

Seed dispersal and environmental heterogeneity in a neotropical herb: a model of population and patch dynamics

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Abstract. We examined the effects of three kinds of seed dispersal on mean fitness in the ant-dispersed perennial herb *Calathea ovandensis* (Marantaceae): (1) local dispersal to safe sites, (2) long-distance dispersal, and (3) dispersal through time, *i.e.*, dormancy. Because persistence of this species depends upon periodic disturbance by treefalls, we propose a matrix model of population dynamics that combines the successional dynamics of the forest with the habitat-specific demographic dynamics of the plant. Using empirically determined values for the demographic parameters for *Calathea ovandensis* in a new gap, and three different models of how stage-specific growth and survival change as succession proceeds, we characterize the overall population dynamics of our study species. For the model best representing the demographic response of *Calathea ovandensis* to succession, the results of our computer simulations predict strong selection for local dispersal to safe sites, and selection against long-distance dispersal. These predictions are consistent with observed patterns of seed dispersal in *Calathea ovandensis*. In addition, the model predicts very weak selection for long-term seed dormancy, a life-history stage currently under investigation. Models combining patch dynamics with population dynamics provide a method of quantifying the demographic consequences of life-history variation for plants occupying variable environments.

Introduction

Spatial and temporal variation in habitat quality are major factors influencing the evolution of dispersal (Gadgil, 1971; Roughgarden, 1979). In many stage-structured organisms, *e.g.*, plants, dispersal is restricted to a single stage (seeds), and early life-history stages are generally far more sensitive to variation in habitat quality than later ones (Harper, 1977). The population consequences of dispersal in such stage-structured organisms depend jointly on stage- and habitat-specific fitnesses, and the spatial and temporal dynamics of habitat change. Because the spatial scale of seed dispersal, *e.g.*, near *vs.* far, often affects plant fitness (Howe and Smallwood, 1982; Augspurger, 1983; Howe *et al.*, 1985), the spatial and temporal distribution of patches will play an important role in the evolution of seed dispersal systems (Platt, 1975, 1976; Werner and Platt, 1976; Werner, 1979).

In this paper we examine the effects of seed dispersal on mean population fitness in the ant-dispersed perennial herb *Calathea ovandensis* (Marantaceae). Examining the response of population growth rate to quantitative changes in particular life-history parameters provides insight into the potential for selection to act on that character (Caswell, 1978, 1982a, b), because population growth rate is a measure of the average fitness of the population (Fisher, 1930). We use simulation mod-

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els which incorporate patch dynamics and patch-specific plant demography to determine how 1) within-patch dispersal, 2) long-distance dispersal, and 3) dispersal through time, *i.e.*, seed dormancy, affect population growth. As is the case with many tropical forest species (Hubbell, 1979; Garwood, 1983; Brokaw, 1985), colonization and persistence of *Calathea ovandensis* depend upon periodic disturbance by treefalls. Thus, to study population growth for this species, we propose a model that combines the successional dynamics of the forest with the demographic dynamics of the plant.

Study species and habitat

We are studying seed dispersal and population demography of *Calathea ovandensis* (Marantaceae) at Laguna Encantada, near San Andres Tuxtla, Veracruz, Mexico. The climate at our site is characterized as warm-humid; the mean annual precipitation is 1996 mm. About 80% of annual rainfall occurs from June-October with a peak in Sept (489 mm); December-May are the driest months with the lowest monthly precipitation in March (28 mm) (Soto, 1976).

Growth, reproduction and germination of *C. ovandensis* are seasonal, in accord with the seasonality in precipitation. Plants lose all above-ground parts during the dry season and re-initiate vegetative growth when rainfall increases during June. Flowering and fruiting occur from August-October, with a peak in fruit production in October (Horvitz, 1980; Horvitz and Schemske, 1984; Schemske and Horvitz, 1984). The seeds have innate short-term (<1 yr) dormancy and do not germinate until the beginning of the next rainy season the following June (Horvitz, 1980; C.C. Horvitz and D.W. Schemske, unpub. data). We are now experimentally investigating the extent of long-term seed dormancy.

The ant-dispersed seeds bear large white, lipid-rich elaiosomes (Horvitz, 1980; Horvitz and Beattie, 1980). At our site, at least five ant species use the elaiosomes for food (Horvitz, 1980, 1981), although only two ant species regularly move seeds beyond the parent plant canopy. The most abun-

dant of these ants, *Pachycondyla harpax*, moves seeds a mean distance of 75 cm, while the rarer *Pachycondyla apicalis* moves seeds 12 times further on average (Horvitz and Schemske, in press).

To study plant demography we established four permanent plots varying in *Calathea* density, substrate and canopy cover. All vegetative individuals ($n = 1860$) in the four plots were mapped and tagged in 1982. Survival, growth, reproduction and recruitment are being recorded annually in these plots as part of a long-term study of the effects of temporal and spatial variation in plant-animal interactions on plant demography (Horvitz and Schemske, 1984; Schemske and Horvitz, 1984). For each year-long census interval and for each plot, a Lefkovich (1965) matrix model of transition probabilities (see below) is constructed based on the census data. In the present paper we utilize data from the 1982-1983 transition matrix for the plot that is most like a treefall gap environment (plot C). At the 1982 census in this 30 sq m plot there were 1275 individuals, including 1020 seeds and 255 vegetative individuals (C.C. Horvitz and D.W. Schemske, unpub. data).

Methods

Forest dynamics

To model rain forest dynamics we assumed a linear Markovian process of forest succession following disturbance caused by treefall gaps (Fig. 1). The forest is divided into patches the size of a treefall gap. Forest dynamics are represented mathematically as a matrix P , where each entry in the matrix, p_{ij} , represents the transition probability from a type- j patch to a type- i patch after one year (Table 1). Let f_t represent the vector of the number of patches of each type at time t , then

$$f(t+1) = P_{ij} \times f(t). \quad (1)$$

Specific assumptions of our model include: (1) The probability that any particular patch becomes a new treefall gap, p_{1j} , depends only upon the 'age' of the patch, defined as the number of years since the last treefall occurred in that patch. (2) The proba-

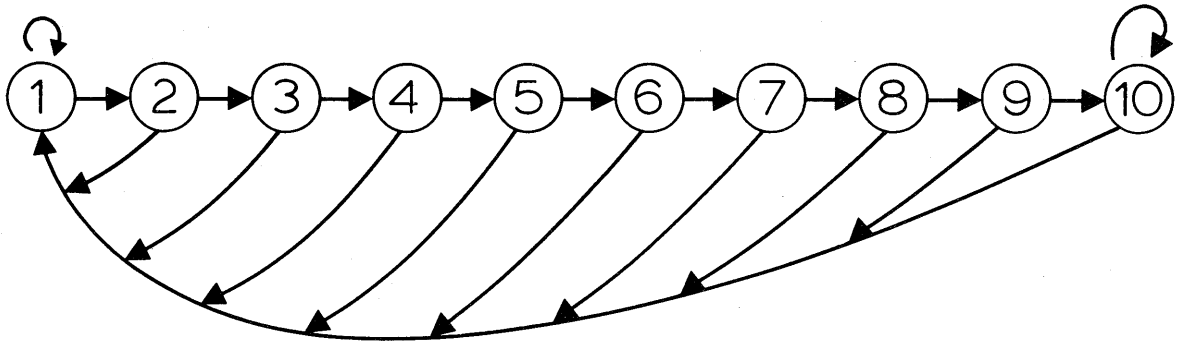


Fig. 1. Forest dynamics model. Each circle represents a distinct patch-type: type 1 is a new treefall gap, type 2 is a one-year old treefall, ... and type 10 is a closed-canopy patch. Arrows indicate transitions between patch types over one time unit.

bility of treefall disturbance is very low in newly formed gaps and increases with gap age. Beyond a certain age (x), it reaches an asymptotic value, k (Fig. 2). (3) Structural changes following gap formation are likely to be most rapid in the first few years of succession (Uhl and Jordan, 1984), as described by a logistic relationship between the probability of gap formation, p_{ij} , and the age of the gap (Fig. 2),

$$p_{ij} = k/[1 + (k/p_{11} - 1)/e^{r(i-1)}]. \quad (2)$$

where ' r ' represents the rate of change of the probability of gap formation. For any particular k , p_{11} , and n (number of patch types), the value of r was approximated by trial and error. The lowest r yielding a $p_{1n} \approx k$ (to four decimal places) was used.

These assumptions lead to an $n \times n$ matrix com-

prised mostly of zeros except the top row, the sub-diagonal, and the lower right hand corner (p_{nn}) (Table 1), where $n = x + 1$ and x = the age at which the asymptote is reached. In the top row, columns 1 to $n-1$ represent the probabilities of gap formation for patches 0 to $x-1$ years old and column n represents the probability of gap formation for patches greater than or equal to x years old. The entries in the sub-diagonal represent the transitions among patch types as a patch ages from 0 to $x-1$ years old. Finally, p_{nn} represents the probability that x -year old and older patches remain as closed-canopy patches. The column eigenvector of this matrix that is associated with its dominant eigenvalue ($\lambda = 1.000$) represents the equilibrium distribution of patch types, hereafter termed the 'stable patch-type distribution.' To interpret the results of our model in

Table 1. Matrix model of forest dynamics, P . Let $f(t)$ = the no. of patches of each type at time t . $f(t+1) = P_{ij} \times f(t)$.

Patch type at $t+1$	Patch type at time t									
	1	2	3	4	5	6	7	8	9	10
1	P_{11}	P_{12}	P_{13}	P_{14}	P_{15}	P_{16}	P_{17}	P_{18}	P_{19}	$P_{1,10}$
2	$1-p_{11}$	0	0	0	0	0	0	0	0	0
3	0	$1-p_{12}$	0	0	0	0	0	0	0	0
4	0	0	$1-p_{13}$	0	0	0	0	0	0	0
5	0	0	0	$1-p_{14}$	0	0	0	0	0	0
6	0	0	0	0	$1-p_{15}$	0	0	0	0	0
7	0	0	0	0	0	$1-p_{16}$	0	0	0	0
8	0	0	0	0	0	0	$1-p_{17}$	0	0	0
9	0	0	0	0	0	0	0	$1-p_{18}$	0	0
10	0	0	0	0	0	0	0	0	$1-p_{19}$	$1-p_{1,10}$

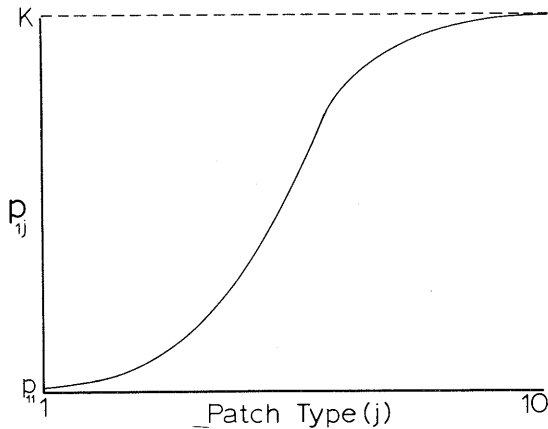


Fig. 2. Probability of gap formation, p_{ij} , as a function of patch type, j . k is the probability of gap formation in closed-canopy patches. See equation (2).

real-world terms, we had in mind a sample of rain forest that would contain 10,000 such patches.

Patch-specific plant population dynamics

To model plant population dynamics within a particular patch type, we assumed a stage-classified demography (Sarukhán and Gadgil, 1974; Harper 1977; Werner and Caswell, 1977; Piñero *et al.*, 1977; Bierzychudek, 1982) and a linear Markovian process. This process can be represented by a life-cycle graph (Hubbell and Werner, 1979; Caswell, 1982a, b, 1983), in which the stages are listed and the

arrows represent the transitions among stages over one time unit (Fig. 3).

The life history depicted in Fig. 3 is based on our demographic field studies of *Calathea ovandensis*. The model includes five life history stages: seeds, seedlings, juveniles and two size classes of reproductives. These stage classifications are a function of plant size. Within one time unit, seeds can either die or germinate, *i.e.*, they can only progress one stage and there is no long-term (>1 yr) seed dormancy. Vegetative individuals that survive one time period do not all progress to the next stage class. For example, surviving seedlings may (1) stay the same size, (2) grow moderately fast and become juveniles, or (3) grow rapidly and skip a stage, becoming small reproductives. Transitions of juveniles are similar to those of seedlings, but displaced one stage class to the right. Note, that both seedlings and juveniles may indirectly contribute to the total numbers of seeds counted at the next time period (represented by dashed lines) if they become reproductives (Fig. 3). For the largest two stage-classes, plants may survive but decrease in size between growing seasons, so that individuals may even regress a stage over one time unit.

The demographic process represented in Fig. 3 can also be represented in matrix form (Table 2). The arrows in the diagram are represented by non-zero entries in the matrix. A stage-classified matrix model of population dynamics is known as a Lef-

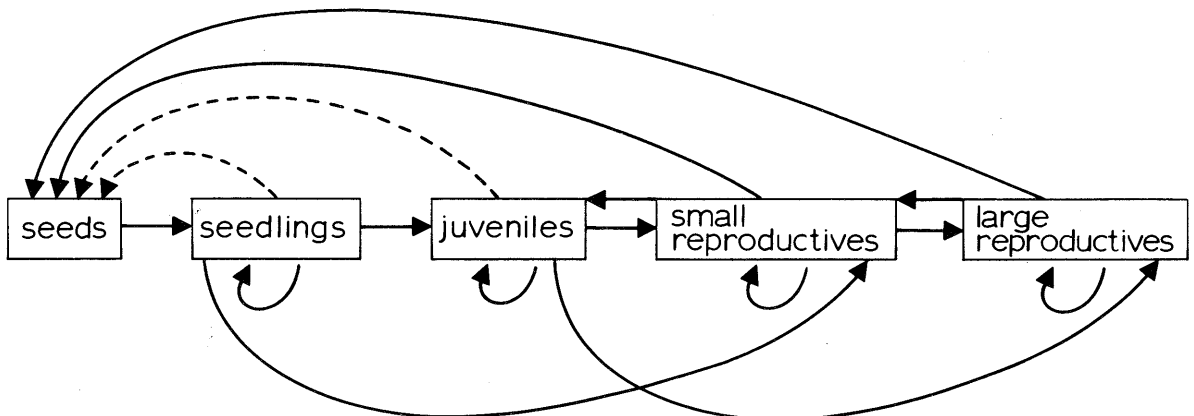


Fig. 3. Life-cycle graph for *Calathea ovandensis*. Arrows indicate transitions between stages over one time unit: solid lines are direct transitions, dashed lines are indirect (see text).

kovitch (1965) stage-projection model (Sarukhán and Gadgil, 1974; Hartshorn, 1975; Werner and Caswell, 1977; Enright and Ogden, 1979; Bullock, 1980; Bierzychudek, 1982; Law, 1983; Hughes, 1984) and is analogous to a Leslie (1945) matrix model except that the population is divided into stage classes rather than age classes (Vandermeer, 1975). The model is as follows. Let there be 5 stages and n_t is a vector representing the number of individuals in each stage class at time t . A matrix, M , can be constructed where the entries in the matrix, m_{ab} , represent the probabilities that an individual in stage class b contributes to or moves to stage class a by time $t + 1$,

$$n(t + 1) = M \cdot n(t). \quad (3)$$

In general, diagonal elements represent survival without stage change, elements below the diagonal represent growth to larger stages, elements above the diagonal (except the top row) represent regression. Total survivorship, S , for a particular stage, say stage k , is equal to the sum of the transition probabilities in column k , summing from row 2 to the last row, row 5. The top row represents either seed dormancy, m_{11} , or the contribution of a stage to next year's seed production, m_{12} , m_{13} , ... m_{15} .

The precise meaning of the elements in the matrix depend upon the timing of the census interval with respect to the phenology of the particular study organism. In our system, censuses are conducted at peak reproduction (in the late rainy season) and seeds are counted on the parent plant. Thus, the top row of the matrix is not simply a listing of the stage-specific fertilities; rather it is

calculated by considering both the probability that individuals in each stage class become reproductives by the next census and the stage-specific fertility (-ies) of the reproductive(s) that they become (C.C. Horvitz, unpub. data). In the present model, where only stages 4 and 5 reproduce; let z_4 and z_5 represent the respective stage-specific fertilities. Then, the top row entry for any non-seed stage k , m_{1k} , is calculated as follows:

$$m_{1k} = m_{4k} \cdot z_4 + m_{5k} \cdot z_5. \quad (4)$$

Also, because seed germination occurs in the early rainy season before our annual census, m_{21} (row 2, column 1 entry) is a parameter that represents the combined effects of seed survival, germination and early seedling survival. Seed dispersal agents are likely to have their greatest effect on this parameter.

The mathematical properties of the matrix correspond to important biological properties of the population. The long-term dynamics of the matrix are governed by its largest positive real root, λ , the dominant eigenvalue, and its associated eigenvectors. λ provides a measure of the long-term population growth rate, *i.e.*, the average fitness of the population (Fisher, 1930). If $\lambda = 1$, the population is not changing size; if $\lambda < 1$, the population is declining, and if $\lambda > 1$, the population is growing. The column eigenvector (normalized such that its elements sum to 1) corresponds to the stable stage distribution of the population, while the elements of the row eigenvector (normalized such that the product of the row x the column eigenvector equals 1) correspond to the stage-specific reproductive

Table 2. Lefkovitch matrix model of population dynamics, M : PATCH 1'S matrix. Let $n(t)$ = the no. of individuals in each stage class at time t . $n(t + 1) = M_{ab} \times n(t)$.

Stage class at $t + 1$	Stage class at time t				
	Seeds	Seedlings	Juveniles	Small rep	Large rep
Seeds	0.0	0.2789	5.1944	11.2876	27.6774
Seedlings	0.5184	0.0744	0.0	0.0	0.0
Juveniles	0.0	0.2220	0.5510	0.2880	0.0
Small rep	0.0	0.0168	0.2240	0.3460	0.4290
Large rep	0.0	0.0	0.0410	0.1540	0.5710

values (*sensu* Goodman, 1967; Caswell, 1978, 1982a,b; Charlesworth, 1980).

Our empirical studies of plant demography of *Calathea ovandensis* (C.C. Horvitz and D.W. Schemske, unpub. data), have indicated that across a range of environments, (1) fertility increases with plant size, (2) mortality is highest for seeds and seedlings, and (3) mortality of reproductives is very low. As a result of these general patterns, the stable-stage distribution is dominated by seeds, and stage-specific reproductive values generally rise in larger stage classes.

The parameter values in Table 2 are based on our empirical data (Horvitz and Schemske, in prep.) and represent the population dynamics of *Calathea* in the most favorable kind of site, a new treefall gap, hereafter called 'PATCH 1'-type of demography. Although none of our study plots is located in a new gap, one plot (C) is in an area with relatively little canopy cover and closely approximates the conditions of a young gap. To obtain demographic transitions that we think are representative of conditions in a new gap, we multiplied all entries in columns 1 and 2 of the transition probability matrix of plot C (for the 1982–1983 census interval) by 1.20, yielding a 20% improvement in both seed germination and seedling survival relative to observed values. We did not change other entries in the matrix. Combining these estimates with changes in demography due to gap closure creates a range of values that spans the observed natural range of demographic transitions (C.C. Horvitz, unpub. data). The observed stage-specific fertilities (z_4 and z_5) of large and small reproductives were 16.6 seeds/plant and 36.0 seeds/plant, respectively.

Effects of forest succession on Calathea demography

We asked: how are forest successional processes likely to affect the demography of an understory herb like *Calathea*? Our field observations indicate that as the canopy closes in and less light reaches the forest floor, growth and survival are likely to decrease for all stages, but that seeds and seedlings are probably more severely depressed than other

stages. Using demographic parameters for a *Calathea* population in a new gap and an intuitively reasonable estimate of how much growth and survival of each stage are likely to be affected as the habitat changes, we can characterize the population dynamics of *Calathea* in the closed-canopy environment and in the intermediate successional habitats.

To do so also requires a model of how rapidly the demography changes as succession proceeds. We consider three models of demographic 'decay' along the successional gradient, (1) a 'non-linear slow' model, (2) a 'linear' model, and (3) a 'non-linear fast' model (Fig. 4). Let c_{bj} represent the proportionate reduction in growth and/or survival to the b th stage in the j th patch relative to the growth and survival in PATCH-1; where C is a matrix of 'demographic-cost' parameters for all stages in all patch types, and the values in the tenth patch have been set as constants. To represent the differential costs of succession to different stage classes, we chose the following values for $c_{b,10}$, the stage-specific demographic costs in the closed-canopy environment: 1.00, 0.70, 0.40 and 0.30 for seeds, seedlings, juveniles and reproductives, respectively. Then, the 'linear' model is represented by the equation:

$$c_{bj} = [(j-1)/9] \cdot c_{b,10}. \quad (5)$$

The 'non-linear fast' model is represented by the equation:

$$c_{bj} = [(j-1)/9]^{1/4} \cdot c_{b,10}. \quad (6)$$

The 'non-linear slow' model is represented by the equation:

$$c_{bj} = [(j-1)/9]^4 \cdot c_{b,10}. \quad (7)$$

These models differ in the rate of change of the demographic-cost parameters as a gap ages. As can be seen in Fig. 4, the shapes are similar for all stage classes, even though the actual values differ among stage classes, depending upon the value of $c_{b,10}$. Conceptually, the models refer to the interaction of the change in the environment as a gap ages with the way the plant 'perceives' that change demographically. Clearly, plants with different kinds of life histories and physiologies will be represented

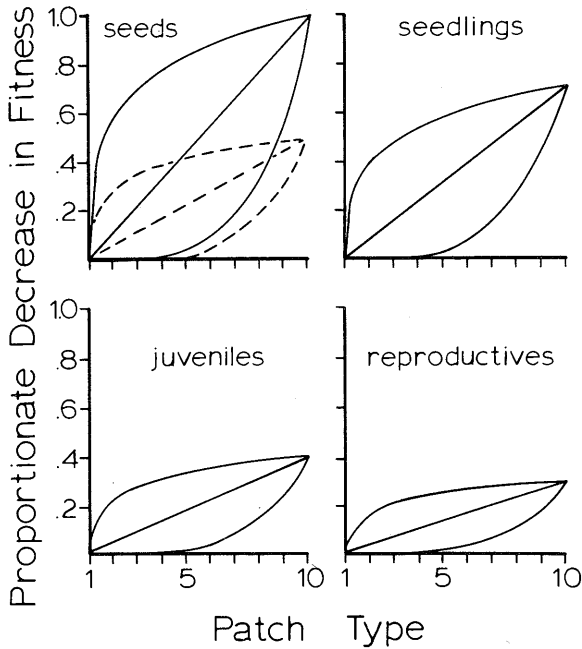


Fig. 4. Models of demographic decay through succession. Three models are illustrated for each stage: 1) Non-linear fast (upper), 2) linear (middle), and 3) non-linear slow (bottom). For each stage class, the proportionate decrease in fitness components is illustrated. For seeds, the solid line represents a 100% decrease in fitness from PATCH 1 to PATCH 10, and the dashed line illustrates a 50% decrease for the same successional sequence.

by different models. For example, species that are relatively more shade-tolerant are likely to more closely follow the 'non-linear slow' pattern, while those that are very shade-intolerant would follow the 'non-linear fast' pattern. To our knowledge, there are no complete empirical data on the demographic 'decay' rates for any plant species (but see Martinez and Alvarez, this volume; Murray, this volume), but we think these three patterns represent, in a general way, the range of possible demographic responses to gap succession. Thus, we will examine the consequences of all three models of demographic 'decay' in the context of the questions posed in the introduction about the relationship between seed dispersal and demography.

For each of these models, we can generate the transition probability matrices for the patch-specific population dynamics for each of the ten patch types in the forest successional sequence, as fol-

lows. We reduced growth and survival by the stage-specific demographic-cost parameters. All entries in row 2 of the matrix represent transitions to the smallest viable vegetative stage. Any reduction in growth of these individuals also results in a reduction in survival, thus these are multiplied by $(1-c_{bj})$. For entries in all other rows, the reduction in growth was modeled by moving a proportion, c_{bj} , of individuals into the next lowest stage class within a column. Then, the reduction in survival was modeled by multiplying all the resulting column entries by $(1-c_{bj})$.

The general formulae for the transition matrix values for any patch type can be written by applying the growth reduction and survival reduction rules. Let m_{abj} represent the entry in the a th row and b th column of the matrix in patch-type j . Let c_{bj} represent the demographic cost to the b th stage in the j th patch. For m_{21j} ,

$$m_{21j} = (1-c_{1j}) \cdot m_{211}. \quad (8)$$

For row 2 ($a = 2$) and columns 2–5 ($b = 2-5$),

$$m_{2bj} = (1-c_{bj}) \cdot [m_{2b1} + (m_{3b1})(c_{bj})]. \quad (9)$$

For rows 3 and 4 ($a = 3, 4$), and columns 2–5 ($b = 2-5$),

$$m_{abj} = (1-c_{bj}) \cdot [m_{ab1} - (m_{ab1})(c_{bj}) + (m_{a+1,b1})(c_{bj})]. \quad (10)$$

For row 5 ($a = 5$) and columns 2–5 ($b = 2-5$),

$$m_{5bj} = (1-c_{bj}) \cdot [m_{5b1} - (m_{5b1})(c_{bj})]. \quad (11)$$

The top rows of these new matrices are calculated as previously described [equation (4)] under the assumption that stage-specific fertility in this plant species is dependent upon plant size and independent of successional status. In other words, we assume that in older patches, there may be fewer plants large enough to reproduce, but those that are large enough produce the same number of seeds as plants of similar size in younger patches.

Overall population dynamics

To characterize overall population dynamics, we combine the model for forest dynamics with the model for patch-specific population dynamics. The

demography in each of the ten kinds of forest environments can be quantified under each of the three models of demographic 'decay' (cf. Fig. 4). We will use these patch-specific demographies to develop the model of overall population dynamics, proceeding in two steps. First, a matrix representing spatial heterogeneity without successional change will be developed, and second, the successional processes will be incorporated into the model. In both of these cases, the population at time t can be fully characterized by a vector that has a dimension equal to the *number of stage classes* \times *the number of patch types*; in our model: $5 \times 10 = 50$. All possible transitions among stages and among patch types are contained in a 50×50 matrix G , such that:

$$n(t+1) = G_{abij} \cdot n(t). \quad (12)$$

G is comprised of one hundred 5×5 submatrices, SUB_{ij} . Each entry g_{abij} represents the probability that an individual in stage class b in habitat j contributes to or becomes stage class a in habitat i after one time unit. i and j index the rows and columns, respectively, among the submatrices; a and b index the rows and columns, respectively, within the submatrices.

A population dynamics model representing spatial heterogeneity without successional change or without migration is depicted in Fig. 5. All the submatrices along the diagonal are equivalent to the patch-specific demographic models for each patch type, where SUB_{11} = the model for PATCH 1, SUB_{22} = the model for PATCH 2. . . . etc. up to $SUB_{10,10}$ = the model for PATCH 10. All other submatrices are comprised entirely of zeros. In such a case, the overall population dynamics is determined only by the dynamics within each patch type. However, this model does *not* allow for temporal changes among patch types.

To include succession, *i.e.*, temporal transitions among patch types, we must change the SUB_{ij} 's, replacing entries in some of the off-diagonal submatrices with non-zero entries as well as changing the entries along the diagonal. These new submatrices will be called $SUBT_{ij}$. In addition to the patch-specific demographies, two factors will determine the values of the entries in the new matrix:

(1) the successional dynamics of the forest and (2) the timing of gap formation with respect to the timing of the annual census. The patch dynamics transition parameters, p_{ij} (Table 1), will determine the probabilities that patch types will change before the next census, while the timing of gap formation will determine if individuals counted in patch type j at time t will undergo the demographic transitions of patch type j for most of the year or if, instead, they will undergo the demographic transitions of patch type i for most of the year. In particular, if tree-falls occur right after the present census, then

$$SUBT_{ij} = (p_{ij})(SUB_{ii}). \quad (13)$$

By contrast, if tree falls occur just before the next census, then

$$SUBT_{ij} = (SUB_{jj})(p_{ij}). \quad (14)$$

Brokaw (1982) reported a peak in tree falls in the mid-rainy season. In our study system, the census is conducted in the late rainy season; thus, we used equation (14) to calculate the entries in the $SUBT_{ij}$ matrices. The resulting 50×50 matrix (not pictured) contains 2,500 entries and represents the overall population dynamics including both successional changes and patch-specific demography. The dominant eigenvalue of this matrix provides a measure of the overall population growth rate. The associated column eigenvector corresponds to the stable-stage \times patch distribution: the relative frequency of individuals of different stages by patch-type at the dynamic equilibrium.

Seed dispersal and population growth rate

To model the effects of seed dispersal on overall population growth rate in an environment undergoing successional changes, we conducted simulations modifying particular aspects of the above-described 50×50 matrix, and then calculated the new population growth rates resulting from these changes. We modeled three kinds of seed dispersal: (1) local dispersal to 'safe sites' (*sensu* Harper, 1977), in which the survivorship of seeds, seed germination and early success of seedlings are affected, (2) long-distance dispersal, in which a cer-

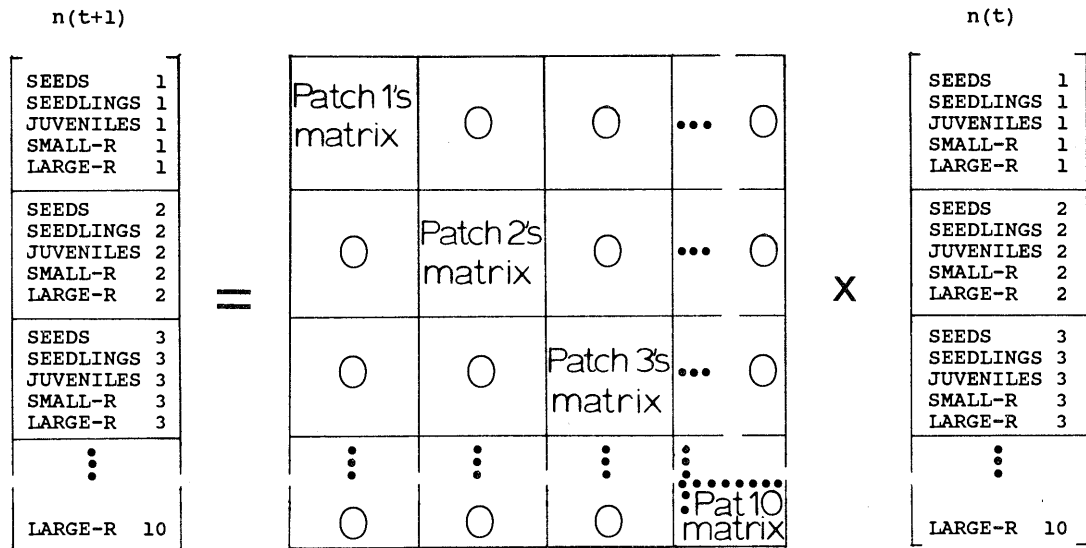


Fig. 5. Matrix model of population dynamics with spatial heterogeneity but no migration or succession. There are 100 submatrices, and each submatrix is 5×5 (see text).

tain proportion of seeds is moved to a different patch and (3) dispersal in time, in which seeds exhibit an enforced dormancy in unfavorable environments, but germinate in favorable environments.

The effects of local dispersal to safe sites was modeled by changing the m_{21} 's within each of the patch-specific demographic models, because this parameter represents the combined effects of seed survival, seed germination and early seedling survival in a particular patch-type. We investigated two ways in which local dispersal could affect these parameters: (a) germination in early successional patch-types could be affected, represented by changing m_{21} of PATCH-1 but keeping the demographic cost to seeds in PATCH-10 unchanged ($c_{1,10} = 100\%$, as above), or (b) the response of seed survival and germination to succession could be affected, resulting in a lower demographic cost to seeds in PATCH-10 ($c_{1,10} = 50\%$) (Fig. 4). For each of the $c_{1,10}$'s (50%, 100%), we examined four different germination levels in patch-1, corresponding to 1.15X, 0.85X, 0.65X and 0.45X the original PATCH-1 m_{21} in Table 2 (spanning the observed natural range of variation).

To model the effects of long-distance dispersal,

we introduced migration of seeds among patch-types into the model of overall population dynamics. Let $y =$ the fraction of seeds that move out of patch type j (y 's are the same for all patches). Let the probability that a dispersed seed reaches patch type i depend upon the relative frequency of type- i patches in the habitat, f_i^* . F^* is a vector representing the stable patch distribution (the leading column eigenvector of the forest dynamics model). Let the 50×50 matrix of overall population dynamics with long-distance dispersal be called D . D is comprised of one hundred 5×5 submatrices, $SUBD_{ij}$. Each entry, d_{abij} , represents the probability that an individual in stage class b and habitat j at time t contributes to or becomes stage class a in habitat i after one time unit. Then D can be defined by defining all of the entries in all the $SUBD_{ij}$'s in terms of the $SUBT_{ij}$'s of the model without migration [see equations (12) and (14)] as follows: $SUBD_{ij} = SUBT_{ij}$ in all entries except d_{21ij} 's, and

$$d_{21ij} = g_{21ij} - (y)(g_{21ij}) + (y)(f_i^*). \quad (15)$$

In other words, the overall population model with long-distance dispersal is very similar to that with no long-distance dispersal, except that in every

submatrix the g_{21} 's are reduced by the fraction that disperses away and increased by the fraction that disperses into a particular patch-type.

To model the effects of dispersal through time, we introduced long-term seed dormancy into the model of overall population dynamics with no long-distance dispersal. We assumed an enforced seed dormancy such that germination is inhibited by the deep shade of the closed-canopy forest, but enhanced by the light and heat of a new gap. Thus, we built dormancy into the patch-specific matrices by assuming (1) that germination is at a maximum (and dormancy is zero) in a gap, (2) germination is at a minimum (and dormancy a maximum) in the closed-canopy, and (3) seed survival is the same in all j patches, although germination differs. Consider the 5×5 patch-specific demographic models for PATCH 1-PATCH 10. With no dormancy, the upper left-hand corner of these, m_{11} , is always 0. To add long-term dormancy to the model is to allow nonzero entries in the m_{11} 's. Let m_{abj} represent the entry in the a th row and the b th column of the matrix for patch type j , then

$$m_{1ij} = m_{211} - m_{21j}. \quad (16)$$

In other words, the dormant fraction in a particular successional phase is equal to the fraction that germinates in PATCH 1 minus the fraction germinating in that particular patch, where the fraction germinating in PATCH j is determined by the model of demographic decay and the value of the demographic-cost parameter as before [see equation (8)].

Matrix analysis

To obtain eigenvalues and eigenvectors of all our matrices, we used the following computer software: 'RG' subroutines from EISPACK (Eigen-system Subroutine Packages), Release 2, distributed under the NATS project by Argonne National Laboratory, Argonne, Illinois. This program finds all the eigenvalues and eigenvectors of a real, general matrix.

Results and discussion

Forest dynamics

The forest structure depends upon k , the probability of gap formation in closed-canopy patches, according to our model. For a sample of 10,000 patches, when $k = 0.01$, there are 95 new gaps, 9,152 closed-canopy patches and 753 patches in intermediate stages of forest succession (Table 3). This kind of forest structure yields a turnover rate of 105.3 years. If k is doubled, the forest structure changes considerably. Although the closed-canopy patches still predominate, there are 1.93 as many new gaps, and 1.90 as many patches in intermediate successional stages as compared to the lower k value, resulting in a much more rapid turnover rate of 54.6 years. The turnover rates generated by our model are similar to observed turnover rates for tropical forests studied empirically (Hartshorn, 1978; Brokaw, 1982; Foster and Brokaw, 1982).

Our proposed model distinguishes only ten

Table 3. Forest dynamics: two disturbance regimes (A sample of 10,000 patches)

Characteristics of the forest structure at the dynamic equilibrium	Probability of gap formation in closed-canopy patches	
	$k = .01$	$k = .02$
No. of new gaps	95	183
No. of patches in succession	753	1,433
No. of closed-canopy patches	9,152	8,384
Proportion of forest in new gap phase	.0095	.0183
Turnover rate, yrs (1/proportion of forest in new gap)	105.3	54.6

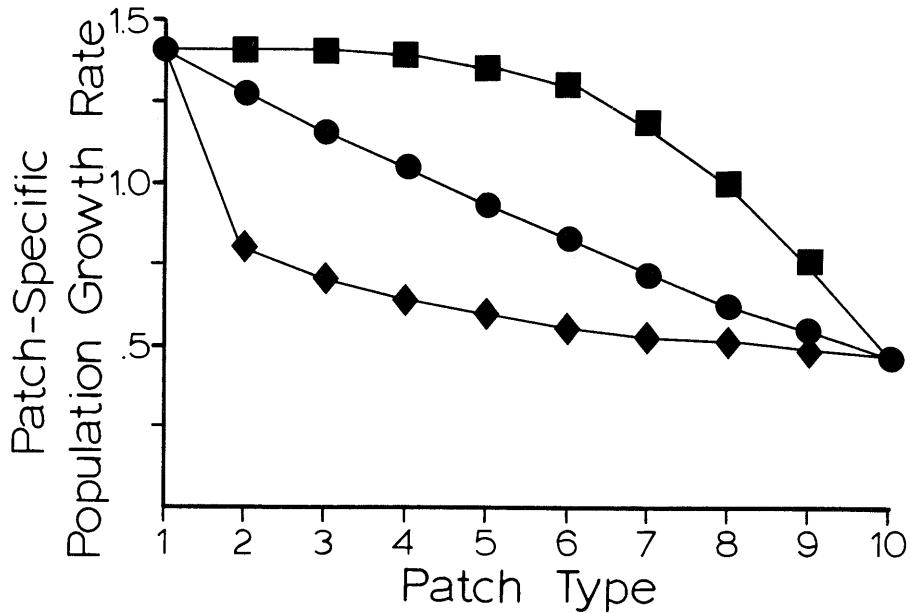


Fig. 6. Patch-specific population growth rates for three models of demographic decay: 1) non-linear slow (squares, 2) linear (circles), and 3) non-linear fast (diamonds).

patch-types and implies that gap maturity occurs at age 9. It could be argued that our model underestimates the number of years it takes for a gap to reach a mature forest closed-canopy stage. Thus, we also examined how the forest structure and turnover rate would respond to a model including more patch types, *i.e.*, one in which the formation of the mature closed-canopy patch is delayed longer. For $k = 0.01$, doubling the number of patch types (from 10 to 20) increased the turnover rate by only 3% (from 105.3 years to 108.7 years). For $k = 0.02$ doubling the number of patch types increased the turnover rate by 9% (from 54.6 to 59.5 yrs). For both k 's, doubling the number of patch types

slightly lowered the equilibrium number of patches in new gaps and considerably lowered the number of mature-forest patches. However, k had a more dramatic effect on forest structure than did the number of patch types (age of gap maturity). In this paper, we are most concerned with the effects of forest succession on an understory herb. We think that the stage of forest development reached after nine years (Uhl and Jordan, 1984; Brokaw, 1985), as it affects *Calathea* demography, is probably sufficiently close to that of a closed-canopy mature forest such that the pattern of demographic decay described earlier is not substantially altered by a longer successional period.

Table 4. Overall population growth rate (λ): Effects of disturbance regime and demographic 'decay'.

Model of demographic 'decay'	Probability of gap formation in closed-canopy patches	
	$k = .01$	$k = .02$
Non-linear slow (environment changes slowly early in succession)	.8762	.9545
Linear (environment changes at a constant rate as succession proceeds)	.6763	.7348
Non-linear fast (environment changes quickly early in succession)	.5219	.5485

Plant population dynamics

The three models representing the different rates of change of demographic response of species to succession result in very different patch-specific demographies (Fig. 6) as well as overall demography (Table 4).

The 'non-linear slow' model represents a situation in which the demographic cost changes slowly early in succession and corresponds to a species that can grow and survive relatively well in an intermediate amount of shade. In this model, the patch-specific population growth rates indicate conditions favoring increasing population sizes in the first eight patch types (Fig. 6). The analysis of overall population dynamics indicates that the population, however, is close to stability but slowly declining (λ close to but <1); the exact rate of decline depending upon the disturbance regime. With $k = 0.02$, λ is quite close to 1, while at $k = 0.01$, λ is lower (Table 4).

The 'linear' model represents a situation in which the demographic cost changes at a constant rate as succession proceeds and corresponds to a species whose growth and survival responds linearly to successional stages. In this model, the patch-specific population growth rates indicate conditions favoring increasing population sizes in only the first four patch-types. The overall population growth rate for this model indicates a declining population, and the rate of decline is affected by the disturbance regime. It is not as rapid for a disturbance regime of $k = 0.02$ as it is for $k = 0.01$ (Table 4).

The 'non-linear fast' model represents a situation in which the demographic cost changes quickly early in succession and corresponds to a species that is very intolerant of shading. For this model of demographic decay, the patch-specific population growth rates indicate an environment favorable for population increase only in PATCH 1 (Fig. 6). The overall population growth rate is much less than 1, indicating a population that is declining dramatically. The disturbance regime does not have as large an effect as in the other two models (Table 4).

It should be pointed out that the λ derived from the analysis of the overall population dynamics

(Table 4) is very different from a simple arithmetic mean of the individual λ 's in the patches. The arithmetic mean is calculated by weighting each patch-type by its relative frequency in the environment. The arithmetic mean of population growth rates underestimates the overall population growth rate given by the dynamic successional model. This discrepancy is almost two-fold under the 'non-linear slow' model ($\bar{\lambda} = 0.5392$ and 0.5995 for $k = 0.01$ and 0.02 , respectively), but it is not as great under the 'linear' model ($\bar{\lambda} = 0.5140$ and 0.5516 for $k = 0.01$ and 0.02 , respectively). Under the 'non-linear fast' model, the arithmetic means ($\bar{\lambda} = 0.4973$ and 0.5100 for $k = 0.01$ and 0.02 , respectively) are closer to the dynamically calculated overall population growth rate (Table 4).

In summary, all three models of demographic decay predict an overall decrease in population size of *Calathea ovandensis*. Only the 'non-linear slow' model predicts a population that is close to stability. We think that this model is probably most representative of the response of *Calathea ovandensis* to forest succession.

Within-patch seed dispersal

To examine the potential selective effects of within-patch dispersal to safe sites (*sensu* Harper, 1977), we examined the response of the overall population growth rate of *Calathea ovandensis* to changes in the life-history parameter most likely to be affected strongly by the microsite of the seed: m_{21} , the parameter representing seed survival, germination and early seedling survival. For convenience, we refer to this parameter as the 'germination' probability. In our simulations, we examined the response of overall population growth rate to changes in germination in the best patches by including four different PATCH-1 germination rates, spanning the range of natural variation (C.C. Horvitz and D.W. Schemske, unpub. data). We also examined the response of overall population growth rate to changes in germination in the worst patch by including two different values of the demographic cost to seeds in PATCH 10, spanning the range of likely values (no data are currently available). For all of these values, simula-

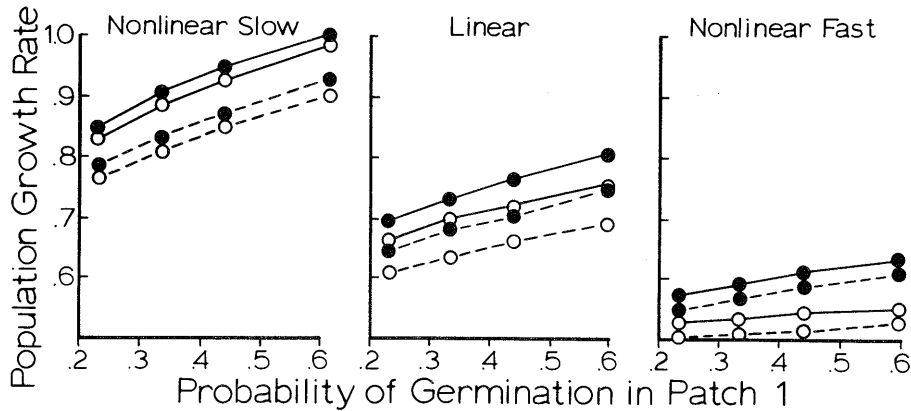


Fig. 7. Effects of within-patch dispersal on overall population growth rate for three models of demographic decay (see Fig. 4), where the effects of local dispersal are modeled by changes in germination. Solid lines are for $k = 0.02$, dashed lines for $k = 0.01$. Solid circles are for a 50% decrease in germination from PATCH 1 to PATCH 10, and open circles are for a 100% decrease over the same successional sequence. Results are presented for four different patch-1 germination rates.

tions were conducted for the three different models of demographic decay and two different disturbance regimes of the forest. The sensitivity of population growth rate to changes in germination is given by the slope of the line, when λ is the dependent variable and germination is the independent variable.

The major result was that both the absolute magnitude of the overall population growth rate and its sensitivity to changes in germination in the best patch were greatest for the 'non-linear slow' model of demographic decay (Fig. 7). In this model the forest disturbance regime had more of an effect than did the demographic cost to seeds in PATCH 10. (Compare the distance between solid and open circles for a particular kind of line with the distance between the dashed and solid lines in Fig. 7, left-hand graph). However, the demographic conditions of the closed canopy become more and more important in determining overall population growth rate, and both the rate of generation of new treefalls and the demographic conditions in treefalls become less important as the rate of demographic decay increases (Fig. 7, middle and right-hand graphs).

These results indicate that selection will act to improve local dispersal for species with any of the three models of demographic decay (positive slopes everywhere) but that the effects on popula-

tion growth rate will be greatest for life histories with the 'non-linear slow' sort of demographic response to succession. Such life histories will also be favored disproportionately by a higher disturbance regime, and selection will act more strongly to increase germination in treefalls than in the closed canopy. By contrast in the 'non-linear fast' life histories, selection will act more on improving germination under the closed canopy than in new treefalls.

Long-distance seed dispersal

We investigated the response of overall population growth rate to changes in the proportion of seeds dispersed a long distance (where long distance = out of the parent's patch). Our empirical data have indicated that a small proportion of the seed crop of *Calathea ovandensis*, an ant-dispersed plant, are moved sufficiently far (>10 m) to be defined as moving out of the parent's patch (C.C. Horvitz and D.W. Schemske, unpub. data). Thus it is interesting to investigate which models predict selection favoring long-distance dispersal.

We conducted simulations including the effects of four different proportions of the seed crop dispersing a long distance (0%, 10%, 50% and 100%). We investigated these effects for two different PATCH-1 germination probabilities (the highest

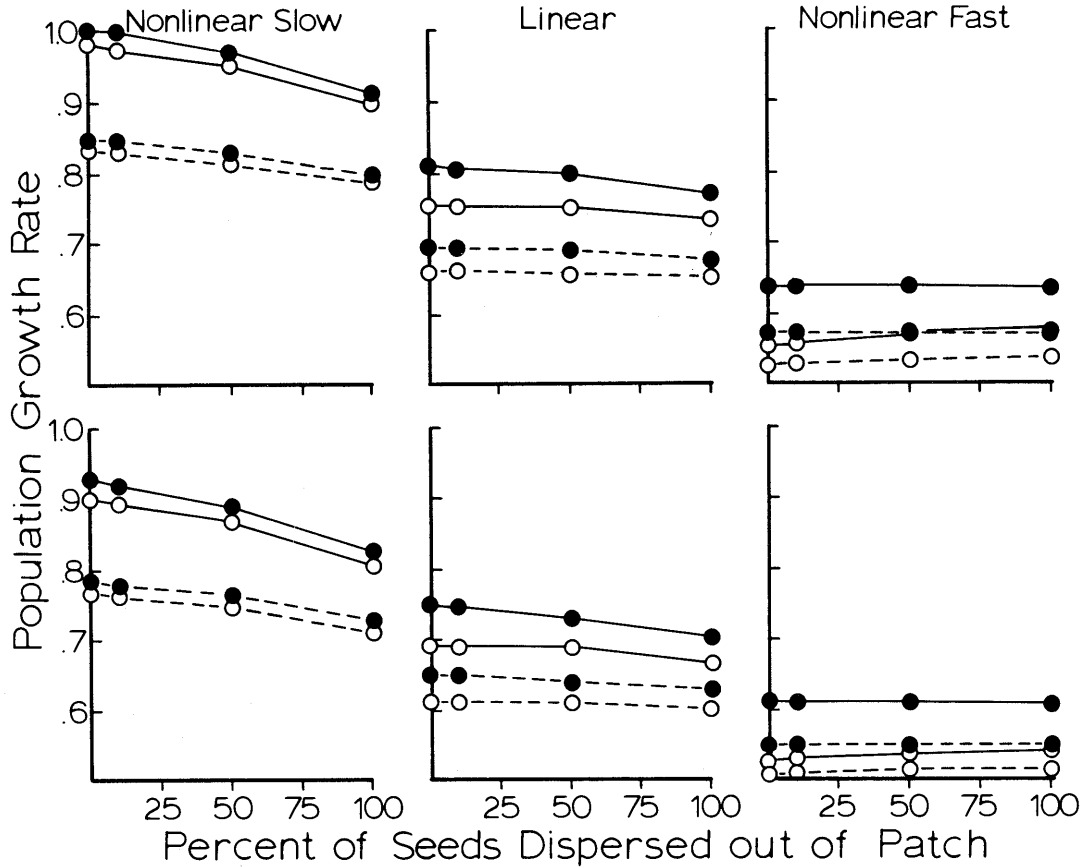


Fig. 8. Effects of long-distance dispersal on overall population growth rate for three models of demographic decay (see Fig. 4). For each model the upper figure is for $k = 0.02$, the lower figure is for $k = 0.01$. Solid lines represent the results for the highest germination rates used in the simulations presented in Fig. 7, and dashed lines represent the lowest germination rates. Solid circles are for a 50% decrease in germination from PATCH 1 to PATCH 10, and open circles are for a 100% decrease over the same successional sequence. Results are presented for four different levels of long-distance dispersal.

and the lowest from Fig. 7, thus spanning the range of natural variation), two different PATCH-10 demographic costs to seeds (the same two as in Fig. 7) and two different disturbance regimes of the forest.

The major result of this simulation was that long-distance dispersal is always disadvantageous (negative slopes) under the 'non-linear slow' model and is generally disadvantageous under the 'linear' model of demographic decay. Under the linear model, when the demographic cost to seeds is high (100% in the tenth patch), there is a very slight advantage to an intermediate amount of long-distance dispersal (10%). Long-distance dispersal is only very slightly advantageous in some cases (small positive slopes) under the 'non-linear fast'

model depending upon the demographic cost to seeds and the disturbance regime (Fig. 8). The advantage is strongest for both disturbance regimes when the demographic cost to seeds is high (100% in the tenth patch). When the demographic cost to seeds is low (50%), there is a slight advantage to an intermediate amount of long-distance dispersal (10% or 50%) only for the higher rate of disturbance ($k = 0.02$). The sensitivity of overall population growth rate to changes in the proportion of seeds dispersed a long distance is highest for the 'non-linear slow' model and decreases as the rate of demographic decay increases (the magnitude of the slopes decreases from left to right in Fig. 8). The effects of both the disturbance regime of the forest,

i.e., the rate of production of treefalls (compare upper and lower panels) and germination rate within treefalls (compare solid and dashed lines) on overall population growth rate are most pronounced in the non-linear slow model. As the demographic decay rate increases (left to right across Fig. 8), the rate of generation of new treefalls and the demographic conditions within treefalls become less important, while the demographic conditions within the closed-canopy patches becomes relatively more important. (Note how the distance between the solid and open circles for a given type of line increases from left to right in Fig. 8).

These results indicate that for species with a demography and a response to succession like that of *Calathea ovandensis* (best represented by the 'non-linear slow' model), we expect there to be selection *against* long-distance dispersal. The results also suggest, however, that species responding to succession as in the 'non-linear fast' model would benefit from long distance dispersal, al-

though other aspects of their life histories would have to be different from that of our study species in order to predict population stability.

Dormancy: seed dispersal through time

We investigated the response of overall population growth rate to long term (>1yr) seed dormancy. Seed dormancy has been suggested as an important strategy for species that depend upon unpredictable disturbances for successful establishment (Platt, 1975; Werner and Platt, 1976; Uhl and Clark, 1983). The extent to which understory herbs in tropical forests have long-term seed dormancy is generally unknown, although many tropical species of gap-dependent 'pioneer' trees are known to maintain long-lived seed banks (but see Martinez and Alvarez, this volume). Thus, it is interesting to investigate which models predict an advantage to long-term seed dormancy.

We conducted simulations investigating the

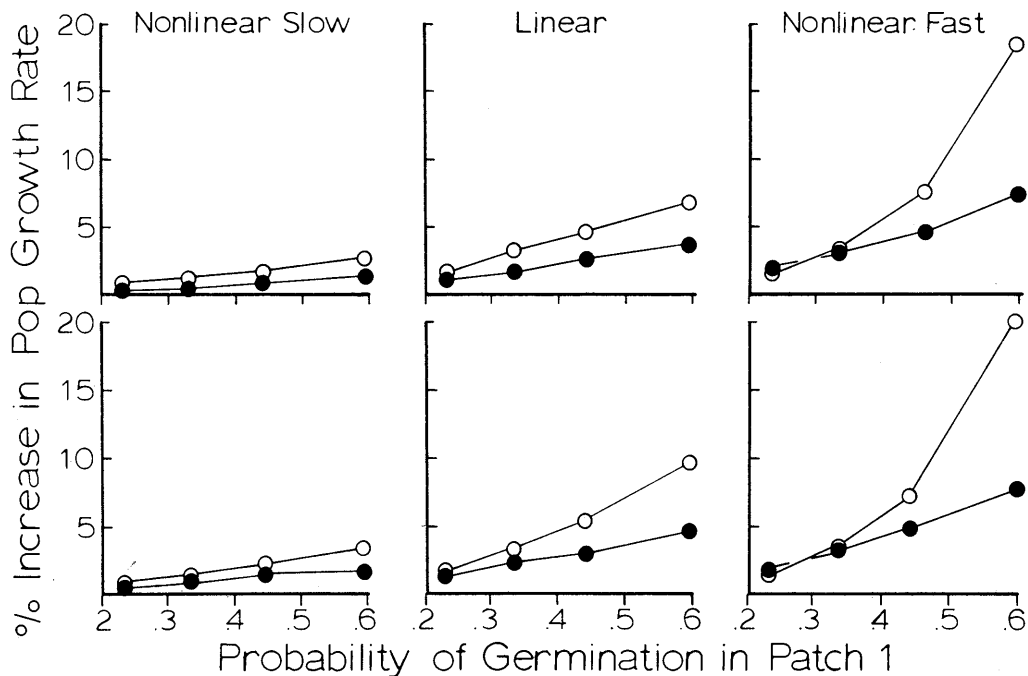


Fig. 9. The effects of dormancy, *i.e.*, dispersal through time, on overall population growth rate for three models of demographic decay (Fig. 4). For each model, the upper figure is for $k = 0.02$, the lower figure is for $k = 0.01$. Solid circles are for a 50% decrease in germination from PATCH 1 to PATCH 10, and open circles are for a 100% decrease over the same successional sequence. Results are presented as the percent increase in overall population growth rate caused by seed dormancy, relative to models without dormancy, for the same PATCH-1 germination rates (*cf.* Fig. 7).

effects of enforced long-term seed dormancy in which germination is inhibited in unfavorable environments and enhanced in favorable environments (see Methods). We investigated these effects for all the parameter values of the within-patch dispersal simulations and we express the effect of dormancy as the % change in population growth rate due to dormancy for a particular combination of parameter values relative to the same set of values for a model with no dormancy. Thus, we examined these effects for four different PATCH-1 germination probabilities, two different values of demographic cost to seeds in PATCH-10 and two different disturbance regimes of the forest (both Fig. 9 and Fig. 7).

The major result was that dormancy had a positive effect on population growth in all three kinds of demographic decay, but the magnitude of this effect dramatically increased as the rate of demographic decay increased (left to right, Fig. 9). Also the advantage to dormancy increased as the rate of germination in treefalls increased (positive slopes throughout in Fig. 9); this increase was faster when the demographic cost to seeds in the closed canopy was relatively high (compare solid circles to open circles in all graphs, Fig. 9). The disturbance regime was not as important as the rate of demographic decay in determining the advantage of dormancy: upper and lower panels within a demographic decay model differ less than panels compared among demographic decay models but within the same forest disturbance regime (Fig. 9). Thus, we predict stronger selection for seed dormancy in species that follow the non-linear fast model, that is, those species that are most shade intolerant. For *Calathea ovandensis*, seed dormancy confers only a slight advantage, the magnitude of that advantage depending upon the effects of within-patch dispersal.

Conclusion

The fitness consequences of dispersal in *Calathea* depend upon the demographic response of the plant to successional changes following treefalls. The model we think is most realistic for *Calathea*

ovandensis (yielding an overall population growth rate close to stability), predicts strong selection for local dispersal to safe sites, and selection against long-distance dispersal. These predictions are consistent with the observed pattern of seed dispersal in *Calathea ovandensis*. In addition, the model predicts very weak selection for long-term seed dormancy, a life history stage currently under experimental investigation in the field.

This study has focused on the overall population level consequences of variation in one life-history stage, the transition of seeds to seedlings. By modeling several processes that may affect this transition, we were able to determine which processes have the most marked effect on overall population growth rate. We also found that including patch dynamics in our model of overall plant population dynamics provided a measure of population processes that was distinct from that which could have been derived from a simple arithmetic mean of the standing variation across patches. Thus, models combining patch dynamics with population dynamics will provide a general method of quantifying the demographic consequences of life history variation for plants occupying variable environments.

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