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Population growth versus population spread of an ant-dispersed neotropical herb with a mixed reproductive strategy

Josiane Le Corff [a,*], Carol C. Horvitz [b]

[a] *Institut National d'Horticulture, UMR A462 SAGAH, 2 rue Le Nôtre, 49045 Angers Cedex 01, France*
[b] *Department of Biology, University of Miami, P.O. Box 249118, Coral Gables, FL 33124, USA*

Abstract

In plants that produce seeds with contrasting genetic background (selfed versus outcrossed), the question arises whether the ecological function of the two types of progeny differ. This paper addresses this issue for the ant-dispersed *Calathea micans* by introducing a novel application of the Neubert–Caswell model for analysis of wave speed for structured populations. Because dispersal as well as vital rates are structured, the model allows for distinct dispersal kernels for different types of progeny and thus permits comparisons of the sensitivity to changes in demographic and dispersal parameters of in situ population growth rate versus population spread across space. The study site was a lowland, evergreen tropical rain forest at La Selva Biological station, Costa Rica, where the species is commonly found throughout the forest. In *C. micans*, seeds produced by open flowers (potentially outcrossed) or by closed flowers (selfed) bear oily arils and are dispersed by ants. Five life-history stages were used to characterize the population: seedlings originating from seeds produced by open flowers, seedlings originating from seeds produced by closed flowers, juvenile vegetative plants, reproductive plants without new shoots and reproductive plants with new shoots. Demography varied seasonally. Transitions were estimated from marking and following the fate of plants ($N = 400$) in a natural population over a dry and a wet season. The population dynamics was described by a 10×10 matrix, with five life-history stages and two habitat states. The habitat states cycle repeatedly, dry–wet–dry–wet. To estimate dispersal kernels for each seed type, individual seeds ($N = 225$ and 306 seeds produced by open and closed flowers, respectively) were color-coded and placed in depots, allowing the ants to redistribute them. Five months later, seedlings with an attached seed coat bearing the intact color-coding, were surveyed around the depots. Radial distances and angles were recorded for each seedling ($N = 67$ and 81 seedlings arising from open and closed flowers, respectively). The results of the model give an asymptotic growth rate of 1.06 per season and an asymptotic rate of spread of 8.36 cm per season. There is a high correlation ($r = 0.99$) between elasticity of growth rate and elasticity of rate of spread of the population. Both rates are most sensitive to changes in stasis of juveniles during the dry season. However, most interesting is the analysis that revealed that population spread is more sensitive than in situ population growth to demographic rates of seedlings arising from open flowers. The analysis suggests a new way of thinking about ecological functions of multiple modes of reproduction.

Keywords: *Calathea micans*; Periodic population projection matrix; Dispersal kernel; Wave speed; Elasticity; Cleistogamy; Mixed reproductive strategy; Seasonal demography

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* Corresponding author.
E-mail addresses: lecorff@angers.inra.fr (J. Le Corff), carolhorvitz@miami.edu (C.C. Horvitz).

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“Mixed reproductive strategy” refers to the production, by the same individual, of seeds with contrasting genetic, energetic or morphological states (Schoen and Lloyd, 1984; Venable, 1985). Plants with cleistogamous (CL) and chasmogamous (CH) flowers are representative of a mixed reproductive strategy because CL flowers remain closed, are obligately selfed, are borne on reduced structures without rewards for pollinators, and often produce large seeds. In contrast, CH flowers open, are potentially outcrossed, are energetically more expensive to produce, have riskier fertilization and often have small seeds (Darwin, 1877). With respect to discussions on the significance of cleistogamy and chasmogamy, the distinction between the genetic, energetic and morphological issues has not always been explicit.

One possible advantage of a mixed reproductive strategy such as CH/CL is that seed production by closed flowers ensures some seed set in conditions where outcrossing is unpredictable due to resource or pollinator limitation. Several studies have empirically investigated differential resource allocation to the two reproductive modes, and have shown that the production of open flowers increased with an increase in soil moisture, soil fertility or light intensity (Koller and Roth, 1964; Schemske, 1978; Waller, 1979; Weiss, 1980; Wilken, 1982; Schoen, 1984; Bell and Quinn, 1987; Trapp and Hendrix, 1988; Cheplik and Clay, 1989). As a consequence, the relative contribution of the two types of seeds to population growth might differ depending on environmental conditions.

Another possible advantage of a mixed reproductive strategy is the production of two types of progeny, each being more successful at establishing in different environments. Differential success of seeds produced by open and closed flowers might be due to differential seed dispersal and/or to differential establishment. Theoretical models have emphasized the genetic contrast between the obligately selfed seeds and the potentially outcrossed seeds and have hypothesized that seeds produced by closed flowers are dispersed and establish short distances from the parent while seeds produced by open flowers are dispersed and establish farther (Schoen and Lloyd, 1984; Holsinger, 1986). As a consequence, either through differential seed dispersal or differential establishment, the two types of seeds might differ in their contributions to local population growth versus population spread. However, differential success of the two types of seeds has been shown only in species with marked seed heteromorphism, or in species where seeds from open and closed flowers differed also in fruit height, or fruiting phenology (Koller and Roth, 1964; Culver and Beattie, 1978; Weiss, 1980; Schmitt et al., 1985; Trapp, 1988; Porras and Muñoz, 2000).

In plants that produce both open and closed flowers with seeds that appear to be morphologically identical, the question is open as to whether the demography and dispersal of the seeds differ. This paper addresses this issue for the ant-dispersed *Calathea micans* by applying the Neubert–Caswell model (Neubert and Caswell, 2000). This model combines stage-specific demography and stage-specific dispersal, and takes into account the fact that in a population, individuals differ both in their vital rates and their dispersal abilities. This model permits calculation of the rate at which a population could spread over space, and more importantly, makes possible the analysis of the sensitivity of the rate of population spread to changes in demographic and dispersal parameters. Our application of this model to a species with a mixed reproductive strategy provides the opportunity to address new questions about the relative ecological roles of the different types of reproduction to population growth versus population spread.

The subject of this study, *C. micans*, is a tropical herb that produces open and closed flowers all year long. Seeds produced by both types of flowers are morphologically identical and are dispersed by ants. To determine whether selfed and potentially outcrossed seeds contribute differentially to in situ population growth versus population spread across space, we combined demographic data from a 2-year field study and dispersal data from a seed depot experiment to answer the following questions: (1) What is the relative contribution of the two types of seeds to population growth? (2) What is the relative contribution of the two types of seeds to population spread? (3) Are potentially outcrossed seeds more important to population spread than to population growth?

1. Study species and site

C. micans (Marantaceae) is an evergreen perennial herb found in lowland tropical rain forests from Mexico to Peru (Hammel, 1984). In this species, an underground rhizome produces acaulescent shoots, which reach about 15 cm in height. Individuals can produce two types of flowers: (1) open flowers on erect peduncles (<10 cm) that require insect visitation for fertilization and (2) closed flowers on short stalks (<3 cm) at the base of the leaves that do not open (Kennedy, 1978). In natural populations, usually a single flower opens per plant per day, which suggests that the majority of the seeds produced by the open flowers are outcrossed.

Both types of flowers are produced throughout the year. However, the production of open flowers is environmentally determined through the effects of habitat quality on plant growth: the production of new vegetative shoots increases the probability of producing open flowers. As a consequence, the production of potentially outcrossed seeds increases in response to an increase in rainfall, light or nutrient availability (Le Corff, 1993). Fruits are capsules with a maximum of three seeds. Both types of seeds appear morphologically identical but their production involves different levels of energetic investment in terms of floral structures (Le Corff, 1993). Peduncles bearing the fruits recurve downward when fruits are mature and both types of fruits open at ground level. Seeds bear oily arils and are dispersed by ants (Horvitz, 1980; Le Corff and Horvitz, 1995). Seeds do not exhibit dormancy and germinate within a few months.

The study site was a lowland evergreen tropical rain forest at La Selva Biological station, Costa Rica, where the species is commonly found throughout the forest. La Selva is owned and operated by the Organization for Tropical Studies. Mean annual precipitation is 3800 mm. January–April are the driest months.

2. Methods

2.1. Empirical work

2.1.1. Demography

To study population dynamics, fecundity, growth and survival were estimated from marking and following the fate of plants in a permanently marked demographic study site. This site, located in a patch of secondary forest, was a recent gap (<5 years) with a large population of *C. micans.* Permanent transects (1-m wide) and 14 plots within those transects were marked. Each shoot within the transects was mapped and marked with a bird ring. At four censuses, April 1990, October 1990, April 1991 and October 1991, we counted the number of shoots, the number and size of the leaves on each shoot and the number of open and closed flowers and marked all new recruits. In 1991, the population was censused every other month for reproduction. The number of plants fluctuated from 334 to 355, with more individuals seen during October censuses (wet season) than April censuses (dry season). Overall, during the 2-year study about 400 individuals were studied. In developing a stage-structured matrix model of population dynamics, only the data from the last three censuses were used in the current paper, because the characterization of the appropriate stage classes was not possible for the first census (see Section 3.1).

Total leaf area was used as an estimate of plant size. Although plant size did not have an effect on the relative number of open and closed flowers produced, there was a threshold below which plants did not reproduce (Le Corff, 1993). At the first census and for all new plants at each census, underground connections were excavated to distinguish seedlings from vegetative shoots, and to determine the relationship between new shoots and established plants.

2.1.2. Dispersal

The seed coat of the seeds can be indelibly marked and it remains attached to the base of the seedlings for at least a few months after germination. We color-coded individual seeds and placed them at nine different “depots” (a total of 225 and 306 seeds from open and closed flowers, respectively), allowing the ants to disperse them. The details of the depot experiment are reported in Le Corff (1996). Here, we recount only those relevant to the new analysis. Five months later, all seedlings within a 3-m radius of each depot were surveyed. The color of the seed coat, radial distance and angle from the original depot were recorded for each seedling. A 3-m radius was chosen because previous observations of ants carrying seeds had indicated that most seeds (97%) were displaced less than 3 m (Le Corff and Horvitz, 1995). A total of 67 and 81 seedlings arising from open and closed flowers, respectively, were recovered around the nine depots (Le Corff, 1996). The ratio of the number of seedlings recovered to the number of seeds placed in depots measured the probability of seedling recruitment and included the components: seed survival, germination and early seedling survival.

2.2. Model

To determine the relative importance of the two types of seeds to population growth versus population spread, we used the Neubert–Caswell approach to analysis of an integrodifference equation model of spatial population dynamics for structured populations (Neubert and Caswell, 2000). The general model is:

$$\mathbf{n}(x, t+1) = \int [\mathbf{K}(x-y) \circ \mathbf{B_n}]\mathbf{n}(y, t)\,\mathrm{d}y \tag{1}$$

where $\mathbf{n}(x, t+1)$ is the population vector at location x at time $t+1$, $\mathbf{B_n}$ the density dependent population projection matrix at location y and $\mathbf{K}(x-y)$ is a matrix of dispersal kernels. The (i, j) entry of $\mathbf{K}$, $k_{ij}(x-y)$ gives the probability that an individual making the transition from stage j to stage i moves from location y to location x. Thus, the model couples population growth rate given by $\mathbf{B_n}$ and individual spread over space described by **K.** The population vector at a given spatial location x at time $t+1$ depends on the population vectors at all other locations y at time t. The population at each point y grows and some individuals are dispersed from point y to location x over one time step. Each stage may have a distinct dispersal kernel and stages that do not move have a dispersal kernel in which all the probability is concentrated at the origin. Integrating this process over all points y gives the population at x after one time step. $\mathbf{B_n}$ is a population projection matrix, which describes survival, growth and reproduction for each life history stage. In general form, the matrix is density dependent. We are interested in the rate of spread of a population into an unoccupied area; this rate depends on the vital rates at low densities, so we substitute the constant matrix $\mathbf{A} = \mathbf{B}_0$ into (1). We also assume that there is no Allee effect. The dominant eigenvalue of $\mathbf{A}$ gives the in situ population growth rate at low density, λ (Caswell, 2001).

If a population governed by (1) grows into a homogeneous and previously unoccupied habitat, it eventually spreads in the form of an invasion wave of constant shape, moving at a constant speed. Neubert and Caswell (2000) provided a means of determining this wave speed. The calculation uses a matrix $\mathbf{M}(s)$ whose (i, j) element is the moment generating function of the dispersal kernel $k_{ij}(x)$:

$$m_{ij}(s) = \int_{-\infty}^{\infty} k_{ij}(x)\,\mathrm{e}^{sx}\,\mathrm{d}x \tag{2}$$

Moment generating functions have a parameter called s, a wave shape parameter. Neubert and Caswell (2000) combined the population projection matrix with the matrix of moment generating functions by elementwise multiplication (an operation called the Hadamard product) to give a new matrix that combines dynamics of demography and dispersal. The dominant eigenvalue of this new matrix is called ρ. They showed that the asymptotic rate at which a structured population spreads across space over one time step is given by c^*,

$$c^* = \min\left[\left(\frac{1}{s}\right)\ln(\rho(s))\right] \tag{3}$$

One intriguing application of this analysis is the comparison of elasticity of population growth to elasticity of population spread. Unlike the elasticities of population growth rate, the elasticities of c^* do not sum to 1 across the matrix, but they can be normalized to sum to 1 for comparison. Then, one can ask whether population growth or population spread is more sensitive to changes in a particular demographic parameter. In the case of a species with a mixed reproductive strategy, one can compare the ecological roles of the different types of offspring by this kind of analysis. We are the first to use this type of analysis to address this issue.

3. Results

3.1. Demography

Five life history stages were necessary to characterize the population dynamics: seedlings originating from seeds produced by open flowers, seedlings originating from seeds produced by closed flowers, juvenile vegetative plants, reproductive plants without new shoots and reproductive plants with new shoots (Table 1). Reproductive plants with new shoots had distinct demographic behavior from those without new shoots: they produced more open flower inflorescences in both the wet and in the dry season. The contribution of the reproductive sized individuals to the seedling

Table 1
Population projection matrix for *Calathea micans*

Stage at $t+1$	Stage at time t									
	April–October transition (wet season)					October–April transition (dry season)				
	open	closed	juv	repwo	repw	open	closed	juv	repwo	repw
open	0	0	0	0	0	0	0	0	0.015	0.103
closed	0	0	0	0	0	0	0	0	0.100	0.138
juv	0	0	0	0	0	0.57	0.57	0.93	0.20	0.16
repwo	0	0	0	0	0	0	0	0.03	0.50	0.53
repw	0	0	0	0	0	0	0	0.01	0.27	0.28
open	0	0	0	0.168	0.339	0	0	0	0	0
closed	0	0	0	0.047	0.049	0	0	0	0	0
juv	0.69	0.69	0.5	0.08	0.08	0	0	0	0	0
repwo	0	0	0.3	0.47	0.53	0	0	0	0	0
repw	0	0	0.2	0.45	0.39	0	0	0	0	0

This matrix is a 10 × 10 matrix with five life-history stages and two seasonal transitions. Stages are seedlings originated from seeds produced by open flowers (open) or by closed flowers (closed), juvenile vegetative plants (juv), reproductive plants with (repw) or without new shoots (repwo). Demography varies between the wet season (April–October) and the dry season (October–April).

classes included the following components: average number of seeds produced per plant (from the demographic censuses) multiplied by the probability of a seed to germinate, grow and survive by the next season (from the seed depot experiment). Growth and survival of seedlings originating from open flowers were assumed to be the same as those of seedlings originating from closed flowers (Le Corff, 1996).

The population of *C. micans* was characterized by very low mortality of all reproductive sized plants throughout the study. There was distinct seasonal variation in vital rates, characterized by higher survival of seedlings, increased growth of juveniles and of reproductives and increased production of open flowers during the wet season as compared to the dry season. However, overall reproduction was extremely low with only 15 inflorescences with open flowers produced from October 1990 to April 1991 (dry season) and 67 from April to October 1991 (wet season).

Since the census intervals for the seasons were of equal length (6-month each), the entire population dynamics could be described by a large matrix, with five life history stages and two seasonal habitat transitions (Table 1). In the 10 × 10 matrix columns 1–5 are the transitions from April to October (wet season) and columns 6–10, the transitions from October to April (dry season). The seasonal habitat cycles repeatedly, dry–wet–dry–wet (Fig. 1). This is a special case of a periodic matrix product where the time step for each component matrix is the same. The growth rate from the matrix is for a 6-month interval; squaring it gives the annual growth rate (Caswell and Trevisan, 1994).

The vital rates used to construct the projection matrix model in this paper were derived from the field data with two caveats. First, plants with new shoots could not be distinguished from plants without new shoots at the first census (April 1990). Therefore, it was not possible to estimate stage transitions from April 1990 to October 1990. Thus, in this paper, the vital rate estimates come only from the transitions among the October 1990, April 1991 and October 1991 censuses. Second, despite our choice of a population that was in a low density, favorable site, the vital rates estimated from the field data did not result in a matrix that had a dominant eigenvalue >1. As we required a growing population to obtain a positive wave speed,

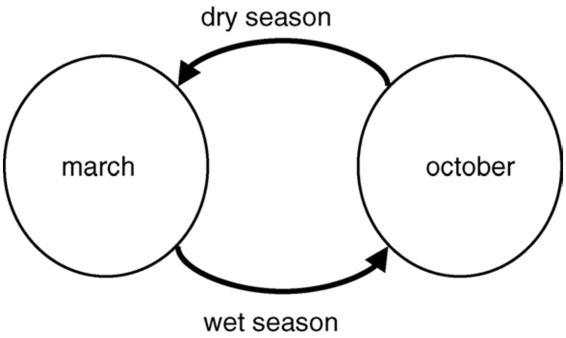

Fig. 1. Diagram of seasonal transitions between demographic states of the habitat.

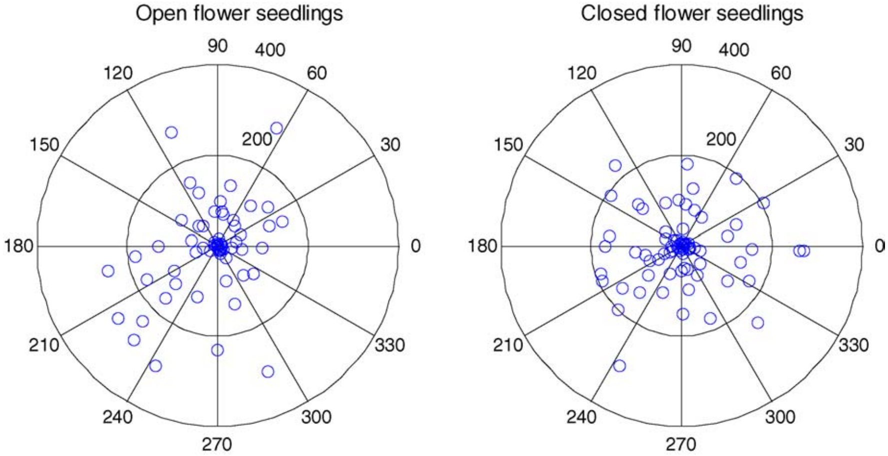

Fig. 2. Seed depot experiment. Distance and polar direction from the original depots for seedlings originated from seeds produced by either open flowers or closed flowers. Data from the nine depots are pooled ($N = 67$ and 81 open flower and closed flower seedlings, respectively).

we made some adjustments to simulate even lower density conditions. Because survival of the reproductive sized plants was already close to 1, the transition most likely to improve at lower density was the survival of the juveniles. For both seasons, we increased the observed survival to nearly 1 (exactly 1 in the wet season and 0.97 in the dry season). The adjusted vital rates are presented in Table 1. The initial rates associated with stasis and growth of the juveniles were $a_{8,3} = 0.62$, $a_{9,3} = 0.15$, $a_{10,3} = 0.07$ in the wet season and $a_{3,8} = 0.71$, $a_{4,8} = 0.02$ in the dry season. We did not change the relative proportion of stasis and growth for the two classes of reproductives in the dry season.

3.2. Dispersal

We pooled results from all nine depots, but separated the open and closed flower seedlings to compare their dispersal patterns. Seedlings that arose from open flowers were dispersed slightly further from depots than seedlings that arose from closed flowers; inspection of the radial distribution of seedlings around depots shows that there are comparatively more seedlings from open flowers in the 2–3 m annulus (Fig. 2). Both the mean distance and the median dispersal distances were slightly higher for the seedlings from open flowers than seedlings from closed flowers, but these differences were not statistically significant (Le Corff, 1996 and Fig. 3). Mean dispersal distances were 92.01 cm (S.D. = 10.62; $N = 67$) and 85.08 cm (S.D. = 8.61; $N = 81$) for seedlings arising from open and closed flowers, respectively. Nevertheless, the dispersal kernels differed subtly in shape with many fewer seedlings from open flowers at the origin and several more in the tail of the distribution compared with seedlings from closed flowers. Such subtle differences could be significant to population spread, which may be especially sensitive to the "tail" (Caswell et al., 2003; Bullock et al., 2003).

We used the two sets of empirical radial distances to describe two different non-parametric dispersal kernels, one for seedlings arising from open flowers and another for seedlings arising from closed flowers. The moment generating function was calculated by marginalizing the two-dimensional set of radial distances. Let d_i, $i = 1, \ldots, N$ be the radial distance to the ith seedling. Then the moment generating function is

$$m(s) = \frac{1}{N} \sum_i I_0(sd_i) \tag{4}$$

where $I_0(\cdot)$ is the modified Bessel function of the first kind (Neubert, personal communication; Neubert et al., in preparation).

The moment generating function matrix has its entries $m_{ij} = 1$ except for the entries corresponding to the stage transitions during which dispersal takes place: $m_{1,9}$, $m_{1,10}$, $m_{6,4}$, $m_{6,5}$ for dispersal of seeds from open flowers; $m_{2,9}$, $m_{2,10}$, $m_{7,4}$, $m_{7,5}$ for dispersal of

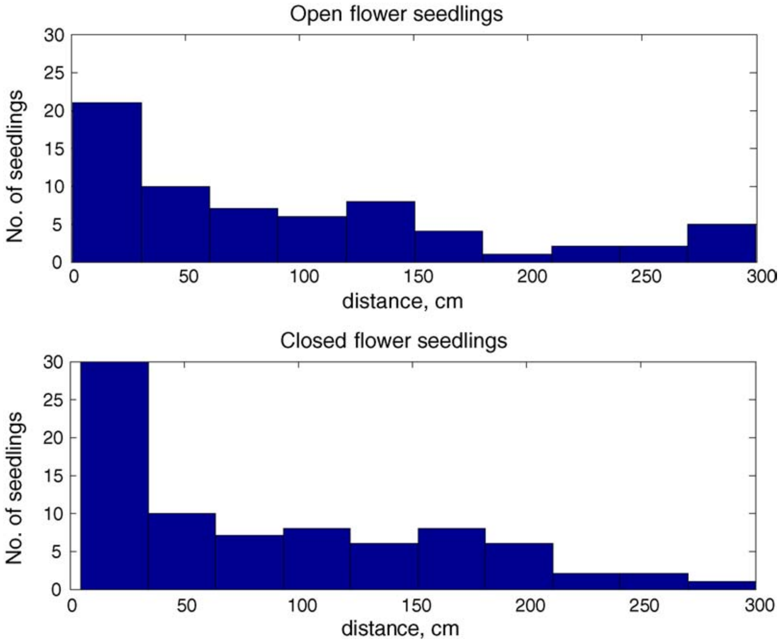

Fig. 3. Seed depot experiment. Seedling shadows ($N = 67$ and 81 open flower and closed flower seedlings, respectively).

seeds from closed flowers. Those entries contain the moment generating function for the appropriate kind of seedlings from open versus closed flowers.

3.3. Population growth, population spread and their elasticities

The population growth rate is $\lambda = 1.06$ per 6 months period (1.12 per year). λ is most sensitive to stasis of juveniles. There is a seasonal difference with higher sensitivity in the dry season than in the wet season (Fig. 4). Furthermore, λ is more sensitive to changes in the production of seedlings arising from open flowers than to changes in the production of seedlings arising from closed flowers. Reproduction by open flowers account for only 3.35% of total elasticity, but it is 1.4-fold more important than reproduction by closed flowers. There is also seasonal difference with an interaction between season and type of reproduction. λ is $3\times$ more sensitive to the production of open flower seedlings during the wet season than during the dry season but $3.5\times$ more sensitive to the production of closed flowers during the dry season than during the wet season.

The asymptotic rate of population spread is 8.36 cm per season. Similar to λ, c^* is most sensitive to changes in stasis of juveniles during the dry season (Fig. 4). There is a very high correlation ($r = 0.99$) between elasticity of the growth rate and elasticity of the rate of spread of the population, and similar to λ, c^* is more sensitive to changes in the production of seedlings arising from open flowers than to changes in the production of seedlings arising from closed flowers.

Finally, we calculated the differences between elasticity of c^* and elasticity of λ to determine whether the rate of population spread is more sensitive than in situ population growth to changes in particular demographic parameters. A positive value would indicate that a small change in a particular entry of $\mathbf{A}$ would have proportionally more impact on c^* than on λ. To make the comparisons, elasticities of c^* were normalized to sum to 1, as do elasticities of λ. In our particular case, the resulting differences between the elasticities were small in magnitude. Nonetheless, the largest values corresponded to the production of the seedlings arising from open flowers during the wet season and their growth during the dry season (Fig. 5). Population spread is thus more sensitive than population growth to small changes in vital rates, which involve seedlings from open flowers.

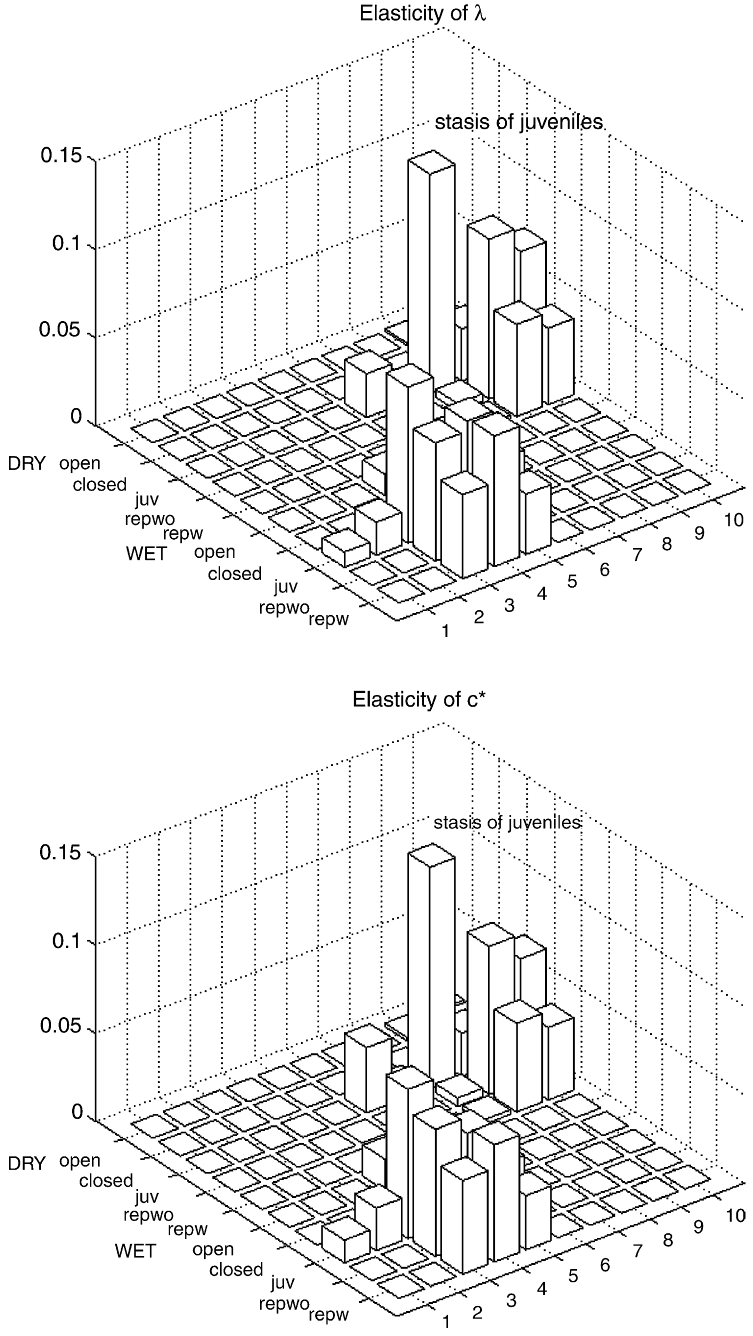

Fig. 4. Elasticities of population growth rate, λ, and elasticities of population rate of spread, c^*, to changes in the transition probabilities of the 10 × 10 population projection matrix.

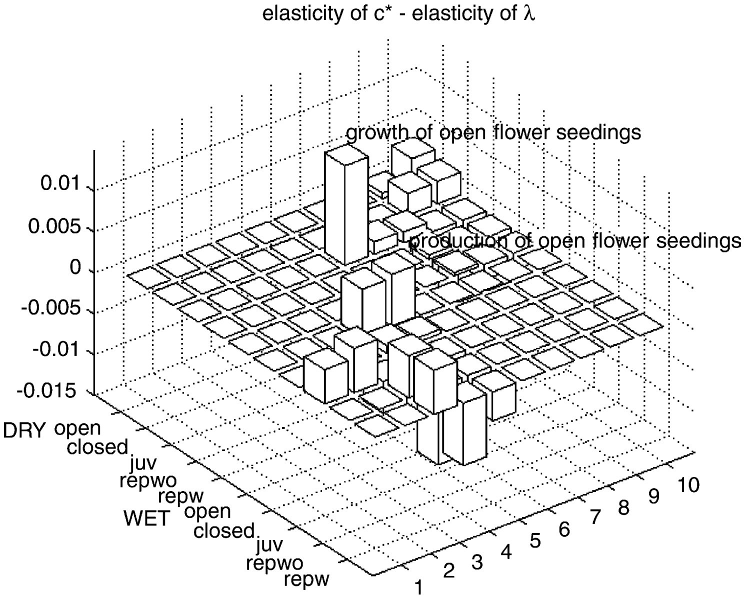

Fig. 5. Differences between the elasticities of c^* and the elasticities of λ. Positive values indicate transitions that are more important to population spread than to in situ population growth.

4. Discussion

The results of the model give an asymptotic population growth rate of 1.06 individuals per capita per season (1.12 per year) and an asymptotic rate of spread of 8.36 cm per season (16.72 per year). Most interesting is the analysis that revealed that population spread is more sensitive than in situ population growth to demographic rates of seedlings arising from open flowers (Fig. 5).

Holsinger (1986) proposed that differential dispersal of outcrossed and inbred progeny could itself account for the maintenance of a mixed reproductive strategy. However, differential success of seeds produced by open or closed flowers has been shown only in species with marked seed heteromorphism either in size, phenology or position on the plant (Koller and Roth, 1964; Weiss, 1980; Schmitt et al., 1985; Trapp, 1988; Porras and Muñoz, 2000). In *C. micans*, seeds from both types of flowers are morphologically identical and are produced throughout the year although the wet season has much higher production of seeds from open flowers. Seeds are dropped on the ground and dispersed by ants. In a separate study in which ants were observed directly and dispersal distances were measured by observing ant-seed interactions, we found that seeds from the two kinds of flowers did not differ in removal rate or mean dispersal distance (Le Corff and Horvitz, 1995). However, the dispersal curve for seeds from open flowers exhibited almost twice the amount of skewness compared to seeds from closed flowers: two of the seeds produced by open flowers ($N = 76$) were dispersed nearly 4 m by a species of *Aphaenogaster* (Le Corff and Horvitz, 1995). Differential seedling establishment was also observed in the seed depot experiment where relatively more seedlings arising from open flowers established further away from the original depots (Figs. 2 and 3). Either subtle differences (perhaps chemical differences, which we did not assay) between the seeds from the different types of flowers that could be distinguishable by the ants that disperse them and/or interactions between the genetic makeup of the seeds and the environment in which the seeds are dispersed could explain why the tail of the dispersal kernel is longer for seeds/seedlings from open flowers than it is for seeds/seedlings from closed flowers.

Despite the diversity of breeding systems encountered in plant species and the ecological consequences of producing progeny with contrasting genetic background, the influence of breeding system on plant population dynamics has been largely ignored, except in a few studies that have examined how dioecy influences population growth (Bierzychudek, 1982; Meagher, 1982). In our analysis, elasticity analysis of the population projection matrix indicated that λ is more sensitive to changes in the production of seedlings arising from open flowers than to changes in the production of seedlings arising from closed flowers. Furthermore, λ is more sensitive to the production of open flower seedlings during the wet season than the dry season. This might be linked to the fact that 4× more open flower inflorescences are produced in the wet season than in the dry season.

Furthermore a specialized ecological function of the progeny from open flowers is indicated. Our analysis explicitly includes the differences in dispersal kernels for different types of progeny in the model. For *C. micans*, the population rate of spread given by c^* (8.36 cm per season) indicated a relatively slow speed across space due in part to the nature of the dispersal agents. Only a few seeds were dispersed relatively long distances. A number of studies have suggested that wave speed is especially sensitive to long distance dispersal events even when they are rare (Goldwasser et al., 1994; Clark et al., 1999, 2003; Neubert and Caswell, 2000). In particular, Caswell et al. (2003) found that c^* was very sensitive to the tail of the distribution for a number of vertebrates. In another ant-dispersed species of *Calathea*, population wave speed was very sensitive to rare long distance dispersal events by one species of ant, *Pachycondyla apicalis* (Neubert and Caswell, 2000). Given the importance of the tail, if we were to repeat this field study in the future, we would probably extend the radius of our sample around depots to at least 5 m to attempt to capture this significant feature. In conclusion, we find that analysis of the combined dynamics of demography and dispersal could be a new and powerful tool to investigate the ecological roles of different progeny produced by a plant with a mixed reproductive strategy. The dynamic significance of the relatively rare dispersal events in the tail of the distribution is only revealed by analyzing the model of spatial population dynamics. The significance of these rare events are obscured by most kinds of statistical analyses comparing dispersal distances, as they are too rare to have an effect on comparisons of means or medians and are thus often discounted or overlooked. For our study species, the analysis revealed that population spread was more sensitive than population growth to vital rates which involved seedlings from open flowers. These differences suggest a specialized ecological function of the seeds from open flowers. Even though in our particular case the effects were rather subtle, this approach suggests a new way of thinking about ecological functions of multiple modes of reproduction and emphasizes the dynamic significance of rare long distance dispersal events. We expect the differences in ecological functions to be more pronounced in cases where the dispersal kernels were more distinct or where the vital rates of the progeny showed more differences.

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