *Jacaranda copaia* seeds in 200 ½ m^2 mesh seed rain traps located across the 50 ha Forest Dynamics Plot, Barro Colorado Island, Panama. Data courtesy of Smithsonian Tropical Research Institute Terrestrial Environmental Sciences Program.

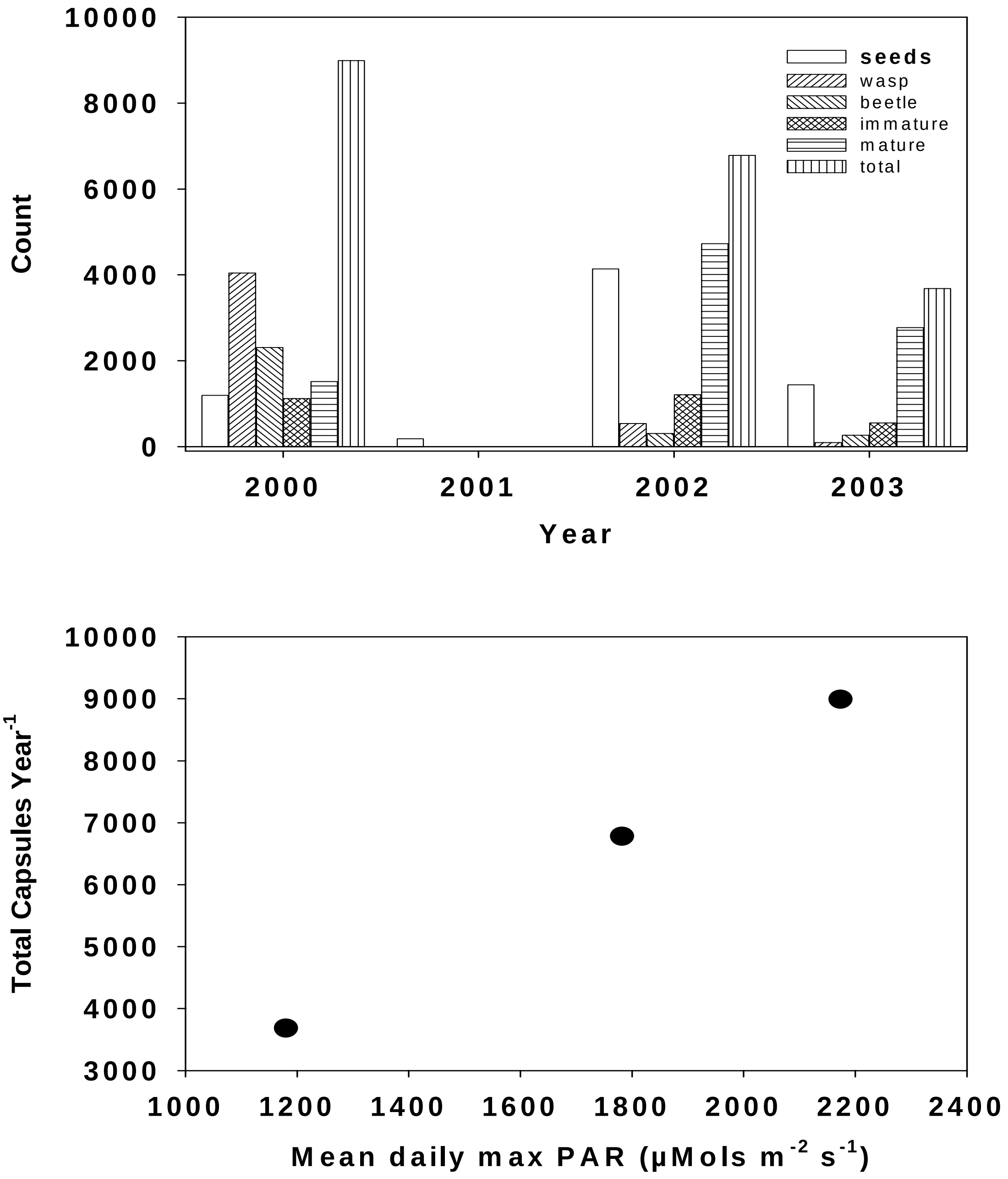

Figure 4.2. Number of seeds, wasp predated, beetle predated, immature, mature, and total capsules for three years in a population of *Jacaranda copaia* on the 50 ha forest dynamics plot on Barro Colorado Island, Panama.

SUMMARY

To my knowledge, this study is among the first undertaken to date using genetic markers to measure dispersal patterns from seed rain within any plant community without confounding the dispersal curve with the recruitment curve. I identified 10 microsatellite loci for *Jacaranda copaia* using an enriched genomic library approach. Most loci showed high levels of heterozygosity and a large number of alleles. A few loci showed evidence of null alleles and were therefore not used in subsequent studies of seed dispersal. Four of these loci were used to genotype all *Jacaranda* adults within the 50ha plot as well as seeds dispersed during two years.

The results of the direct genetic study of seed dispersal distances showed that seeds of *Jacaranda copaia* can be dispersed well beyond the edge of the canopy of the tree, often to hundreds of meters. I found that a mixture model consisting of a local Gaussian dispersal kernel and a long distance fat tail described by a negative exponential function best-fit the observed data better than single component models. Greater than 20% of dispersal distances examined in each year occurred at distances > 100 m. Differences among years in population-wide observed dispersal distances are interpreted to be due to differences observed in wind profiles in each year as well as differences in seed production and fecundity across different years. I found no support for the hypothesis that wind-dispersed seeds are disproportionately dispersed to tree fall gaps over understory sites.

Inverse modeling has been a popular and economical way to study seed dispersal within closed forest canopies. However, I have shown that it may produce significantly biased over- and underestimates of seed dispersal within forest communities. In particular, it may underestimate the tail of the curve. Furthermore, I have shown that inverse modeling, as it is typically described, does not adequately address process error in fecundity estimation. The implications of this finding are that sources of diserpsal limitation in forest communities in some species may not solely be due to limited dispersal capacity, but rather limited numbers of propagules, or variable numbers of propagules, available to be dispersed. The results further suggest caution in interpreting previous findings using inverse techniques, namely that as currently formulated, they may not adequately characterize the tail of the dispersal curve. Therefore, these methods have the potential to overestimate the degree of dispersal limitation within communities which might potentially obscure other biotic and abiotic factors that may limit recruitment and regeneration.

Finally, I have shown that positive density dependence, as measured by increased fecundity of *Jacaranda copaia* trees growing in higher densities, may operate within tropical forests. When we controlled for the effect of individual size, neighborhood (heterospecific size and density, liana presence, genetic relatedness) and habitat, we found that *Jacaranda* individuals growing in neighborhoods within high density of other reproductive *Jacaranda* showed increased fecundity above that explained by the other factors. These results also suggest positive density dependence or spatial autocorrelation in seed production may be an additional cause, along with limited dispersal and habitat preferences, in explaining the commonly observed pattern of spatial aggregation in tropical trees.

Pros and cons of the genetic measurement of dispersal distances

Direct measurement of dispersal distances by genotyping maternally derived tissue on seeds is a powerful tool for dissecting population levels of seed dispersal within large natural populations of trees. Although not examined here, the technique also has the potential to explore patterns of individual variation in seed dispersal patterns and how they relate to recruitment of seedlings. Given enough variability in markers and unique genotypes of all putative maternal plants in the population, the technique allows for the exact identification of the maternal source of dispersed seeds and the determination of seeds that have moved from beyond study areas, allowing for a direct measurement of seed mediated gene flow. Because the seed may also remain viable after removal of maternal tissue, tandem parentage analysis of seed parent and pollen parent is also possible (F. A. Jones, unpublished data).

Despite the power of this type of analysis, the technique also has several drawbacks that may prevent its' widespread application in the near future. The first drawback is the potentially large amount of time and resources required to develop effective markers for such an analysis. For species in which there are no pre-existing markers, development of these markers may be cost prohibitive and extremely time consuming, with no guarantee of success. However, my progress was greatly accelerated by using an enrichment technique (Chapter 1) and time required to develop such markers has certainly decreased during the course of my dissertation.

Anonymously amplified genetic markers, such as AFLPs could potentially reduce the time and cost of such development. However, because a limited amount of maternal tissue is usually available and because DNA obtained from this tissue can often be of limited quantity and low quality, care must be taken in that reliable genotypes are obtained and are repeatable. Furthermore, contamination of seeds by fungal spores or other exogenous sources of DNA (fecal matter for animal dispersed seeds, endophytes, fungal spores, etc.) could lead to errors in genotyping and subsequent exclusion of seeds when in fact they are locally dispersed. Therefore, unless individual seeds are genotyped several times to provide confidence in the maternal identity of the seed, anonymous markers methods have the potential to overestimate the scale and frequency of long distance dispersal.

A second potential drawback for the maternally derived tissue approach, and to seed trap studies in general, is that no adequate sampling theory has yet been developed to deal with the impact of trap placement relative to tree position and its' influence on the determination of dispersal patterns on the population and individual level. Ultimately, the application of genetic techniques to dissect individual patterns of dispersal and reproductive success could be extremely useful. However, without a thorough statistical examination of the effect of seed trap placement and sampling frequency on observed patterns, this will remain an open question. The combination of inverse modeling techniques or Bayesian analysis and the direct genetic approach could more directly address sampling issues and deserves further development. In short, the number of seeds captured in a trap, genotyped and non-genotyped, is potentially useful information that was not fully used in this study in a combined analysis. The application of Bayesian methods and the use of historical seed dispersal patterns to these questions is a potentially fruitful avenue for further research.

Ultimately, the question remains as to the importance of seed dispersal distances in the survival and recruitment of seedling, juvenile, and adult life-history stages. Although I did not explicitly address these questions in my research, they are critical in closing the loop between adult reproduction and fecundity, seed dispersal, and seedling and adult recruitment. This method is useful only in determining the primary dispersal distances, it offers little information to the prediction of successful germination and recruitment without further investigation. Future studies could incorporate dispersal kernels measured using maternally derived tissue to predict parentage of established seedlings, with the probability of maternal parentage assignment preconditioned on the predictions made by the dispersal kernel and this parentage ultimately evaluated in light of the genotype of the seedling. This would allow for more detailed studies of demography and individual plant fitness as it relates to the process of dispersal.

The technique is also limited in terms of the spatial scale over which dispersal can be measured. Indeed, I suspect that this study may push the limit in terms of tractable spatial scale over which dispersal can be directly measured. Therefore, it is an impractical method for measuring truly long distance dispersal events >1km simply because of the large numbers of individuals that would need to be genotyped and the need to explicitly map these individuals over an unrealistically large area.

Finally, these techniques may only be truly practical in populations where the number of potential adults is relatively small. For very common species with thousands of individuals in a local population, the number of potential adults as well as the number of seeds that would need to be genotyped would be large and potentially prohibitive. In populations with large numbers of adults, the effect will be to either reduce the spatial scale of the study to include a tractable number of the adults, which will ultimately reduce the scale over which dispersal can be direct measured, or to increase the time and resources required to complete such a study. For example, a study as described here may be totally intractable in a grassland system, in large populations of clonal plants, in herbaceous communities, or even in low diversity, high density temperate and boreal forest ecosystems. What is required is a compromise between methods, analogous to the TWOGENER model described by Smouse et al., that represents a compromise between indirect and direct methods.

There are a number of theoretical considerations that are brought up by the results of my dissertation. Among the most important, we found evidence for separate physical mechanisms that may govern local and long distance dispersal. Each of these mechanisms has implications for both local and regional processes. Abundant dispersal to local sites may be advantageous in terms of the numbers of seeds that can potentially recruit, however, these seeds and seedlings may suffer disproportionately due to distance and density dependent biotic factors. Seeds that are dispersed long distances may avoid distance and density dependent factors, but seeds dispersed long distances will also be at a numerical disadvantage versus local seeds, since the probability of any single seed surviving to adulthood is exceedingly small.

We also found evidence lending support that other factors besides limited dispersal ability of individual species can lead to dispersal limited populations. *Jacaranda* is one of the most effective dispersers on the FDP. However, one factor that contributes to dispersal limitation in this species is variation in fecundity within and among individuals within and among years. Future empirical and theoretical studies of dispersal limitation should consider the role of periodic reproduction in assessing the degree of dispersal limitation within populations.

Local population genetic structure is increased by local dispersal, while long distance dispersal decreases regional or among population genetic structure. Separate studies have indeed revealed that *Jacaranda* shows a high degree of genetic structure within adult populations on the FDP due to limited seed dispersal (Jones, unpublished data). However, populations of *Jacaranda* across the Isthmus show relatively little genetic differentiation. Although this lack of genetic differentiation could be due to long distance seed movement, other lines of evidence suggest that pollen movement may occur on even greater scales than seed movement in *Jacaranda* (FAJ unpublished data). Future studies have been planned to separate the effect of pollen versus seed dispersal in explaining regional patterns of genetic differentiation.

I found a great deal of individual variation in fecundity among individuals within years, and within the population among years. As revealed by the inverse modeling, the variation in fecundity had a direct impact on spatial patterns of dispersal as well as the number of seeds moving long distances. Although several theories, including the storage effect and various lottery models have explored species level temporal variation in reproduction and it's implications for the maintenance of diversity, few theoretical studies have yet to incorporate spatial and temporal variation in reproduction and dispersal and the role that it plays in species regeneration within communities or coexistence. Variation in fecundity, both spatially and temporally, can reduce a populations' effective size below that of the census size. Furthermore, variation in fecundity and dispersal patterns within and among years has yet to be incorporated into a general theory of dispersal and recruitment limitation and the role that it may play in the maintenance of genetic and species diversity. Future theoretical efforts should focus on the role of population and individual level variation in reproduction and dispersal and its role in the origin and maintenance of biological diversity.