

## Seed Dispersal of a High Quality Fruit by Specialized Frugivores: High Quality Dispersal?<sup>1</sup>

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### ABSTRACT

Dispersal quality, as estimated by the cumulative effects of dispersal, germination, seed predation, and seedling survival, was examined for *Beilschmiedia pendula* (Lauraceae) in Monteverde, Costa Rica. I determined the pattern of dispersal by finding seeds deposited by birds, protected the seeds from seed predators with cages to assess germination and seedling survival, and examined seed predation rates with marked seeds. Seed predation, germination, and seedling survival were compared between seeds naturally dispersed by birds and seeds placed at randomly located sites.

Approximately 70 percent of seeds dispersed by birds ( $N = 244$ ) were deposited <10 m from crown edges of fruiting *B. pendula* trees, although some seeds were dispersed at least 70 m away. Larger seeds were more likely to be dispersed under or close to the parent trees, and larger seeds produced larger seedlings. Seed size was not correlated directly with seedling survival, but larger seedlings at three months were most likely to survive one year. Seed predation by mammals and insects and seedling mortality due to fungal pathogens were concentrated beneath the crowns of parent trees. Seedlings and saplings were more abundant beneath fruiting *B. pendula* trees, but individuals farther away were taller on average. Thus, dispersal is beneficial for *B. pendula*, but such benefits appear most pronounced at a small spatial scale; seeds dispersed >30 m from the crown edges actually had a lower probability of survival than those dispersed 10–20 m. Only 10 percent of *B. pendula* seeds received high-quality dispersal in terms of landing in the zone with the highest per seed probability of seedling survival 10–20 m from parental crowns.

### RESUMEN

La calidad de dispersión, estimado del efecto acumulativo de dispersión, germinación, predación de semillas, y sobrevivencia de plantulas fue examinada por *Beilschmiedia pendula* (Lauracea) en Monteverde, Costa Rica. Determiné el patrón de dispersión, encontrando semillas defecadas o regurgitadas por aves, protegí semillas de predadores con jaulas para determinar germinación y sobrevivencia de plantulas, y examiné la proporción de predación de semillas con semillas marcadas. Predación de semillas, germinación y sobrevivencia de plantulas fueron comparadas con semillas dispersadas naturalmente por aves y con semillas localizadas en lugares al azar.

Aproximadamente 70 por ciento de las semillas dispersadas por aves ( $N = 244$ ) fueron depositadas cerca de 10 m del borde de la corona de árboles en fruto de *B. pendula*, aunque algunas semillas fueron dispersadas hasta 70 m más lejos. Semillas grandes tuvieron la tendencia de ser dispersadas debajo o cerca del árbol parental, y semillas grandes produjeron plantulas grandes. El tamaño de la semilla no estaba correlacionada directamente con sobrevivencia de plantulas, pero plantulas grandes a 3 meses tuvieron la tendencia de sobrevivir. Predación de semillas por los roedores y insectos, y mortalidad de plantulas por hongos patogénicos fueron lo mas comun debajo de la corona de los árboles parentales. Plantulas y arbolillos fueron más abundantes debajo de árboles en fruto de *B. pendula*, pero individuos distantes fueron en promedio más altos. Dispersión es favorable para *B. pendula*, pero estos beneficios aparentan ser más pronunciados a una escala espacial menor; semillas dispersadas más de 30 m del borde de la corona en realidad tienen una probabilidad menor de sobrevivencia que las que son dispersadas entre 10–20 m. Solamente 10 por ciento de las semillas de *B. pendula* recibieron dispersión de calidad alta en terminos de aterrizar en una zona con la más alta probabilidad de sobrevivencia de plantulas entre 10–20 m de la corona parental.

*Key words:* *Beilschmiedia pendula*; *Costa Rica*; *dispersal quality*; *Lauraceae*; *seed dispersal*; *seedling recruitment*; *seed size*; *tropical cloud forest*.

IN A SEMINAL PAPER, McKEY (1975) PROPOSED that tropical trees producing nutrient-rich fruits attract specialized frugivores providing high quality seed dispersal. He noted that this strategy of high quality fruits gaining high quality dispersal from spe-

cialized frugivores could be viewed as one endpoint in a continuum of plant/disperser relationships. High quality, or specialist, plants produce large fruits with one or a few large seeds and lipid- or protein-rich pulp. At the other end of the continuum, generalist plants produce large crops of fruits with many small seeds and pulp composed mostly of sugars and water. Small, opportunistic birds that eat generalist fruits were expected to be less reliable

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dispersers because they were purportedly less dependent on fruit than specialized frugivores. Although components of the specialist/generalist framework have been supported, data to fully test it are still lacking (Howe 1993, Schupp & Fuentes 1995).

Howe (1993) suggested that the main reason the framework remains untested is because zoologists and plant ecologists study different aspects of the multiple stages in the plant recruitment process. Quantifying dispersal quality is key to testing the model; yet to examine dispersal quality, it is necessary to study both the dispersal pattern and post-dispersal fate of seeds (Janzen 1983, Howe 1993, Jordano & Herrera 1995, Schupp & Fuentes 1995). Previous studies have addressed components of dispersal quality such as gut treatment of seeds (Traveset & Willson 1997, Wahaj *et al.* 1998), animal movement or deposition patterns (Murray 1988, Wheelwright 1991, Mack 1995, Laman 1996), or microsite suitability for seedling growth (Howe *et al.* 1985, Laman 1995), but few have integrated these aspects to examine survival of naturally dispersed seeds. Difficulty in finding seeds dispersed by animals has limited such studies to parasitic mistletoes, which have specific and easily quantifiable safe sites (Davidar 1983, Reid 1989, Sargent 1995, Larson 1996), and to ant-dispersed species that are disseminated over relatively small scales (Horvitz & Schemske 1986, Hanzawa *et al.* 1988, Gibson 1993).

Another reason that the specialist/generalist framework has not been tested adequately is because species-specific coevolution between plants and dispersers, an underlying theme of the original model, now is considered unlikely. Diffuse coevolution between groups of plants and groups of dispersers is thought to be more typical (Janzen 1980, Wheelwright & Orians 1982, Janzen 1983, Howe 1984, Herrera 1985, Levey *et al.* 1994). Even though species-specific mutualisms are not expected, some species may provide high quality dispersal (Wenny & Levey 1998).

Dispersal quality originally was discussed mainly as a function of the reliability of frugivore visitation to fruiting trees and the effects of gut treatment on germination (McKey 1975). Because seed dispersal is one phase of plant reproduction, dispersal quality should also include post-dispersal factors. In Howe's (1993:4) summary of the characteristics found in specialized dispersal systems, the only post-dispersal component listed that could be construed as dispersal quality was "seed dispersal away from parents [is] critical for recruitment."

More generally, the quality of dispersal can be defined as the probability that a dispersed seed will survive to reproductive age (Schupp 1993).

My goal was to estimate the quality of seed dispersal for a tropical tree with high quality fruits (*Beilschmiedia pendula*, Lauraceae; hereafter *Beilschmiedia*) dispersed by highly frugivorous birds. The specific objectives were to determine the spatial distribution and microsite characteristics of naturally dispersed seeds and then monitor seed predation, germination, seedling establishment, and seedling survival. I also compared survival of dispersed, non-dispersed, and randomly placed seeds. With this combination of descriptive and experimental data, I used the cumulative effects of post-dispersal sources of seed and seedling mortality as an estimate of dispersal quality. The specialist/generalist hypothesis that specialized frugivores provide high quality dispersal leads to the predictions that: (1) dispersed seeds should have higher survival than non-dispersed seeds; and (2) naturally dispersed seeds should have a higher probability of survival than randomly placed seeds.

## METHODS

**STUDY SITE.**—This study was conducted January 1995–June 1996, in the Monteverde Cloud Forest Preserve (10°12'N, 84°42'W) in the Cordillera de Tilarán, Costa Rica. The study area was in relatively undisturbed lower montane rain forest along the continental divide at 1600 m elevation. A 5-ha area, 500 m from the beginning of the Valley Trail (Sendero El Valle), was mapped and marked into 10- × 10-m quadrats with PVC tubing at every grid point. The site's vegetation is described in more detail by Nadkarni and Wheelwright (1999). The average annual rainfall is *ca* 2500 mm, with most of the precipitation occurring between May and November (Nadkarni & Wheelwright 1999).

**STUDY SPECIES.**—*Beilschmiedia pendula* [(Sw.) Hemsl.] is a common canopy tree in Costa Rican montane forests from 600 to 2000 m elevation. In the Monteverde area, it occurs from 1500 to 1600 m (Haber *et al.* 1996). *Beilschmiedia* begins flowering in the late dry season (March) and fruits ripen from mid-January through late April. Fruits have black skin and lipid-rich pulp (Wheelwright *et al.* 1984). Most of the fruit volume is a single seed (length:  $48.55 \pm 7.65$  mm, width:  $20.70 \pm 1.78$  mm, mass:  $12.89 \pm 3.60$  g;  $\bar{x} \pm SD$ ,  $N = 293$ ) which is composed of a small embryo and two large cotyledons. Compared to other genera of

Lauraceae, *Beilschmiedia* has a relatively thick (2.5 mm) endocarp, and the pulp is attached more tightly to the seed. Seven *Beilschmiedia* trees were in the 5-ha study site. Data for two trees that had adjacent crowns were pooled for analyses. Fruits and seeds for some experiments were collected from trees outside the main study area. Large fruit crops ( $1837 \pm 1024$  fruits/tree) were produced by the seven trees in 1995, but not in 1994 or 1996. Individual *Beilschmiedia* trees typically fruit at two-year intervals (Wheelwright 1986).

*Beilschmiedia* fruits are eaten primarily by four species of birds: Emerald Toucanet (*Aulacorhynchus prasinus*), Resplendent Quetzal (*Pharomachrus mocinno*), Three-wattled Bellbird (*Procnias tricarunculata*), and Black Guan (*Chamaepetes unicolor*; Wheelwright *et al.* 1984). The first three species typically remain in a fruiting tree after eating several fruits and regurgitate viable seeds under the same tree or nearby (Wheelwright 1983, 1991). Guans defecate seeds in viable condition, and they generally leave a fruiting tree before defecating the seeds from that foraging bout. All four species can be considered fruit specialists in the sense that they depend on fruit for most (if not all) of their dietary requirements, at least at some times of the year (Wheelwright 1983, Avila H. *et al.* 1996). Quetzals and toucanets also eat large insects and small vertebrates (Skutch 1967, Wheelwright 1983, Riley & Smith 1992, Avila H. *et al.* 1996), while guans also eat leaves (Haber *et al.* 1996). Bellbirds apparently eat only fruits, although diets of female bellbirds are poorly known (Snow 1982).

Dropped or fallen fruits are eaten by agoutis (*Dasyprocta punctata*) and possibly pacas (*Agouti paca*) and other rodents. Agoutis chew off pulp and sometimes the endocarp, and leave the seeds under the trees, but do not eat or bury seeds (D. Wenny, pers. obs.). Squirrels (*Sciurus* sp.) also eat the pulp and drop seeds under the trees (D. Wenny, pers. obs.; N. Wheelwright, pers. comm.) Thus, these species probably do not provide major dispersal for *Beilschmiedia*.

SEED DISPERSAL.—Seeds were located by systematically searching the ground for freshly regurgitated or defecated seeds from late January through mid-April. The ground searches started at the base of a fruiting tree and proceeded along 10-m-wide transects (delineated by the PVC markers) to 100 m from each *Beilschmiedia* trunk. Additional sites away from the focal trees also were searched; some were selected randomly and others were chosen due to bird activity in the area. It was impossible to

search the entire site with equal intensity; however, an effort was made to cover the entire site at least once every three weeks, so that over the course of the study each 10- × 10-m plot was checked at least four times. I assumed defecated seeds were dispersed by black guans because guans are the only avian disperser in the area that defecates large seeds. Sites were classified as non-dispersed if directly under the crown of a fruiting *Beilschmiedia* tree, or as dispersed if not under such a tree. The closest fruiting *Beilschmiedia* tree to a seed was assumed to be the parent of that seed, although this method likely underestimated dispersal distances for some seeds (Gibson & Wheelwright 1995, Wenny & Levey 1998). All the dispersed and non-dispersed seeds, as well as the seeds placed at random sites (see below), were covered with wire mesh cages to protect them from vertebrate seed predators. By doing so, I was able to calculate accurate estimates of germination and seedling establishment in the absence of seed predation by mammals.

In addition to these naturally dispersed and non-dispersed seeds, other seeds were placed at 50 randomly selected sites to compare seed predation, germination, and survival at dispersed, non-dispersed, and random sites. These sites were selected with random numbers generated by a hand calculator and used as coordinates within the study site. The post-dispersal fate of seeds at these random locations was compared to the fate of seeds at the dispersed and non-dispersed locations to determine how the probability of recruitment differed among the three types of sites.

GERMINATION AND SEEDLING SURVIVAL.—The original dispersed and non-dispersed seeds, and all seeds placed at randomly located sites were protected by 4- × 8- × 4-cm cages made of 1-cm galvanized wire mesh held in place by two 25-cm metal stakes. Caged seeds were used to determine germination rates and insect predation rates in the absence of mammalian seed predators. Each site was checked weekly for at least 12 weeks and once in late June 1996, ca 16 months after dispersal (hereafter, seedling survival). Germination was defined as the splitting of the seed coat and spreading of the cotyledons. Typically, the radicle had emerged by the census after germination, and a week later the stem was visible. As each seed germinated and the shoot began to grow, the cage was removed to allow normal seedling growth. The seedling location was marked with one of the stakes from the cage. Causes of seedling mortality were classified as mammal, insect, fungal pathogen, physical, or unknown.

Mammals either ate the seed and left the damaged shoot behind (seed predators) or removed the entire shoot (herbivores). Some seeds that appeared to have germinated eventually were killed by beetles inside the cotyledons. Insect-killed seeds frequently developed a root but never had a shoot >2 cm tall. Seedlings killed by fungal pathogens were characterized by a wilted and discolored shoot (Augspurger 1990). A seed was considered alive as long as it remained firm, even if the shoot had been eaten or otherwise damaged. Such seeds resprouted repeatedly.

**POST-DISPERSAL SEED FATE.**—At each dispersed, non-dispersed, and random site, a marked seed was used to assess rates of seed predation, identify seed predators, and determine if secondary dispersal occurred. Seed predation and secondary dispersal could alter any pattern generated by dispersers, and thus be more important in determining the probability of recruitment than primary dispersal (Wheelwright 1988, Herrera *et al.* 1994). For this treatment, I used regurgitated seeds collected under fruiting trees outside the study site. Seeds were marked by gluing 50–75 cm of unwaxed dental floss to the seed, and tying *ca* 50 cm of flagging tape to the distal end of the floss. Because the glue held best on seeds with a dry seed coat, seeds were taken inside and allowed to dry for one to three hours before gluing. Each marked seed was placed at a site the next morning. Such marking procedures have been used for other species in the same study site with no evidence of negative effects on seed removal (Wenny *in press*).

All marked seeds were censused on days one, three, and seven and once each week afterwards until week five. If a marked seed was removed, the surrounding area was searched to find the flagging tape–dental floss assembly. When the marking assembly was found, seed fate was scored as present or absent. In the few cases in which seeds were consumed partially, teeth or bill marks were examined to identify the consumer.

**SEEDLING AND SAPLING PLOTS.**—To determine if *Beilschmiedia* seedlings and saplings were more likely to recruit under or away from conspecifics, seedlings and saplings (up to 5 m height) were measured and mapped in paired 10- × 10-m plots. For each of five trees, one plot was located near the tree with approximately half of the plot directly under the crown. The second plot was located at least 20–40 m from the crown edge.

*Beilschmiedia* did not fruit in the study site in

1994, so most individuals were presumably at least two years old. Such seedlings could be distinguished from new seedlings by the lack of a seed, presence of a woody stem, and presence of epiphylls.

**MICROHABITAT CHARACTERISTICS.**—For all sites and seeds, I measured seed characteristics and microhabitat variables that might influence seed predation, germination, or seedling survival. Seed length and width were measured with dial calipers and seed mass was measured with a handheld digital scale accurate to 0.01g. Canopy cover was estimated with a spherical densiometer held *ca* 1.1 m above the ground. Leaf litter depth was measured as the number of leaves pierced by a metal stake thrust into the soil at the site. Vegetation density was the number of stems within a 50-cm radius of the site. The distances to the nearest woody stem, tree >10 cm DBH (diameter at breast height), crown edge of fruiting *Beilschmiedia* tree, and fallen log were measured with a measuring tape.

**PROBABILITY OF SURVIVAL.**—I estimated dispersal quality by calculating the cumulative probability of post-dispersal survival with the formula:  $P \times G \times E \times S$ , where P is the proportion of seeds surviving seed predators, G is the proportion germinating successfully, E is the proportion establishing seedlings with at least two leaves, and S is the proportion of seedlings surviving 16 months. Each of the four stage-specific survival values and the cumulative probability of survival were calculated for each tree and then averaged among all trees (Jordano & Herrera 1995).

**STATISTICAL ANALYSES.**—Data were analyzed with tests from SAS JMP (SAS 1989). Parametric tests were used unless data violated the assumptions of normality and equal variance, in which case non-parametric procedures were employed. Survival proportions were arcsine square-root transformed before analysis. Rates of seed removal were compared among treatments with survival analysis and the Mantel log-rank test, which gives equal weight to all survival times (Pyke & Thompson 1986). The importance of microsite characteristics on survival was assessed with multiple logistic regression, which is analogous to multiple linear regression with a binomial response variable. After starting with the full model including all predictor variables, the model was run with and without each variable until only significant predictors were retained (Trexler & Travis 1993). At each step, var-

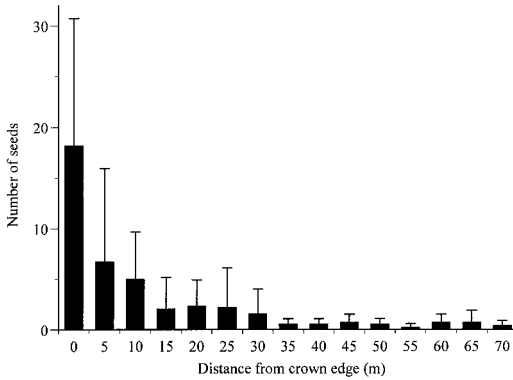


FIGURE 1. The average number of regurgitated or defecated *Beilschmiedia* seeds ( $\pm 1$  SD) at 5-m intervals from crown edges of six fruiting *Beilschmiedia* trees. The first category (distance 0) includes all non-dispersed seeds, while the remaining categories include only dispersed seeds.

tables were selected manually to avoid the problems of automatic stepwise procedures (James & McCulloch 1990). Lack-of-fit tests indicated that the single-term models were adequate, and thus interaction terms were not required (SAS 1989). Throughout this paper, mean values are followed by  $\pm 1$  SD.

## RESULTS

Over the three-month fruiting season, 217 regurgitated and 27 defecated seeds were found. Of these, 129 (53%) were deposited beyond the crowns of fruiting trees (dispersed) and 115 (47%) were directly under the trees (non-dispersed). Of the dispersed seeds, 67 percent landed within 20 m of crown edge, but some seeds were found up to 70 m away (Fig. 1). Dispersal distance (for dispersed seeds) was not correlated with seed mass, length, or width (Spearman's rank tests,  $P > 0.3$ ).

Seeds defecated (presumably by guans) tended to be lighter (Wilcoxon  $\chi^2 = 6.7$ ,  $P = 0.009$ ) and shorter ( $\chi^2 = 9.9$ ,  $P = 0.002$ ), but not narrower ( $\chi^2 = 0.8$ ,  $P = 0.2$ ) than seeds regurgitated by the other three species (Table 1). Defecated seeds were dispersed significantly farther ( $39.6 \pm 17.2$  m) from the parental crowns than regurgitated seeds ( $14.3 \pm 13.4$  m; Wilcoxon  $\chi^2 = 30.5$ ,  $P < 0.001$ ).

Very few marked seeds (17%) were eaten or removed after dispersal (or placement at random sites), but removal rates were significantly different among the three treatments (Mantel  $\chi^2 = 8.6$ ,  $df = 2$ ,  $P = 0.01$ ; Fig. 2). Non-dispersed seeds had

TABLE 1. Average ( $\pm 1$  SD) mass, length, and width of *Beilschmiedia* seeds defecated (presumably by black guans) or regurgitated by quetzals, toucanets, and bellbirds. Sizes of regurgitated and defecated seeds were compared with Wilcoxon rank sum test. Measurements for all seeds, including seeds placed at random sites ( $N = 294$ ), are shown for comparison.

	Defecated $N = 27$	Regurgitated 217	All Seeds 294
Mass (g)	11.3 (2.8)	13.0 (3.5)**	12.9 (3.6)
Length (mm)	43.1 (5.5)	48.2 (7.8)**	48.6 (7.6)
Width (mm)	20.4 (1.5)	20.8 (1.2) <sup>NS</sup>	20.7 (1.8)

\*\*  $P < 0.01$ .

<sup>NS</sup>  $P = 0.2$ .

lower survival than dispersed seeds (Mantel  $\chi^2 = 7.5$ ,  $df = 1$ ,  $P = 0.006$ ), but survival of seeds at random sites did not differ from that of dispersed (Mantel  $\chi^2 = 0.02$ ,  $df = 1$ ,  $P = 0.9$ ) or non-dispersed seeds (Mantel  $\chi^2 = 3.0$ ,  $df = 1$ ,  $P = 0.08$ ).

The most conspicuous post-dispersal seed predators were two species of beetles, one of which (Nitidulidae) buried the seeds and fed upon the rotting cotyledonary reserves. The second beetle species (Curculionidae) consumed the seed by tunneling through the endocarp to reach the seed. None of the seeds buried by beetles ( $N = 24$ , 8.2%) produced seedlings (although a few germinated), and thus the beetles likely do not act as secondary dis-

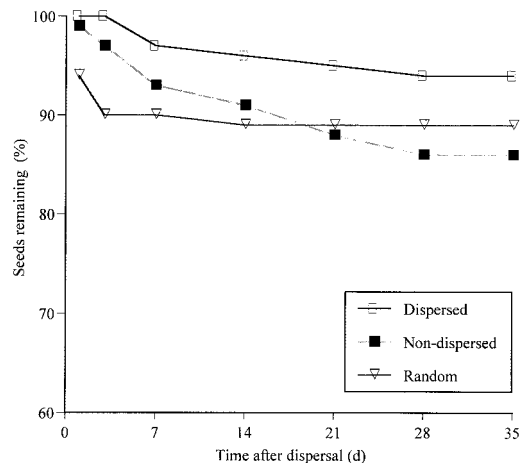


FIGURE 2. Post-dispersal predation of seeds from dispersed ( $N = 129$ ), non-dispersed ( $N = 115$ ), and random ( $N = 50$ ) locations. Non-dispersed seeds had a lower survival rate than dispersed seeds, but the other pairwise comparisons did not differ.

TABLE 2. Results of logistic regressions for post-dispersal survival of marked seeds after 5 weeks, and 16-month seedling survival of initially caged seeds against habitat variables. Only significant effects are listed. Nonsignificant variables included seed mass, seed length, seed width, canopy cover, distance to log, distance to woody stem, and distance to 10-cm tree. The abbreviations for type of site are: D = dispersed; N = non-dispersed; and R = random.

Response	$R^2$	$\chi^2$	Predictors <sup>a</sup>
5-wk seed survival	0.3	72.7***	+ Leaf litter* + Dispersal date*** + Vegetation density*** + Distance from parent* Type (N < D = R)*
16-mo seedling survival	0.1	21.2***	+ 3-mo seedling height** - Dispersal date***

\*  $P \leq 0.05$ , \*\*  $P \leq 0.01$ , \*\*\*  $P < 0.001$ .

<sup>a</sup> Sign in front of each predictor indicates positive or negative correlation with the response.

persers. Small rodents removed 8 seeds (2.7%) and took them into burrows at least 50 cm deep. Such a depth would preclude seedling establishment. Therefore, rodents probably are not secondary dispersers of *Beilschmiedia*. Black-breasted Wood-Quail (*Odontophorus leucolaemus*) pecked apart 7 seeds (based on one direct observation and bill marks left on pieces of seeds). An additional 11 marked seeds were removed but were not found.

Width, length, and mass were not significant effects in logistic regression models predicting five-week seed survival (Table 2). Seeds dispersed beyond the parental crowns and seeds at randomly located sites were more likely to survive five weeks

than non-dispersed seeds (Wald  $\chi^2 = 7.0$ ,  $P = 0.03$ ) and similarly, seed survival was positively correlated with dispersal distance (Wald  $\chi^2 = 7.3$ ,  $P = 0.03$ ; Table 2). Seed survival was also positively correlated with amount of leaf litter (Wald  $\chi^2 = 6.0$ ,  $P = 0.05$ ), vegetation density (Wald  $\chi^2 = 11.6$ ,  $P = 0.003$ ), and date of dispersal (Wald  $\chi^2 = 14.0$ ,  $P < 0.001$ ).

Virtually all caged seeds initiated germination (98%) and the majority (68%) had established seedlings by late July, three to five months after dispersal. The average proportion per tree of seeds that germinated, established seedlings, or survived 16 months, did not differ among the three treatments (Kruskal-Wallis tests,  $P > 0.05$ ; Fig. 3). Overall, however, the number of non-dispersed seeds that established seedlings was greater than expected if all three treatments had equal survival ( $\chi^2 = 9.4$ ,  $df = 2$ ,  $P = 0.009$ ).

Germination usually occurred two to three weeks after dispersal ( $18 \pm 9$  d). Germination time was slightly faster for regurgitated ( $18 \pm 9$  d) than for defecated seeds ( $22 \pm 11$  d; Mann-Whitney  $U$ -test,  $P = 0.04$ ). Time to germination was not related to seedling establishment (Mann-Whitney  $U$ -test,  $P = 0.9$ ) or 16-month seedling survival (Mann-Whitney  $U$ -test,  $P = 0.2$ ). Seed mass was not correlated with time to germination after dispersal ( $r = -0.09$ ,  $P = 0.2$ ), but shoots from larger seeds grew faster after germination ( $r = -0.2$ ,  $P < 0.001$ ). Seeds that established seedlings by July 1995 (3–5 mo after dispersal) were significantly heavier on average ( $13.5 \pm 3.5$  g,  $N = 165$ ) than seeds that did not establish seedlings ( $12.1 \pm 3.6$  g,  $N = 127$ ;  $t = 3.2$ ,  $P < 0.002$ ), but those that survived 16 months ( $13.1 \pm 3.6$  g,  $N = 143$ ) were not from seeds larger than those of seedlings that

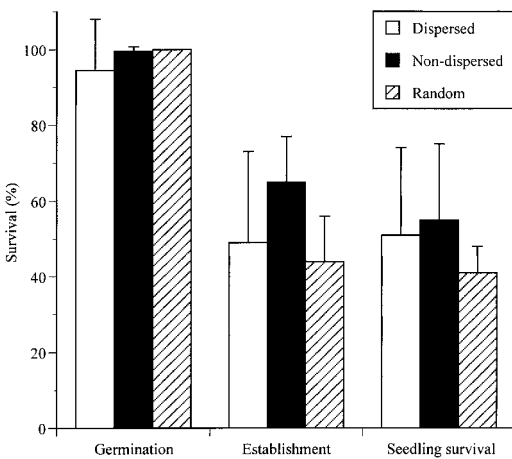


FIGURE 3. Proportion of seeds germinating, establishing seedlings 3 months after dispersal, and surviving 16 months, at dispersed ( $N = 129$ ), non-dispersed ( $N = 115$ ), and random ( $N = 50$ ) locations. The proportion surviving each stage did not differ among the three treatments.

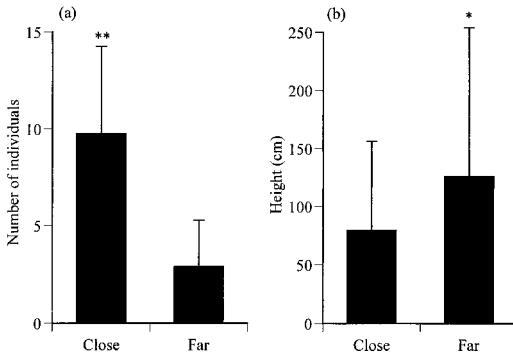


FIGURE 4. (a) Average ( $\pm$  SD) number and (b) height of seedlings and saplings up to 5 m tall in paired 10-  $\times$  10-m plots ( $N = 5$  pairs) under (close) and 20–40 m away (far) from *Beilschmiedia* crowns. Asterisks indicate significance levels (\*\* $P = 0.005$ , \* $P = 0.02$ ).

did not survive ( $12.7 \pm 3.5$  g,  $N = 149$ ;  $t = 0.9$ ,  $P = 0.4$ ). Of the seedlings that survived, seedling height was positively correlated with initial seed mass ( $N = 143$ ,  $r = 0.4$ ,  $P < 0.001$ ).

The predominant source of seedling mortality was fungal pathogens, although many seeds resprouted several times even after fungal attack. Fungal pathogens killed more seedlings directly beneath the parental crowns (non-dispersed) than seedlings at dispersed or random locations ( $\chi^2 = 20.3$ ,  $df = 4$ ,  $P < 0.001$ ). As for the marked seeds, some caged seeds (6.8%) were buried or eaten by beetles. Herbivory by insects and mammals was probably the primary cause of seedling mortality after seedling establishment, but the effect of herbivory was difficult to quantify because the seedlings were examined too infrequently.

Seedling survival was predicted by only two variables in the logistic regression analysis (Table 2). In contrast to seed survival at 5 weeks, 16-month seedling survival was negatively correlated with dispersal date ( $\chi^2 = 9.7$ ,  $P = 0.002$ ). Seedling survival was positively correlated with seedling height at 3 months ( $\chi^2 = 6.6$ ,  $P = 0.01$ ; Table 2).

The abundance of seedlings and saplings (up to 5 m tall) was higher in plots close to the fruiting trees (paired  $t$ -test = 3.4,  $df = 4$ ,  $P = 0.005$ ), but the median height of individuals was greater in the plots 20–40 m away from the trees (Wilcoxon rank sums test,  $\chi^2 = 5.1$ ,  $df = 1$ ,  $P = 0.02$ ; Fig. 4). Most seedlings (58%) in the plots close to fruiting trees were  $< 50$  cm in height, while most individuals (70%) in the plots far from adult trees were  $> 50$  cm and ranged up to 5 m.

The cumulative probability of survival per seed

as a function of distance from parent trees was calculated as the product of the probabilities of surviving seed predation, germination, seedling establishment, and 16 months. Seed predation and germination were not as important in limiting survival as were seedling establishment and seedling survival (Fig. 5). Establishment and 16-month seedling survival were higher for seeds under the crown and up to 20 m from the crown than for seeds dispersed 30–40 m from the crown (Fig. 5). The overall probability of survival varied with distance (One-way ANOVA on arcsine transformed data,  $F_{5,20} = 5.8$ ,  $P = 0.002$ ). The cumulative probability of survival was higher 10–20 m from the crown than within 10 m (Fisher's LSD,  $P < 0.01$ ) or beyond 20 m ( $P < 0.008$ ; Fig. 5e). Note that these probabilities do not include the number of seeds per distance interval (Fig. 1), because that is a component of dispersal quantity, not quality.

## DISCUSSION

The results do not support the hypothesis that specialized dispersers predictably provide high quality dispersal. Differences in survival of dispersed, non-dispersed, and randomly located seeds were minor, and in some cases, contrary to the prediction. The majority (71%) of seeds disseminated by birds landed under or within 10 m of the crowns of parent trees where survival was moderate; only 10 percent landed in the zone with the highest probability of survival 10–20 m from adult crowns, and the remainder were dispersed beyond 20 m where the probability of *Beilschmiedia* survival dropped considerably (Fig. 5). These results may be explained by: (1) the confounding effects of seed size on the relationship between dispersal distance and survival probability; (2) the lack of clearly definable safe sites for germination and seedling survival; and (3) the short-term nature of the study.

Large seeds had the best chances of surviving (all else being equal) because larger seeds produced larger seedlings initially, and larger seedlings were more likely to survive 16 months. Unfortunately, large seeds were taken predictably to poor sites for establishment and survival. Most seeds, and especially most large seeds, landed under and near the trees where mortality from seed predation and fungal pathogens was most prevalent. Small seeds tended to be dispersed farther but had poorer chances of survival. The lack of a correlation between seedling survival and initial seed mass is probably because most large seeds landed under or near parents where fungal attack and seed preda-

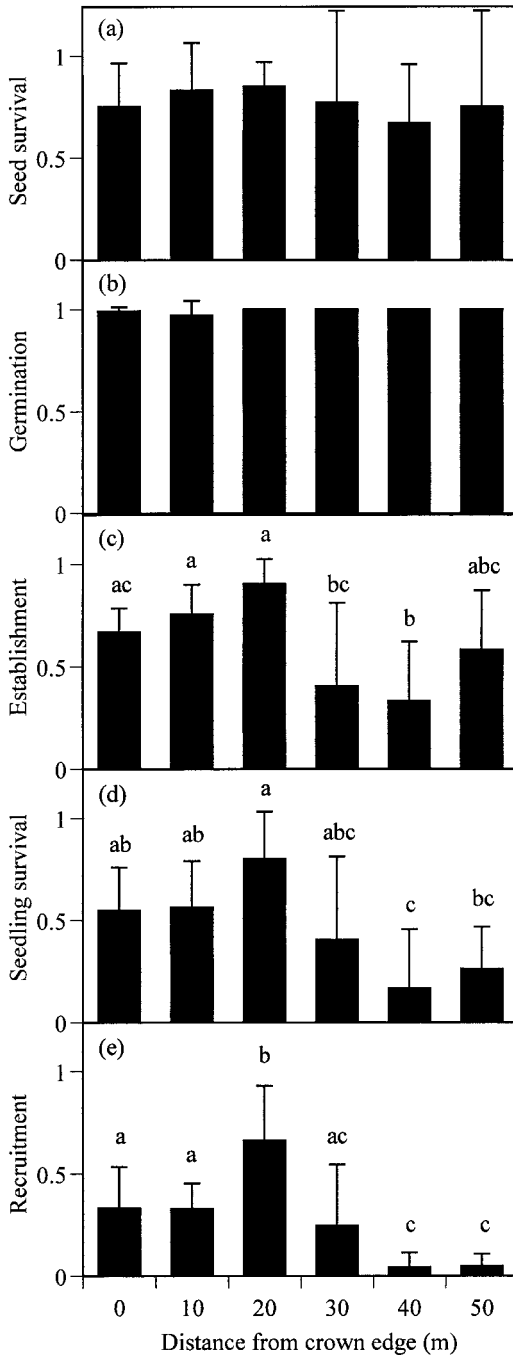


FIGURE 5. (a) Average ( $\pm 1$  SD) proportion of seeds surviving post-dispersal seed predators, (b) germinating, (c) establishing seedlings, and (d) surviving 15-months as functions of distance from the crown edge. Seeds deposited directly beneath the parental crowns (non-dispersed) are included in distance 0. The cumulative probability of recruitment (e) was calculated as the product of each of the four previous stages for each tree. Different letters

tion were higher than for seeds dispersed farther. The large seeds of *Beilschmiedia* enable the seedlings to resprout several times, but resprouts tend to be shorter than the first shoot (D. Wenny, pers. obs.). Therefore, one- to two-year seedlings from seeds of various sizes may be about the same height if large seeds resprout disproportionately. Thus, the relatively inefficient dispersal of *Beilschmiedia* was moderated by the survival advantages of large seeds.

Survival of seeds and seedlings was similar at random and naturally dispersed sites, suggesting a lack of specific habitat features important for *Beilschmiedia* seedling survival. Although microhabitat had some role in escape from seed predators (Table 2), the rate of seed predation was low compared to other Lauraceae species (Wheelwright 1988, Wenny in press). Thus, even though seed and seedling survival was slightly density- or distance-dependent (Table 2; Fig. 5d), recruitment of *Beilschmiedia* appears to be limited more by the number of seeds dispersed than by safe-site availability. Safe sites for large-seeded species with shade tolerant seedlings could be considered superabundant relative to those for species requiring certain substrates or light regimes for germination and establishment (McKey 1975, Foster & Janson 1985, Laman 1995). Large seeds can survive on cotyledonary reserves for several months, thus rendering variation in microsites relatively unimportant for short-term survival.

Although this study provides data on dispersal pattern and subsequent survival, it is only a short-term view. Growth to reproductive age for large canopy trees like *Beilschmiedia* takes decades. The peak in survival probability appears to be relatively close to parent trees, but this zone may shift farther away over time, as suggested by the size distribution of saplings. In this study, dispersal of a large seed long distances (*i.e.*, by regurgitators rather than defecators) was a relatively rare event, but these rare events may be important for recruitment. Whether or not seedlings in the zone of highest initial survival noted in this study retain that advantage through recruitment to reproductive age awaits data from longer-term studies. Processes such as herbivory, physical damage, drought, and changes in light availability are likely important for

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above bars indicate significantly different means ( $P < 0.05$ ) based on ANOVA and Fisher's LSD on arcsine-transformed data. Panels with no letters had no significant differences.

longer-term seedling/sapling survival, especially for large-seeded, shade tolerant species.

In McKey's (1975) original framework, dispersal quality of high quality fruits was greater relative to that of low quality fruits. *Ocotea endresiana* is a small-seeded (0.8 g) lauraceous tree in the same study site, and is dispersed by the same four bird species as *Beilschmiedia* along with several other bird species (Wheelwright *et al.* 1984, Wenny in press). Due to its smaller size, larger fruit crops, and larger disperser assemblage, *Ocotea* is lower on the specialist/generalist continuum than *Beilschmiedia*. Thus, one might expect *Ocotea* to have lower quality dispersal than *Beilschmiedia*; however, *Ocotea* fruits later in the year than *Beilschmiedia* at a time when male bellbirds are fully active on display perches, which are often on emergent snags near canopy gaps. Bellbirds dispersed many seeds in canopy gaps where seedlings had a survival advantage over seedlings in closed canopy forest (Wenny & Levey 1998). In that respect, *Ocotea* had higher quality dispersal than *Beilschmiedia*. Some low quality fruits (Phytolaccaceae, Solanaceae) in the area are more difficult to compare directly to *Beilschmiedia* because they had different dispersers, dormancy, and germination requirements (Murray 1988); but dispersal quality for *Beilschmiedia* was in no way obviously higher than for the low quality fruits.

The data on *Beilschmiedia* illustrate how multiple sources of selection on seed and seedling traits limit coevolution between plants and their dispersers (Herrera 1985, Wheelwright 1988). It is difficult to see how selection could simultaneously favor seedling survival via large seed size and increased dispersal via smaller seed size. The large investment per seed in *Beilschmiedia* limits dispersal

to areas near the parent trees, but favors persistent shade tolerant seedlings. A similar trade-off between dispersal and seed survival has been noted for some African trees (Chapman & Chapman 1996).

Dispersal quality for tropical trees has received little attention from ecologists despite the potential insights it could provide about forest dynamics (Howe 1993, Schupp 1993). In this study, I have shown that estimating short-term dispersal quality in the field is feasible. The next steps could include longer-term studies of recruitment from natural and experimental seed shadows, comparisons of recruitment in species with different fruit and seed morphologies dispersed by similar disperser assemblages, and detailed studies of recruitment for a plant species (or group of related species) at multiple sites. Such studies could lead to fruitful comparative analyses that address the underlying evolutionary factors involved in plant/disperser interactions.

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