

A model of patch dynamics, seed dispersal, and sex ratio in the dioecious shrub *Lindera benzoin* (Lauraceae)

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Summary

1 We used a combined model of forest canopy dynamics and patch-specific demography to examine the response of a forest understorey shrub, *Lindera benzoin*, to changes in rates of forest disturbance, rates of long distance seed dispersal, and relative effects of canopy closure on males and females. Because *L. benzoin* is dioecious, our analysis allowed an examination of sexual dimorphism and its effect upon habitat-specific patterns of sex ratio.

2 The matrix modelling approach followed that of Horvitz & Schemske (1986), in which demographic parameters of a population experiencing new treefall gap conditions are modified using functions describing changes in growth, survivorship and reproduction as gaps close.

3 In our analysis, effects of full canopy closure were estimated by comparing growth of adults in new treefall gaps with those in fully closed understorey, and by comparing mortality of seedlings and juveniles within subplots classified according to mean light level. Growth, survival and reproduction in intermediate successional patches leading to fully closed canopy followed a response pattern expected for shade-tolerant species, where declines in fitness components only become important as full canopy closure approaches.

4 Our results suggest positive effects of an increased rate of canopy disturbance and increased long-distance seed dispersal on mean population growth rate (fitness) in *L. benzoin*.

5 Our analyses predict only slightly male-biased adult sex ratios that result from relatively lower growth and survivorship for adult females (assumed to be associated with greater reproductive costs).

6 We discuss our results with respect to observed patterns of sexual dimorphism, seed dispersal, and adult sex ratio in *L. benzoin*, and in terms of the overall potential influence of forest gap dynamics on the demography of understorey shrubs.

Keywords: dioecy, Lefkovich matrix, metapopulation, population demography, seed dispersal, sex ratio, treefall gap dynamics

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Introduction

Spatial and temporal environmental variation is a major factor influencing the demography of populations, and thus the evolution of seed dispersal (Gadgil 1971). For stage-structured plant species, different life history stages may vary independently in their responses to environmental variation. The

overall demography of such populations depends upon stage- and habitat-specific demography, the spatial and temporal dynamics of the environment, and the pattern of seed dispersal.

In this paper, we use a matrix model (Horvitz & Schemske 1986) to examine the effects of forest dynamics and long-distance dispersal on mean population fitness in *Lindera benzoin* (L.) Blume, an understorey shrub. Responses of population growth rate to changes in life-history parameters provides information concerning selective pressure on those characters (Caswell 1989), as population growth rate is a

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measure of mean population fitness (Fisher 1930). The type of matrix model we used is one of two general approaches to the study of the demographic effects of spatial and temporal heterogeneity, the other being simulation models based on the behaviour of individuals (Alvarez-Buylla & Garcia-Barrios 1993). The matrix model approach assumes that overall 'metapopulation' (cf. Levins 1969) dynamics is a function of demography in a mosaic of contrasting habitat patches coupled with the dynamics of patch change. Because canopy treefall gaps represent a major source of habitat heterogeneity in mature forests (cf. Runkle 1985), such models generally focus on population demography in a series of successional patches ranging from newly formed gaps to fully closed understorey (cf. Horvitz & Schemske 1986; Martinez-Ramos *et al.* 1989; Alvarez-Buylla & Garcia-Barrios 1991). Dispersal among habitats, which may be of major demographic consequence (Murray 1986; Levey 1988; Murray 1988; Schupp *et al.* 1989), can be readily modelled using these techniques. Matrix models allow general results concerning population dynamics, evolution, and the management of plant species in fragmented landscapes (Alvarez-Buylla & Garcia-Barrios 1993). While both modelling approaches may suffer from assumptions of linearity, matrix models have an advantage in their ability to be solved analytically and in allowing patch dynamics to be easily linked with patch-specific population dynamics. Few studies (e.g. Perry & Gonzalez-Andujar 1993) have attempted to link individual-based models with metapopulation matrix models.

The simulations we applied were designed to examine three general questions:

- 1 How might population dynamics be affected by changes in the forest disturbance rate, defined as the probability of treefall gap formation? This information allows an assessment of the relative importance of habitat heterogeneity on population dynamics and can be of utility for forest management.
- 2 How does modelled variation in long-distance seed dispersal, defined as the proportion of seed dispersed out of patches, influence overall population demography? This question relates to the selection pressures exerted upon characters influencing seed dispersal. While primarily evolutionary in orientation, information concerning the potential influence of long-distance dispersal can also be used to address questions concerning the effects of local extinction of biotic dispersal agents.
- 3 How does sexual dimorphism in costs of reproduction affect population growth and adult sex ratio? Classic sex ratio theory generally predicts 1:1 offspring sex ratios in dioecious species (Fisher 1930). Thus, biased sex ratios in dioecious plants have been of much interest to evolutionary ecologists (cf. Allen & Antos 1993). While adult sex ratios in *L. benzoin* tend toward 1.0 (Niesenbaum 1992a), sex ratios may vary significantly among populations, ranging from

female bias (< 0.4) to male bias (> 1.2) (M. Cipollini, A. Mills, & D. Whigham, unpublished data). Sex ratio in plants has been examined using matrix models by at least two authors (Bierzychudek 1982; Meagher 1982). Effects of varying costs of reproduction in hermaphroditic plants have also been addressed using matrix methods (Calvo & Horvitz 1990; Calvo 1993). Nevertheless, sex ratio variation in plants has never been examined using a combined model of patch dynamics and patch-specific demography.

Materials and methods

STUDY SPECIES AND SITE

Individuals (genets) of the woody shrub *L. benzoin* bear unisexual flowers (Boyle 1980) and grow via the production of stems (ramets) from a central root bole. While considered shade tolerant, individuals show morphological and growth responses to increased light (Moore & Willson 1982; Veres & Pickett 1982; Niesenbaum 1993). In the north-eastern United States, plants flower in early April followed by new leaf and shoot initiation in early May. Although there are occasional hermaphroditic and sexually inconstant plants, sex expression is usually constant (Primack 1985). Female plants mature single-seeded fruits that are dispersed by birds in the fall (Stiles 1980; Johnson *et al.* 1985). Seeds either germinate the following May or die (C. Baskin, personal communication; M. Cipollini, personal observation).

At our study site, Smithsonian Environmental Research Center (SERC), Edgewater, Maryland, *L. benzoin* occurs in moist locations within understoreys of mid- to late-successional 'tulip poplar association' forests (Brush *et al.* 1980). The site of our primary study population, Fox Point, is a mid-successional site about 40 years since abandonment as a pasture (D. Higman, personal communication) situated on Aldelphia sandy loam (Kirby & Matthews 1973). The site was dominated by *Liriodendron tulipifera* L., *Liquidambar styraciflua* L., and *Prunus serotina* L. in the overstorey and was occupied almost exclusively by *L. benzoin* in the shrub layer.

CENSUS METHODS

To provide data for formulation of the basic population transition matrix, we censused plants at Fox Point. In June 1991, we tagged all adult genets within a 30-m × 50-m area and measured the height and basal diameter (at 5 cm above the ground) of all ramets. In April 1992, we added 96 newly flowering adults. As of this census, there were 251 female and 87 male genets tagged. In June 1992, we remeasured basal diameter and height of each living ramet. Ramet volume (RV) was estimated from basal radius (R) and ramet height (H), using the equation for a cone: $RV = (3.1416 \times R^2 \times H)/3$. For each genet, we esti-

mated genet volume (cm^3), by summing the volumes of the individual ramets. In August 1991 and 1992, we counted mature fruits on all females.

In order to estimate survivorship of juveniles and seedlings, 52 subplots ($1 \text{ m} \times 2 \text{ m}$) were randomly established at Fox Point. Individuals within subplots were censused and mapped in June 1991 ($n = 245$ seedlings, 176 juveniles) and June 1992 ($n = 130$ seedlings, 148 juveniles [including seedlings from 1991]). On four dates in 1992 (20 July, 29 July, 1 August, and 4 August), we measured light intensities ($\mu\text{mol m}^{-2} \text{ s}^{-1}$) at 0.3 m above 35 randomly-selected subplots by recording the mean of four light meter readings (LICOR # LI-185A) taken at 1-minute intervals.

COMPARISON OF GAP AND UNDERSTOREY ADULTS

In July 1992, we located adults in newly-formed tree-fall gaps (40 females, 37 males) and in nearby full understorey conditions (41 females, 38 males), within forest areas adjacent to Fox Point. Height (cm), basal diameter (cm), and ramet volume (cm^3) were determined for the largest ramet within each genet. Additionally, we measured terminal shoot (height) growth (cm) for the largest ramet and counted the number of fruits on the terminal stem. We analysed these data using ANCOVA (main effects = sex and site, using initial ramet volume as a covariate). Comparisons between gap and understorey adults provided an estimate of the relative effects of canopy closure on growth, under the assumption that relative differences in ramet growth corresponded with relative differences in genet growth.

FOREST GAP DYNAMICS

In order to assess forest canopy dynamics, we collected data in mid-to-late successional forest (about 40–150 years since abandonment as cattle pasture) adjacent to Fox Point. In July 1992, we located treefall gaps that had been mapped in 1991 within a 442.5 hectare tract (D. Whigham & D. Higman, unpublished data) and surveyed area adjacent to these gaps to locate previously unmapped gaps. Gaps included canopy treefalls and standing dead canopy trees. For 54 gaps, we used the decomposition state of the tree and the growth of the surrounding herbaceous layer to estimate whether the gap had formed within the previous year or in a previous time period. This qualitative assessment served to distinguish newly formed gaps from those that had been missed previously. We measured the minimum and maximum axis of the ground projection of each gap, and estimated gap area (m^2) as an ellipse.

The ratio of newly formed gaps to the total number of gaps visited was used to estimate the number of newly-formed gaps for the entire survey area. Area occupied by new gaps was then estimated by mul-

tiplying by the average area of such gaps. Area in fully closed canopy at the start of the previous year was calculated by subtracting the total area in gaps ≥ 1 year old from the total survey area. The ratio of the area in new gaps to the area in closed canopy at the start of the previous year was considered the rate of new gap formation in closed canopy (k ; see Matrix model construction, below). Using an estimate of the rate of radial encroachment by canopy trees (0.35 m year^{-1} ; G. Parker, personal communication), we estimated the time to full canopy closure for each new gap as the minimum radius of the gap divided by twice the mean radial encroachment (mean = 8.33 years).

MATRIX MODEL CONSTRUCTION

We used a modification of the model of forest dynamics and patch-specific population dynamics described by Horvitz & Schemske (1986):

Treefall gap dynamics

Forest dynamics are modelled as a linear Markovian process of succession (cf. Fig. 1 of Horvitz & Schemske 1986) following patch formation caused by death of canopy trees. This is represented by the matrix \mathbf{P} (Table 1), whose entries p_{ij} are the probabilities that type- j patches become type- i patches in one year's time (a patch is defined as an area equal to that of an average treefall gap). In one-year's time, patches either age one year or revert to a new treefall gap; thus, the number of patch types (successional stages) is determined by the years required for canopy closure (in our case, 8.33 years). The column eigenvector, \mathbf{f}^* , associated with the dominant eigenvalue of the \mathbf{P} matrix is proportional to the stable patch type distribution; i.e. the proportion of patches of various successional stages in the environment. Values for p_{ij} are shown for two forest disturbance levels (k) in Table 1, under the assumption that the probability of treefall gap formation (p_{1j}) has a very low value within new treefall gaps and increases to an asymptotic value, k , in closed canopy (cf. Fig. 2 of Horvitz & Schemske 1986).

Patch-specific population dynamics

For population dynamics, one assumes an age- or stage-classified model (Leslie 1945; Lefkovich 1965; Caswell 1989), which can be illustrated by a life cycle diagram showing transitions among stages. The life cycle for *L. benzoin* (Fig. 1) included five stages for males and females: seeds (1,6), seedlings (2,7), juveniles (3,8), small adults (4,9), and large adults (5,10). Adults were plants that have flowered at least one time in the past, a definition with implications for sex ratio analysis. While it is possible that small adults may regress to a juvenile state, within the relatively

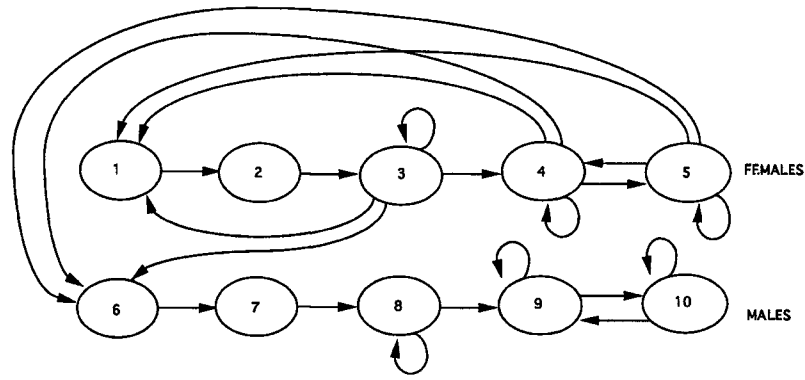


Fig. 1 Life-history diagram for *Lindera benzoin*. Circles represent various life-history stages for males and females (1,6 = seeds; 2,7 = seedlings; 3,8 = juveniles; 4,9 = small reproductive; 5,10 = large reproductive). Arrows represent transitions or contributions of a given stage class to another stage class over one year's time.

young Fox Point population, adult-to-juvenile transitions have not been observed across three census years (see Cipollini & Whigham 1994). We thus assumed these transitions to be negligible for this analysis. Additionally, we assumed that transitions were equal for male and female seeds, seedlings, and juveniles, although they could not be sexed at these

stages. Adult size classes were determined using Moloney's (1986) algorithm.

Reproduction is represented by arrows leading to the seed stage in Fig. 1. Our model was female-dominant (Caswell & Weeks 1986); that is, seed set in females was assumed to be unaffected by the sex ratio. This assumption was based upon data showing no

Table 1 Patch dynamics transition matrices (\mathbf{P}) and stable patch type distributions (\mathbf{f}^*) for two levels of canopy disturbance rate (k). Each element p_{ij} represents the transition from patch type- j to patch type- i in 1 year's time

(a) Probability of new gap formation in closed canopy (k) = 0.0086

0.000100	0.000903	0.004638	0.007921	0.008527	0.008593	0.008599	0.008599	0.008600
0.999900	0	0	0	0	0	0	0	0
0	0.999097	0	0	0	0	0	0	0
0	0	0.995362	0	0	0	0	0	0
0	0	0	0.992079	0	0	0	0	0
0	0	0	0	0.991473	0	0	0	0
0	0	0	0	0	0.991407	0	0	0
0	0	0	0	0	0	0.991401	0	0
0	0	0	0	0	0	0	0.991400	0.991400

(b) Probability of new gap formation in closed canopy (k) = 0.0172

0.000100	0.001092	0.007566	0.015497	0.017038	0.017186	0.017199	0.017199	0.017200
0.999900	0	0	0	0	0	0	0	0
0	0.998908	0	0	0	0	0	0	0
0	0	0.992434	0	0	0	0	0	0
0	0	0	0.984503	0	0	0	0	0
0	0	0	0	0.982962	0	0	0	0
0	0	0	0	0	0.982814	0	0	0
0	0	0	0	0	0	0.982801	0	0
0	0	0	0	0	0	0	0.982800	0.982800

(c) Stable patch type distribution (\mathbf{f}^*):

Patch type $k = 0.0086$ $k = 0.0172$

1 (new gap)	0.00842	0.01646
2	0.00842	0.01646
3	0.00841	0.01644
4	0.00837	0.01632
5	0.00831	0.01606
6	0.00823	0.01579
7	0.00816	0.01552
8	0.00809	0.01525
9 (understorey)	0.93354	0.87167

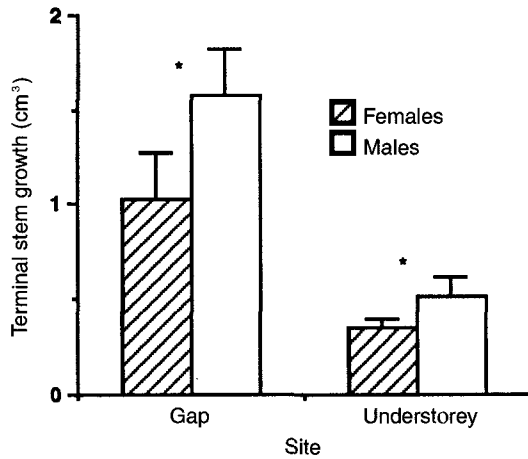


Fig. 2 Terminal stem growth of female and male *L. benzoin* located within new treefall gaps (GAP) or in adjacent understorey (UNDERSTOREY). Vertical bars are standard errors. Asterisks denote significant differences between males and females based upon two-way ANCOVA (covariate = initial ramet volume).

effect of sex ratio and/or pollen:ovule ratio on fruit set in *L. benzoin* (M. Cipollini, unpublished data; Niesenbaum 1992a), and a two-sex frequency-dependent model showing only negligible effects of sex ratio imbalance on female fertility in *L. benzoin* (M. Cipollini, A. Mills, & D. Whigham, unpublished data).

The life cycle is represented as the matrix **M** in Table 2(a), whose entries, m_{ab} , represent transitions from stage *b* to stage *a* in one year's time. In our model, intersexual transitions were not possible, except for row 6, which represented the contribution of females to male seeds (assuming a 1:1 primary sex ratio). Juveniles, small adults, and large adults contribute to seed production via the product of their transitions to reproductive stages 4 and 5 (m_{4b} , m_{5b}) and the stage specific fertilities of those stages ($z_4 = 18.2$, $z_5 = 189.5$):

$$m_{1b} = m_{6b} = ((m_{4b} \times z_4) + (m_{5b} \times z_5)) / 2. \quad (1)$$

The dominant eigenvalue of **M**, λ , is an estimate of asymptotic multiplicative population growth. The associated right eigenvector, **w**, is proportional to the stable stage distribution, while the associated left eigenvector, **v**, is proportional to stage-specific reproductive values (Caswell 1989). The elements of the elasticity matrix **E**, e_{ab} , are the relative effects of proportional changes in the elements of **M** with respect to λ (de Kroon *et al.* 1986).

The numerical values in Table 2b were obtained from our analysis of *L. benzoin* at Fox Point (Cipollini & Whigham 1994; M. Cipollini, A. Mills, & D. Whigham, unpublished data), and represent dynamics in the most favourable site, a new treefall gap (NEWGAP demography). Although the population was not entirely in a new treefall gap, the plot was in a very young forest with a relatively open canopy containing several large treefall gaps (about 20–33% canopy openness).

We know that growth, survival and reproduction

in *L. benzoin* is depressed in low-light microsites (see Results, below); however, we do not have census data for subpopulations occupying a range of habitats along the gap-understorey continuum. To address this problem, Horvitz & Schemske (1986) obtained estimates of the degree with which growth, survival and reproduction of each stage is depressed in full understorey relative to new gaps. These estimates are used to create demographic matrices corresponding to the intermediate stages leading to fully closed canopy. This is done by applying cost parameters, c_{bj} (i.e. the 'demographic decay' values of Horvitz & Schemske 1986), that represent the proportionate reduction in growth, survival, and/or reproduction of the *b*th stage in the *j*th patch, relative to the NEWGAP matrix. For our analysis, the stage-specific costs of full canopy closure (c_{b9}) had the following values: Seeds (c_{19} and c_{69}): 0.20, seedlings (c_{29} , c_{79}): 0.50, juveniles (c_{39} and c_{89}): 0.50, adults (c_{49} , c_{59} , c_{99} , $c_{10,9}$): 0.6651. These values were estimated by comparing seedling and juvenile survivorship in 'high-light' and 'low-light' subplots at Fox Point, and by comparing ramet growth rates of adults in treefall gaps and full understorey (see Results, below). The slight (0.20) cost for the seed stage was an estimate based upon the observation of high germination rates even under low light, and the assumption that survival of seedlings from the May germination period to the late June census period would be affected only slightly by canopy conditions. We estimated a cost to fruit production (c_{29}) = 0.0929, based upon growth-independent reduction in fruit production in understorey plants (see Results, below).

For *L. benzoin*, we applied a model of response to canopy closure considered appropriate for shade-tolerant plants and termed 'non-linear slow' by Horvitz and Schemske (1986):

$$c_{bj} = [(j-1)/8]^4 \times c_{b9}, \quad (2)$$

with an analogous expression for costs to fruit production (c_{zj}). In this response pattern, reductions in growth, survivorship, and reproduction are very slow during the early stages of gap closure, then rapidly accelerate as full canopy closure is approached (cf. Fig. 4 of Horvitz & Schemske 1986). Transition matrices corresponding to the nine successional patch types leading from newly formed gaps (the NEWGAP matrix) to fully closed understorey (the UNDERSTOREY matrix), were produced by using the cost parameters to reduce growth, survival and reproduction of each stage relative to the NEWGAP matrix. For adults, we modelled only reductions in growth and reproduction, without decreasing survivorship. We based this modification from Horvitz & Schemske (1986) on our observations of extremely low mortalities for adults, even in the most shaded habitats.

Overall population dynamics

Subsequent modelling of overall population dynamics and long-distance seed dispersal followed explicitly

Table 2 Generalized and numerical examples of the population dynamics transition matrix (**M**). Each element m_{ab} , represents the transition from stage class b to stage class a over 1 year's time

(a) Generalized matrix									
0	0	m_{13}	m_{14}	m_{15}	0	0	0	0	0
m_{21}	0	0	0	0	0	0	0	0	0
0	m_{32}	m_{33}	0	0	0	0	0	0	0
0	0	m_{43}	m_{44}	m_{45}	0	0	0	0	0
0	0	0	m_{54}	m_{55}	0	0	0	0	0
0	0	m_{63}	m_{64}	m_{65}	0	0	0	0	0
0	0	0	0	0	m_{76}	0	0	0	0
0	0	0	0	0	0	m_{87}	m_{88}	0	0
0	0	0	0	0	0	0	m_{98}	m_{99}	$m_{9,10}$
0	0	0	0	0	0	0	0	$m_{10,9}$	$m_{10,10}$
(b) NEWGAP matrix (newly formed gap)									
0	0	0.1367	31.714	91.783	0	0	0	0	0
0.1344	0	0	0	0	0	0	0	0	0
0	0.6168	0.6927	0	0	0	0	0	0	0
0	0	0.0158	0.7332	0.0355	0	0	0	0	0
0	0	0	0.2668	0.9645	0	0	0	0	0
0	0	0.1367	31.714	91.783	0	0	0	0	0
0	0	0	0	0	0.1344	0	0	0	0
0	0	0	0	0	0	0.6168	0.6927	0	0
0	0	0	0	0	0	0	0.0158	0.7000	0.0173
0	0	0	0	0	0	0	0	0.2977	0.9827
(c) UNDERSTOREY matrix (understorey)									
0	0	0.0310	15.134	33.386	0	0	0	0	0
0.1075	0	0	0	0	0	0	0	0	0
0	0.3084	0.1771	0	0	0	0	0	0	0
0	0	0.0040	0.9105	0.6769	0	0	0	0	0
0	0	0	0.0894	0.3231	0	0	0	0	0
0	0	0.0310	15.134	33.386	0	0	0	0	0
0	0	0	0	0	0.1075	0	0	0	0
0	0	0	0	0	0	0.3084	0.1771	0	0
0	0	0	0	0	0	0	0.0040	0.9002	0.6708
0	0	0	0	0	0	0	0	0.0997	0.3292

the methods of Horvitz & Schemske (1986). Transitions among stages and patch types were contained in a matrix **G**, comprised of eighty-one 10×10 submatrices, **SUB_{ij}**. Each entry in **G**, g_{abij} , represented the probability that an individual in stage class b in patch type j contributed to or appeared as an individual in stage class a in patch type i after one year's time. All submatrices of **G** were initially zeros, except for the diagonal (**SUB_{ij}**) matrices which were the nine patch-specific demographic matrices (NEWGAP through UNDERSTOREY matrices). The patch dynamics transition parameters, p_{ij} (Table 1) determined the probabilities that patches change between censuses. We assumed that most treefalls occur during times of high wind in the springtime, just before the annual census. We thus post-multiplied the diagonal **SUB_{ij}** matrices by p_{ij} to obtain the submatrices **SUBT_{ij}**:

$$\mathbf{SUBT}_{ij} = \mathbf{SUB}_{ij} \times p_{ij} \quad (3)$$

The resulting matrix represented overall dynamics including patch-specific demography and successional change.

Long-distance seed dispersal was modelled by

defining y as the proportion of seeds that are dispersed out of patches and by assuming that the probability that dispersed seeds reach a particular habitat (patch type) depends only upon the relative frequency of that habitat in the environment, \mathbf{f}^* .

Matrix analysis and modelled parameters

AT-MATLAB (The Mathworks, Inc. 1989) was used to construct the matrices and to calculate λ , \mathbf{w} , \mathbf{v} , and **E**. We modelled variation in three sets of parameters:

1 New treefall gap formation (k) at the observed rate of 0.0086, and at a doubling of that rate to 0.0172;
2 Long-distance seed dispersal (y) at values ranging from 0 to 1.0;

3 The cost of full canopy closure for adult females at a value equal to that of males and at a value 25% greater (c_{49} and $c_{59} = 0.8313$ for females; c_{99} and $c_{10,9} = 0.6651$ for males). While our analyses indicated sexual dimorphism in growth, but no differences between the sexes in the effects of canopy closure (see Results, below), Niesenbaum (1992b) suggested that

growth may be disproportionately reduced for female *L. benzoin* under low light conditions.

We estimated the variance, $V(m_{ab})$, associated with the transition elements in the NEWGAP matrix, using bootstrap resampling with replacement of the census data ($n = 1000$ bootstraps; Efron & Tibshirani 1986). Variances for elements of modelled matrices (i.e. the submatrices of \mathbf{G}) were estimated from coefficients-of-variation for the elements of the NEWGAP matrix. For each patch-specific matrix (NEWGAP through UNDERSTOREY) we estimated the variance associated with λ , $V(\lambda)$, using the equation of Caswell (1989),

$$V(\lambda) = \sum_{i,j} ((\delta_{\lambda}/\delta m_{ab})^2) \times V(m_{ab}), \quad (4)$$

with a similar expression for the full matrix \mathbf{G} . Assuming random distribution, small variances and independence of matrix elements, 95% confidence limits are $\pm 1.96 \times (\sqrt{V(\lambda)})$.

Results

LIGHT-LEVEL VARIATION AND PLANT DEMOGRAPHY

For adults at Fox Point, we could find no relationship of light level to growth (basal growth, height increase, ramet and genet volume growth) or seed production (M. Cipollini, D. Wallace-Senft, & D. Whigham, unpublished data). This was true for light intensities estimated from light meter readings and for estimates from canopy fisheye photos (cf. Chazdon & Field 1987). We thus focused on adults located in and out of treefall gaps to estimate the effects of canopy closure on adults. Results of these comparisons are illustrated by Fig. 2, which shows shoot growth of males and females located in and out of gaps. Males and females showed a similar reduction in growth in understorey conditions (65.92% reduction for females, 67.09% reduction for males). Based upon two-way ANCOVA, the effects of sex and site were significant ($F_{1,153} = 11.65$, $P < 0.001$ for sex; $F_{1,153} = 17.10$, $P < 0.0001$ for site), while the sex-site interaction was not. This indicates that males and females responded equally to canopy condition (site) at SERC. Additionally, upon controlling for variation in plant size (ramet volume) using one-way ANCOVA, fruit production was reduced by 9.29% in full understorey ($F_{1,79} = 4.22$, $P < 0.05$ for site). These values were used to estimate the costs of full canopy closure for adult transition elements (c_{49} , c_{59} , c_{99} , $c_{10,9} = 0.6651$) and for adult seed production ($c_{29} = 0.0929$).

For 'high-light' subplots (mean light level $\geq 100 \mu\text{mol m}^{-2} \text{s}^{-1}$), survival of seedlings from 1991 to 1992 was 18/24 = 75.0%, whereas survival for 'low-light' subplots (mean light level $< 100 \mu\text{mol/m}^2/\text{s}$) was 44/116 = 37.9% ($\chi^2_1 = 6.27$, $P < 0.05$). We chose the light level of $100 \mu\text{mol m}^{-2} \text{s}^{-1}$ as a threshold value between low-light and high-light subplots because this

was close to the minimum light level recorded in nearby treefall gaps. Comparison of these values gave an estimated cost of full canopy closure of 0.5053 for seedlings. Comparisons for juveniles yielded survival values of 17/25 = 68.0% for high light subplots and 32/95 = 33.7% for low light subplots ($\chi^2_1 = 5.71$, $P < 0.05$), which provided an almost identical cost of full canopy closure of 0.4956 for juveniles. For simplicity, we used a value of 0.50 for both seedlings (c_{29} , c_{79}) and juveniles (c_{39} , c_{89}).

FOREST CANOPY DYNAMICS

Data concerning forest canopy dynamics are summarized in Table 3. We estimated that new treefall gaps in 1992 comprised 0.86% of the area that had been closed canopy in 1991. Given the assumed rate of radial encroachment (0.35 m year^{-1}), time to canopy closure was 8.33 years, which yielded the nine successional stages used in the forest dynamics model. Treefall gaps had light levels that were, on average, about 7 times higher than those of adjacent understorey (M. Cipollini, D. Wallace-Senft, & D. Whigham, unpublished data).

At $k = 0.0086$, the stable patch type distribution, \mathbf{f}^* , was dominated by understorey; over 93% of patches were understorey (Fig. 3). The relative area in gaps of all ages (sum of \mathbf{f}^*_1 through \mathbf{f}^*_8) was 0.0665, which compares favourably with our empirical estimate of 0.0623 (Table 3). Additionally, the predicted proportion of area in new gaps (0.0084) was very close to our empirical estimate (0.0080). When k was doubled to 0.0172, \mathbf{f}^* was shifted accordingly, with an increased relative abundance of early successional patches (Fig. 3).

Patch-specific demography

Analysis of the patch-specific demographic matrices (NEWGAP through UNDERSTOREY matrices) indicated that population growth rate (λ) was significantly higher than 1.0 in all habitat types (Fig. 4a). This suggests that *L. benzoin* may be not be dependent upon treefall gap formation for maintenance of population growth. As expected, large adult females had the highest reproductive values (data not shown), and as expected from the female-dominant model formulation, elasticities were zero for all parameters involving males (Table 4a,b). Elasticity analysis suggested that the most influential elements shifted from the large adult-to-large adult transition for females (m_{55}) in new gaps (Table 4a) to the small adult-to-small adult transition for females (m_{44}) in full understorey (Table 4b).

When costs of canopy closure were held equal for males and females, sex ratios within each habitat type remained very close to 1.0, with a trend toward slight male-bias in the understorey (Fig. 4b). When costs of canopy closure were made 25% higher for females,

Table 3 Summary of data used to estimate forest canopy dynamics parameters. Where applicable, means are presented with standard errors in parentheses

Variable	Mean
Total forest area surveyed 1990–91*	442500 m ²
Gaps mapped 1990–91	429
Gaps relocated in 1992	43
New gaps located in 1992	11
Mean minimum gap diameter ($n = 54$)	5.83 (0.39) m
Mean maximum gap diameter ($n = 54$)	9.54 (0.92) m
Mean area of existing gaps ($n = 43$)	55.90 (12.27) m ²
Mean area of new gaps ($n = 11$)	41.30 (10.11) m ²
Estimated parameters:	
Mean time to new gap closure ($n = 54$)	8.33 (0.55) year
Total number of new gaps	87.4
Total area in new gaps 1992	3609.6 m ²
Proportion of area in new gaps 1992	0.00816
Total area in existing gaps 1991	23981.1 m ²
Total area in closed canopy 1991	418518.9 m ²
Rate of new gap formation in closed canopy (k)	0.00862
Total area in gaps 1992	27590.7 m ²
Proportion of area in gaps 1992	0.06235

*SERC forest canopy gap inventory (D. Higman, personal communication)

sex ratios still remained very close to 1.0 within each habitat type, but showed a shift toward slightly greater male-bias in the understorey (Fig. 4b). Patch-specific sex ratios never exceeded 1.005 in any case.

POPULATION DYNAMICS COUPLED WITH FOREST CANOPY DYNAMICS

When the model of patch-specific demography was combined with forest canopy dynamics, overall population growth rate reflected not only patch-specific plant demography, but also the dynamic equilibrium of forest patch types. Under all conditions of seed dispersal, doubling the rate of canopy gap formation (k) had a positive effect on overall population growth rate (Fig. 5a), an effect that became statistically significant at higher levels of seed dispersal ($\gamma \geq 0.4$).

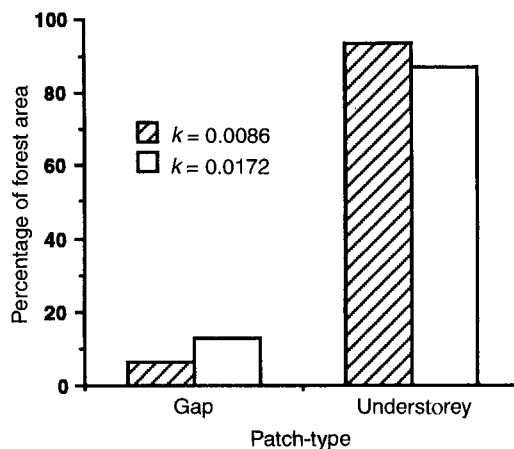


Fig. 3 Stable patch type distribution under two assumed rates of forest canopy disturbance (k). Patch types 1–8 have been combined to represent gaps of all ages (GAP), while patch type 9 represents area in full understorey (UNDERSTOREY).

Table 4 Results of eigenanalysis of patch-specific demographic matrices PATCH-1 and PATCH-9, with costs of canopy closure identical for males and females. Confidence limits (95%) on λ are in parentheses, and **E** represents the elasticity matrix

NEWGAP matrix					
$\lambda = 1.155$ (1.127 – 1.184)					
Adult sex ratio = 1.00003					
E (rows 1 to 5, columns 1 to 5)					
0	0	0.0016	0.0149	0.0599	
0.0763	0	0	0	0	
0	0.0763	0.1152	0	0	
0	0	0.0748	0.1483	0.0097	
0	0	0	0.0696	0.3535	
Stable population distribution (w)					
	Seeds	Seedlings	Juveniles	Small adults	Large adults
Females	0.3819	0.0444	0.0672	0.0027	0.0038
Males	0.3819	0.0444	0.0672	0.0024	0.0041
Overall	0.7639	0.0889	0.1343	0.0051	0.0081
UNDERSTOREY matrix					
$\lambda = 1.003$ (0.991 – 1.015)					
Adult sex ratio = 1.00047					
E (rows 1 to 5, columns 1 to 5)					
0	0	0.0000	0.0022	0.0006	
0.0029	0	0	0	0	
0	0.0029	0.0006	0	0	
0	0	0.0029	0.7965	0.0769	
0	0	0	0.0776	0.0369	
Stable population distribution (w)					
	Seeds	Seedlings	Juveniles	Small adults	Large adults
Females	0.4130	0.0443	0.0187	0.0212	0.0028
Males	0.4130	0.0443	0.0187	0.0209	0.0031
Overall	0.8261	0.0886	0.0373	0.0422	0.0059

This resulted from an increased proportion of the landscape occupied by gap habitats, where growth, survivorship and reproduction was increased. For instance: for $y = 0.2$, a doubling of k from 0.0086 to 0.0172 increased the proportion of each stage class within gaps by over 50% (Fig. 6).

Under conditions of increased canopy gap formation, slightly male biased adult sex ratios become less male biased, although sex ratios still remained very close to 1.0 (Fig. 5b). In all cases, sex ratios were more male biased in the large size class, relative to the small size class. This was a consequence of the relatively greater probability of males moving from the small to the large size class ($m_{10,9}$ relative to $m_{5,4}$) and their relatively greater probability of staying in that size class ($m_{10,10}$ relative to $m_{5,5}$). Adult sex ratios were also slightly less male-biased in gaps under all conditions (Fig. 4b). This result was associated with shifts in the stable population distribution (Table 4b) showing a relatively greater proportion of small adults (i.e. adults with risk of mortality) in the understorey. Because females are relatively more abundant in the

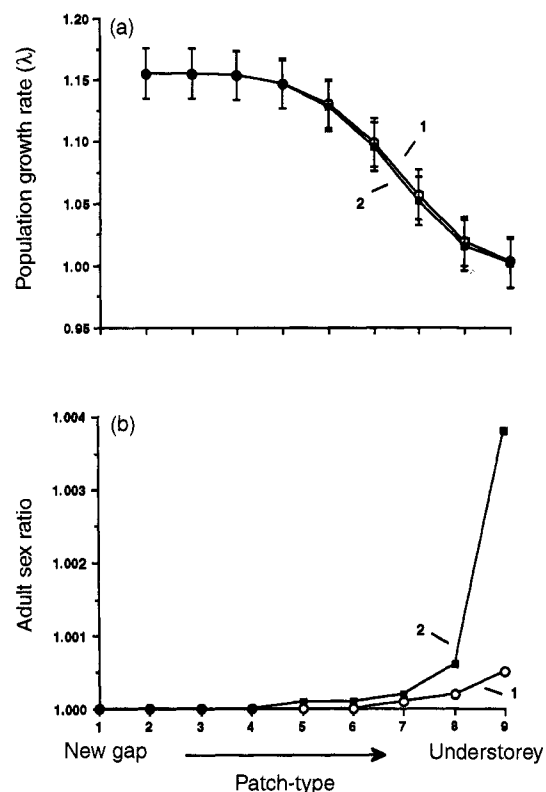


Fig. 4 Effects of habitat type and differential demographic behaviour on (a) population growth rate ($\lambda \pm 95\%$ confidence limits) and (b) adult sex ratio (males/females). This analysis is for demography within each patch-type, with patch-types characterized along a continuum from newly formed gaps (NEWGAP matrix) through fully closed understorey (UNDERSTOREY matrix), in absence of patch dynamics and seed dispersal. In each figure, the curve labelled '1' represents results for effects of canopy closure held equal for male and female adults, while the curve labelled '2' represents results for such effects made 25% greater for females.

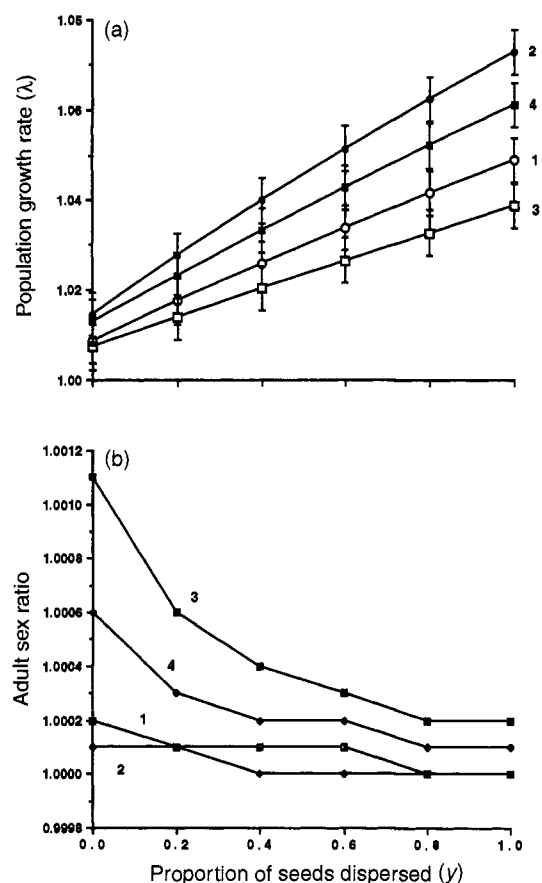


Fig. 5 The effects of forest disturbance rate (k), seed dispersal (y), and differential demographic behaviour of males and females on (a) overall population growth rate ($\lambda \pm 95\%$ confidence limits) and (b) adult sex ratio. This analysis incorporates patch-specific demography, patch dynamics, and migration of seeds among patches. The curves represent results for variation in rate of seed dispersal under four different sets of modelled conditions: Curves 1 and 2, $k = 0.0086$ and 0.0172 , respectively, with effects of canopy closure on growth held equal for males and females, Curves 3 and 4, $k = 0.0086$ and 0.0172 , respectively, with effects of canopy closure made 25% greater for females.

small adult size class in the understorey (Table 4b), they are relatively more likely to suffer mortality.

At both levels of forest disturbance, increasing seed dispersal rate (y) increased population growth (Fig. 5a). The primary stage classes influenced by increased long-distance seed dispersal were seedlings and juveniles, whose presence was increased in both gap and understorey conditions (Fig. 7). According to elasticity analyses of patch-specific submatrices (Table 4), seedling and juvenile stages have little effect on population growth in understorey conditions, whereas transitions involving these stages have a more significant impact on population growth within gaps. This suggests that the slightly increased proportion of seedlings and juveniles in gaps is associated with the increased population growth rates seen under conditions of increased long-distance dispersal.

Overall adult sex ratios become slightly less male-biased with increasing seed dispersal (Fig. 5b). This

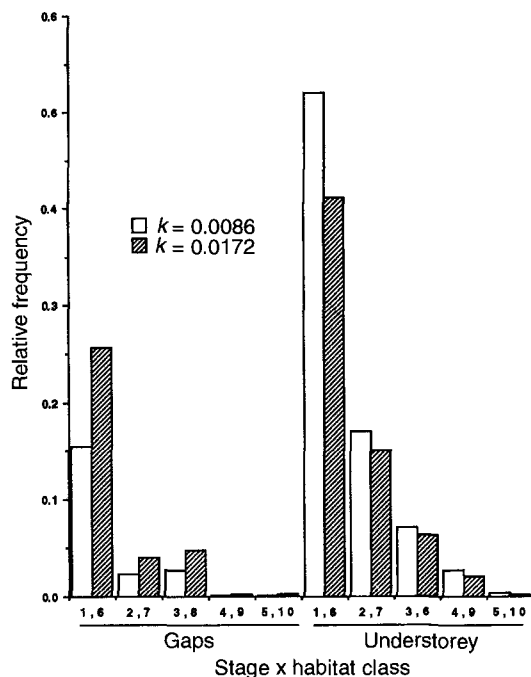


Fig. 6 Effects of forest disturbance (k) on the distribution of life history stages among patches at equilibrium. As with Fig. 3, results for patch types 1 to 8 have been combined to represent gaps of all ages (GAP), while patch type 9 represents understorey conditions (UNDERSTOREY). Results are for two levels of canopy disturbance (low disturbance, $k = 0.0086$; high disturbance, $k = 0.0172$), holding seed dispersal rate constant ($\gamma = 0.2$).

was a consequence of a relatively greater proportion of the adult population occupying gap conditions (an increase in the ratio of adults in gaps to adults in understorey), where sex ratios are less male-biased (Fig. 4b). Nevertheless, overall adult sex ratios remained very close to 1.0.

As expected, population growth rates were depressed when the costs of full canopy closure for females were increased by 25% over those of males (Fig. 5a). This resulted from a decrease in the representation of large adult females in the stable stage \times patch-type distribution (results not shown). Although showing slightly stronger male-bias, sex ratios remained close to 1.0, only ranging up to 1.0015 for $k = 0.0086$, $\gamma = 0$; Fig. 5b).

Discussion

Our empirical estimate of $k = 0.0086$ compared favourably with values ranging from about 0.004 to 0.02 for mature forests (Hartshorn 1978; Brokaw 1982; Runkle 1985; Runkle & Yetter 1987). Present rates of disturbance at SERC may be somewhat lower than those of more mature forests because fully mature forests may contain a greater abundance of large canopy individuals more prone to death (Lorimer 1989). In fact, the mean size of a new gap at SERC (40–50 m²) was at the low end of the range of gap sizes for temperate hardwood forests (Runkle

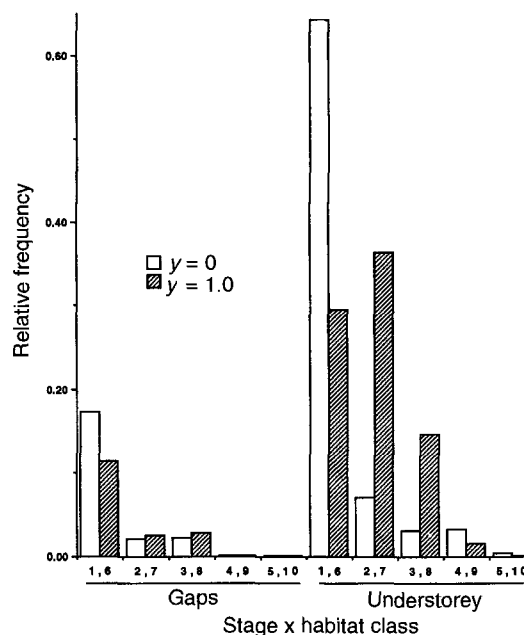


Fig. 7 Effects of long-distance seed dispersal (γ) on the distribution of life history stages among patches at equilibrium. As with Fig. 3, results for patch types 1 to 8 have been combined to represent gaps of all ages (GAP), while patch type 9 represents understorey conditions (UNDERSTOREY). Results are for two levels of seed dispersal (no dispersal, $\gamma = 0$; 100% dispersal, $\gamma = 1.0$), holding forest disturbance rate constant ($k = 0.0086$).

1985; Lorimer 1989). In addition to varying with age of the forest, disturbance rates can be expected to vary depending upon the pattern and timing of events such as wind storms, disease and insect outbreaks. Thus, our single year estimate should be taken only as a rough estimate of current rates of canopy opening.

Similarly, the rate of canopy closure was estimated in a crude fashion. Unlike several other models (cf. Alvarez-Buylla & Garcia-Barrios 1991), our analysis did not distinguish among gaps of various sizes or with respect to the pattern of canopy closure; i.e. radial encroachment versus vertical and horizontal expansion of subcanopy trees. We assumed that all gaps progress toward full canopy closure at the same rate. Despite this, our estimate of mean time to full gap closure corresponds closely to published reports (e.g. Runkle 1985), thus may be considered a realistic approximation. The observed relative area in gaps (0.0623) was close to the value derived from the stable patch type distribution (0.0665), which suggests that the forest model we used was a fairly good predictor of current canopy conditions.

Our results suggest that *L. benzoin* should exhibit population growth in all habitats including full understorey, which is consistent with its classification as shade-tolerant (Veres & Pickett 1982). Demographic analysis of all life-history stages in gaps of various sizes and ages would assist in producing more accurate patch-specific matrices (Howe 1990; Phillips & Shure 1990; Dirzo *et al.* 1992; Cipollini *et al.* 1994).

To our knowledge, the only analyses that incorporate a broad range of patch ages and sizes are studies of the demographics of *Cecropia obtusifolia* (Alvarez-Buylla & Garcia-Barrios 1991) and *Astrocaryum mexicanum* (Martinez-Ramos *et al.* 1989) at Los Tuxtlas, Mexico.

Our analyses suggests that a doubling of the rate of new gap formation would be associated with increased population growth rate. These results are consistent with the increased growth, survivorship and reproduction of *L. benzoin* in gaps relative to full understorey, and an increase in the relative abundance of gaps at higher rates of disturbance. Thus, even for shade-tolerant species such as *L. benzoin*, forest canopy dynamics can have important consequences for population structure and dynamics. Because actual responses depend not only on patch-specific demographics, but also on patterns of forest canopy dynamics, better data on rates of canopy opening and closure will be necessary to address these predictions more precisely. Such data are presently being collected at SERC via a forest gap inventory (D. Whigham & D. Higman, unpublished data).

Increasing the seed dispersal rate increased population growth rate, which is indicative of selection for long-distance dispersal. This result was associated with an increased proportion of seedlings and juveniles occupying both gap and understorey conditions. Under conditions of little or no seed dispersal, all seeds produced in the understorey remain there. Under conditions of increased dispersal, seeds produced in the understorey can be dispersed to gaps, where subsequent growth and survivorship is enhanced, and where proportional effects upon population growth are higher (as indicated by relatively higher elasticities for seedlings and juveniles in gaps). While seeds are also dispersed out of gaps to the understorey, the stable stage \times patch-type distribution shows that the relative proportion of seeds in gaps (seeds in gaps/seeds in understorey) increases with long-distance seed dispersal (Fig. 7). These results suggest selection for long-distance dispersal is likely for *L. benzoin*, which is consistent with observations of high rates of seed dispersal by birds (generally > 60%; Moore & Willson 1982; White & Stiles 1992; M. Cipollini, personal observation). We know that seed removal and dispersal by frugivores may be influenced by the presence or absence of canopy gaps (cf. Levey 1988; Murray 1988; Schupp *et al.* 1989). Such effects could be readily modelled by using appropriate vectors describing patch-specific rates of seed migration and immigration.

Our finding of a consistent benefit for long-distance dispersal for *L. benzoin* is contrary to that of Horvitz & Schemske (1986) for *Calathea ovandensis*. Horvitz & Schemske reported that, for all modelled conditions (variation in k , variation in pattern of demographic response), there was little or no benefit of long-distance dispersal (y) for *C. ovandensis*. The

contrasting results we report here for *L. benzoin* suggest that the results of Horvitz & Schemske may not be generalizable to species with different demographic matrices and hence different demographic elasticities. In fact, one would expect shade-tolerant and gap-dependent plants to exhibit fundamentally different demographic matrices (Silvertown *et al.* 1993). Unlike Horvitz & Schemske, we modelled reduction in growth of adults with canopy closure but did not alter survivorship. Our contrasting results might thus have been due to differences in application of the model. To address this possibility, we altered both growth and survivorship for adults and modelled other potential response functions (i.e. linear and gap-dependent or 'non-linear fast' models) and still found positive benefits of long-distance dispersal (results not presented). Additionally, we have found a slightly positive benefit of long-distance dispersal for the understorey herb *Cynoglossum virginianum* using an analogous metapopulation model (Cipollini *et al.* 1994).

Our estimates of the effects of canopy closure were greater for adult plants than they were for seeds, seedlings, and juveniles. This contrasts with the values used by Horvitz & Schemske (1986) for *Calathea ovandensis*, in which negative effects of full canopy closure were highest for younger stages. Three items qualify our assumptions concerning the effects of canopy closure.

1 Changes in gap conditions not directly related to light level variation may also play a role in affecting patch-specific demographics; e.g. variation in nutrients, seed predators, etc. Comparisons of plants in high-light and low-light microsites may not be entirely appropriate for analyses based strictly upon treefall gap dynamics.

2 Because of their proximity to the ground, seedlings and juveniles may commonly experience less variation in light intensity than do adult plants. For large-seeded, shade-tolerant species such as *L. benzoin*, it is thus possible that effects of canopy closure on seedlings and juveniles may be relatively lower due to a lower magnitude of light variation.

3 In some species, the effects of canopy closure may be exacerbated for later stages as a result of reproductive costs incurred in these stages. We have previously demonstrated that reproductive costs play a role in influencing vegetative growth in *L. benzoin* (Cipollini & Whigham 1994).

Despite slight shifts, sex ratios never achieved the levels of bias occasionally seen in the field, levels which can range from 0.354 to 1.340 among populations occupying rather similar forest habitats (M. Cipollini, A. Mills & D. Whigham, unpublished data). Our analysis thus suggests that differences in the growth of adult males and females, which are assumed to be associated with differential costs of reproduction (Cipollini & Whigham 1994), are insufficient to explain widely varying sex ratios – even when effects

of canopy closure are made more severe for female plants. It remains to be determined whether observed sex ratios result from intrinsic, but unobserved, demographic differences or from extrinsic ecological mechanisms such as differential herbivory (cf. Boecklen & Hoffman 1993). We currently have no means of distinguishing the sexes prior to reproduction, and have assumed that survivorship and growth of the sexes is identical prior to reproduction (see Cipollini & Whigham 1994). Better data on the performance of males and females of all life history stages under variable canopy conditions would address more directly the issue of sex ratio variation.

Our analysis illustrates the utility of matrix models in incorporating the effects of habitat heterogeneity and temporal dynamics into demographic analyses. This study is unique in quantifying the effects of sexual dimorphism in a dioecious plant from the metapopulation perspective. In a practical sense, the analysis has proven beneficial in narrowing the potential source of sex ratio bias in *L. benzoin* to mechanisms involving seeds, seedlings or juveniles, thus providing focus for future work on this species. We encourage research into sex ratio variation that takes similar approaches.

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