OIKOS 86: 320–330. Copenhagen 1999

Seed shadows, survival and recruitment: how simple mechanisms lead to dynamics of population recruitment curves

Sébastien Barot, Jacques Gignoux and J.-C. Menaut

Barot, S., Gignoux, J. and Menaut, J.-C. 1999. Seed shadows, survival and recruitment: how simple mechanisms lead to dynamics of population recruitment curves. – Oikos 86: 320–330.

According to the Janzen-Connell hypothesis, seedling recruitment around tropical trees is more likely away from parent trees because of density- or distance-dependent predation or pathogen attack on seeds and seedlings. This was expected to lead to a more regular distribution of conspecific adults than would be expected by chance, and to favour coexistence. We first show theoretically that, even if yearly survival increases only slightly with distance to parent trees, an outward shift of seedling recruitment curves with time is very likely simply because seedlings live more than one year before recruiting to the juvenile stage. We tested this hypothesis for a humid savanna, dioecious palm tree, *Borassus aethiopum*, for which three discrete stages were defined by clear morphological traits. We found that (1) individuals of the second seedling stage are found on average further from their mother than individuals of the first seedling stage, and juveniles are found even further away (relative outward shifts between the three successive stages), and that (2) the older a female is, the further away its seedlings are (temporal outward shifts of distributions of seedlings). Both yearly recruitment (transition between two stages) and survival of seedlings are distance dependent and not density dependent. A matrix population model was used to demonstrate that, during the reproductive part of female palm life cycle, the cumulative effects of these distance-dependent variations in yearly recruitment and survival rates are sufficient to explain qualitatively the observed outward shifts.

S. Barot, J. Gignoux and J.-C. Menaut, UMR 7625, Ecole Normale Supérieure, F-75230 Paris Cedex 05, France (barot@biologie.ens.fr).

Seed dispersal is thought to enable seeds to (1) escape competition with their parents, competition between seedlings, and density-dependent mortality (escape hypothesis), to (2) reach newly created favourable sites that are unpredictable in space and time (colonisation hypothesis), or to (3) reach predictable suitable sites (directed dispersal hypothesis) (Howe and Smallwood 1982). Venable and Brown (1993) presented another classification that emphasises the bet hedging (risk reduction) function of seed dispersal. All of these functions of seed dispersal imply spatial variation in some demographic parameter, usually seed or seedling survival. Janzen (1970) and Connell (1971) pointed out that seed shadows and distribution of recruited seedlings around parent trees (Population Recruitment Curve, PRC) are often discordant around tropical forest trees, and attributed this discordance to distance-dependent survival. The further a seed or a seedling is from its parent tree, the more likely it is to germinate and to recruit later as an adult. This process is closely related to the escape hypothesis above and would be able to cause an outward shift of the PRCs of cohorts of tree seedlings relative to seed shadows in tropical forests. Here we studied a savanna palm tree and tested whether seed and immature stages distributions around parent palms are discordant. These stages were defined by morphological traits. We also tested whether seedling distributions around females of increasing age

Accepted 5 November 1998

ISSN 0030-1299

are concordant, which has never been tested, as far as we know.

Janzen and Connell hypothesised (Janzen 1970, Connell 1971) that tropical forests are characterised by a very high frequency of host-specific seed predators and pathogens (as opposed to temperate forests) and that these predators and pathogens are the main cause of both the commonly observed distance-dependent survival and the outward shift of PRCs. They argued that this phenomenon should lead to a less aggregated intraspecific spatial pattern of adult trees than would be predicted otherwise, promoting coexistence and high tree diversity in these forests. Since the issue of biodiversity and coexistence is among the most challenging in ecology, many empirical studies have tried to test the Janzen-Connell hypothesis on particular tree species. Many cases of distance-dependent seed survival (Janzen 1972a, Janzen et al. 1976, Howe et al. 1985, Schupp 1988, Chapman and Chapman 1996, Cintra 1997) and seedling survival (Augspurger 1983a, b, 1984, Clark and Clark 1984, Connell et al. 1984, Schupp 1988, Cintra 1997) have been documented. Nonetheless, the Janzen-Connell predictions are still controversial.

First, mechanisms inducing spatial variation of survival rates and their possible consequences on PRCs are difficult to investigate thoroughly. Since the density of offspring generally decreases away from parent trees it is difficult to determine whether the underlying process is density dependent or distance dependent. In these two cases, both distance and density may have statistically significant effects because they are highly positively correlated. Few field studies have made the distinction (Clark and Clark 1984, Cintra 1997). It could be argued that distinguishing density dependence from distance dependence is useless because they both cause an outward shift of the PRCs, and because in most cases the mortality pattern is probably not purely distance dependent or purely density dependent. However, distance and density dependence have been widely discussed by Janzen (1970) and are likely to lead to different selection pressures on fecundity and seed dispersal pattern. Furthermore, the distinction between distance and density dependence can help clarify the underlying process which can be interesting for its own sake. Primarily, predation and pathogens have been invoked to explain observed PRCs and can be both distance or density dependent. Nevertheless, distance-dependent survival of seedlings due to competition with the parent tree (Smith 1984, Coomes and Grubb 1998) or density-dependent survival due to competition between seedlings are other possible mechanisms that have rarely been mentioned in the context of the PRCs and Janzen-Connell hypothesis although they could lead to outward shifts of seedling distributions as well as seed or seedling predators and pathogens. Here, we aimed at distinguishing density dependence from distance dependence. We tested the dependence of both survival without recruitment and recruitment rates (recruitment was defined as the transition between two discrete stages) of seedlings on their distance to their parent, and on their own density.

Second, it has been argued whether distance-dependent survival could really favour coexistence between tropical tree species (Hubbell 1980, Becker et al. 1985, Condit et al. 1992), and even whether distance-dependent survival could prevent the maximum of the PRCs to be at the parent (Hubbell 1980, Becker et al. 1985). In this context, McCanny (1985) showed that any case of PRCs is possible after just one occurrence of distance-dependent survival (e.g. after one year if this is the time step chosen for the study) and Augspurger (1983a) mentioned that PRCs around a reproductive tree depend not only on last year seedling mortality but on the whole past mortality pattern since the tree dispersed its first seeds. We want to develop these ideas and to emphasise the fact that even with only one cause of density- or distance-dependent mortality (survival increases with distance or decreases with density), and even if the mortality pattern is constant all through the reproductive life of a tree, the PRC of a cohort is very likely to shift outwards. As shown by Fig. 1, this shift will increase over years for a single cohort, if the stage that is vulnerable to the considered mortality (seedling, sapling, or even seed if dormancy is present) lasts more than one year, since differences in yearly survival probabilities accumulate. Fig. 1 demonstrates theoretically that even with small (but constant over years) differences in survival rates (small positive slope of the relation between yearly survival and distance), after several years, offspring of a cohort will be more numerous away from parents than directly at the parents.

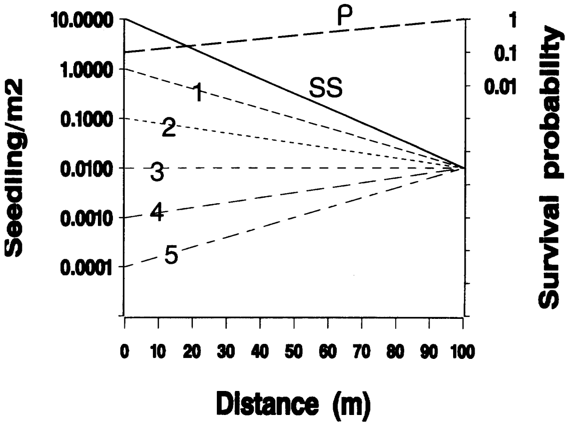


Fig. 1. Idealised distribution of a cohort of seedlings around a mother plant given a seed shadow (SS) and the yearly survival probability of seedlings (P); 1, 2...5: seedling distribution after 1, 2...5 yr. Logarithmic scale is used both for seedling density and probabilities that are exponentials of linear combinations of distance as in Hubbell's (1980), Augspurger's (1983a) and McCanny's (1985) original graphical models. The positive slope of the survival probability was chosen to be smaller than in these models.

Finally, we develop a matrix population model, parameterised with our dynamic data and incorporating as many subpopulations as distance classes around a parent. This model permits us to emphasise how the PRCs evolve through the life of a parent and when many cohorts are considered as in our field data (and not only one as in Fig. 1). It also permits us to test whether our results on the pattern of survival and recruitment could explain by themselves the observed seedling distributions.

Study site and study species

We studied a population of the palm tree *Borassus aethiopum* Mart. at the Tropical Ecology Station of Lamto, Côte d'Ivoire (6°13′N, 5°02′W). Lamto lies in the Guinean bioclimatic zone (Monod 1957, Menaut 1983). The mean annual temperature is 27°C and rainfall averages 1200 mm a year. Savanna vegetation is composed of three strata (Menaut and César 1979): the herbaceous stratum (2 m), the shrub stratum (5 m), and the highest stratum composed of *B. aethiopum* adults (up to 20 m). The savanna experiences a dry season between December and February, and the herbaceous layer burns in January.

B. aethiopum is a dioecious species, and females can produce more than 80 fruits a year (Vuattoux 1965). The palm is long-lived, and it can be assumed that adults are commonly more than 120 yr old and that females can produce fruits during about 60 yr (Barot and Gignoux 1999). Fruits contain up to 3 seeds, and weigh 500–1500 g. Nowadays, they are mainly dispersed by barochory. There may be some secondary dispersal by greater cane rats (*Thryonomys swinderianus*, Temminck), but this dispersal is likely to be insignificant since the cane rats are light in comparison to palm fruits (pers. obs.). Baboons and elephants were probably efficient secondary dispersers (Vuattoux pers. comm.) but have not been significantly present in the reserve surrounding Lamto ecology station, at least since its creation, 36 yr ago. There is no seed dormancy and germination is hypogeal and remote (Tomlinson and Jeffrey 1990): seedling roots and leaves develop from an embryo that has been buried down to 50 cm deep by the cotyledonary axis. Three immature stages can be easily distinguished from younger to older: entire-leaved seedlings (EL-seedlings), slit-leaved seedlings (SL-seedlings), and juveniles (with the same fan shaped leaves as adults)(Barot and Gignoux 1999). *B. aethiopum* is relatively resistant to fire; seedling and juvenile leaves (for juveniles under 2 m high) burn each year, but the terminal bud (which is below ground for seedlings and smaller juveniles) and the stipes are not harmed by fire. Juvenile stems are covered by old-leaf petioles, that fall off when they become adults, and reproduce for the first time.

Methods

Field data

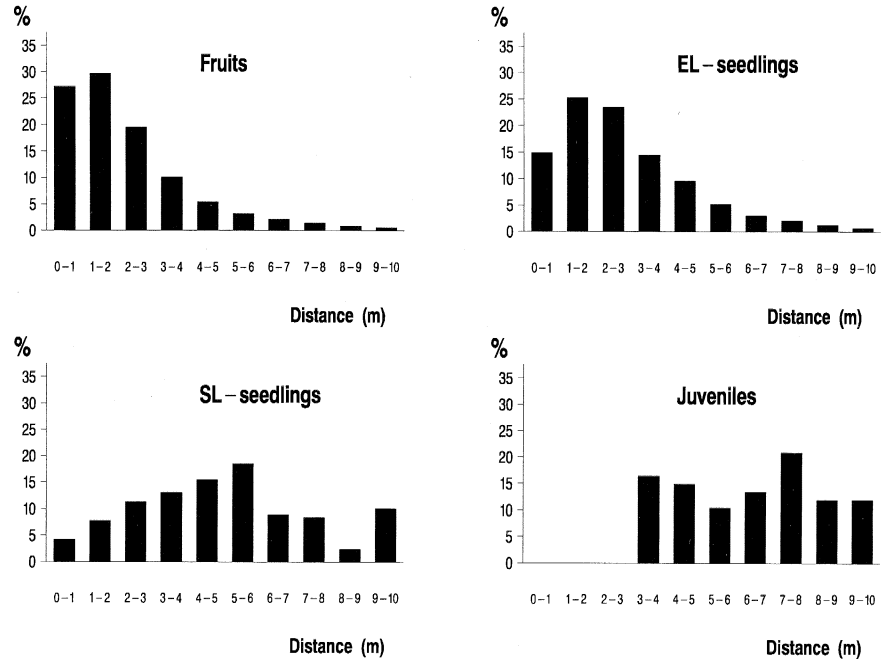
All fruits (about 800) of 31 females that fell during a 6-month period were collected on the soil and their distance to the female (base of the stipe) was measured. EL-seedlings, SL- seedlings, and juveniles were counted in 10 1-m-wide concentric bands around 25 females; very few seedlings could be found further away. Spatially isolated females (each female was more than 15 m away from any female) were chosen so that fruits, seedlings, and juveniles could be undoubtedly attributed to them. Females were classified in 3 age classes (young, middle-aged, and senescent) defined by their number of leaves and their height: numbers of leaves are maximal for adults that have just reached sexual maturity (up to 25 leaves) and then decrease till death (down to 2 or 3 leaves) (Barot and Gignoux 1999). The youngest females can be estimated to be about 110 yr old, whereas senescent females are probably more than 150 yr old (ages estimated through a matrix population model, unpubl. results).

EL-seedlings ($n = 999$) of 6 females were labelled during the 1996 wet season, their distance to the mother's stipe was measured, and their fates (death, survival in the same stage, or recruitment to the SL-seedling stage) were registered during the next wet season in 1997.

Log likelihood ratio tests (*G* tests) (Sokal and Rohlf 1981) were used to compare distributions of seedlings and juveniles classified according to their distance to the mother palms. When samples where too small (too many expected frequencies smaller than 5), the nonparametric Kolmogorov-Smirnov two-sample test was used instead (Sokal and Rohlf 1981).

Logistic regression (SAS LOGISTIC procedure) (SAS 1989) with the cumulative logit link function was used to test both the effect of distance (to the mother's stipe), and local density (mean per 1-m-wide band) on the fates of EL-seedlings: probabilities of death, survival in the same stage, or survival and recruitment to the SL-seedling stage. Since density of EL-seedlings and distance to the mother palm are strongly correlated (Figs 2,3) it was not possible to directly test the effect of these variables in the same logistic regression model. Thus, we used the regression model of density as a linear function of ln(distance) ($n = 1054$, $R^2 = 0.60$, $F = 1628$, $P = 0.0001$) to separate the part of the density variability that is not due to distance from the part of this variability that is only due to distance (this analysis was relevant because EL-seedlings densities were very different for the 6 females, Fig. 3). We then used the residuals of this model (representing the effects of density) and distance as independent variables in a single logistic regression model (Table 2).

Fig. 2. Distribution of fruits (836 fruits found around 31 females), EL-seedlings, SL-seedlings, and juveniles (respectively 2734, 131, and 65 individuals found around 25 females) in 1-m-wide concentric bands around females.



Model description

We designed a multiregional matrix population model (Caswell 1989) focusing on only one part of the life cycle (cf. Appendix): (1) there were two nonreproductive stages (EL-seedlings and SL-seedlings) which were divided into 10 regional classes according to their distance to the female, (2) there was only one reproductive individual with a survival probability equal to 1 (the purpose is to add new seedlings each year without considering dynamics of adults), and (3) there was no recruitment from the nonreproductive classes into the reproductive class.

Survival probability of SL-seedlings was the same in all distance classes (q). Survival and recruitment probability depended on the distance class (d). At each time step (a year) a constant number (F) of EL-seedlings was produced and allocated to the 10 distance classes according to the following equations: for each distance class we calculated $s(d)$ (the function s determined the shape of the dispersal curve) (Portnoy and Willson 1993) and allocated $f(d)$ new EL-seedlings to each distance class (d takes the following values, which are mid-point distances of each 1-m-wide distance class: 0.5, 1.5,...8.5, 9.5):

$$s(d) = d^{\alpha} e^{(-\beta d^{\gamma})} \qquad (1)$$

$$f(d) = \frac{s(d)F}{\sum_{d=1}^{10} s(d)} \qquad (2)$$

Each year, an EL-seedling may die, survive without recruiting to the SL-seedling stage, or survive and recruit. If P_d, P_p, and P_r denote the respective probabilities of these events, $P_d + P_p + P_r = 1$. Probability of survival in the same stage and of survival and recruitment to the SL-seedling stage ($P_p(d)$ and $P_r(d)$) depended on the distance class (d) according to the logistic regression model with the cumulative logit link function. Two linear functions (*fp*(d) *and fr*(d)) of the independent variables were estimated:

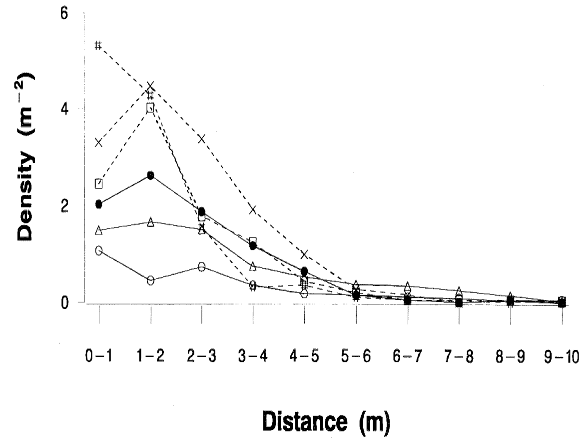


Fig. 3. Average density (number of individuals per m^2) in 1-m-wide concentric bands of the EL-seedlings labelled around six females.

Table 1. Log likelihood ratio (G) tests for the comparisons of the distributions in 1-m-wide concentric bands around females of (a) fruits, EL-seedlings, and SL-seedlings; (b) fruits (all females) and EL-seedlings around females of increasing age classes. df = 9 for each test. ELS, entire-leaved seedlings; YF, young females; MF, middle-aged female; SF, senescent female; n_1 and n_2, respective numbers of fruits or seedlings in the compared distributions; *, $P<0.05$; **, $P<0.005$.

			n_1	n_2	G	P
a	Fruits	EL-seedlings	821	2734	77.48	**
	EL-seedlings	SL-seedlings	2734	131	148.43	**
	SL-seedlings	Juveniles	131	65	19.33	*
b	Fruits	YF ELS	821	574	37.70	**
	YF ELS	MF ELS	574	1845	76.46	**
	MF ELS	SF ELS	1845	315	20.88	*

$$fp(d) = ap + dbp = \ln(P_d(d)/(1 - P_d(d))) \tag{3}$$

$$fr(d) = ar + dbr = \ln(P_{d+p}(d)/(1 - P_{d+p}(d))) \tag{4}$$

where P_{d+p} is the probability of death or survival without recruitment (this parameterization is due to the use of the cumulative logit link function).

We derived from eqs 3–4:

$$P_p(d) = \frac{e^{fr(d)}}{e^{fr(d)} + 1} - \frac{e^{fp(d)}}{e^{fp(d)} + 1} = P_{d+p}(d) - P_d(d) \tag{5}$$

$$P_r(d) = 1 - \frac{e^{fr(d)}}{e^{fr(d)} + 1} = 1 - P_{d+p}(d) \tag{6}$$

u_t is the vector composed of the numbers of EL-(EL_{dt}) and SL-seedlings (SL_{dt}) in each distance class d, after t reproductive years: $u_t = (\mathrm{EL}_{1t},\ldots,\mathrm{EL}_{10t},\ \mathrm{SL}_{1t},\ldots,\mathrm{SL}_{10t},\ 1)$ (the last entry of the vector is the constant number of reproductive females, i.e. 1). In this context, $u_t = A^t u_0$ (Caswell 1989) where A is the transition matrix. Its upper left submatrix contains (on the first diagonal) EL-seedling survival probabilities ($p(d)$), its lower right submatrix contains (on the first diagonal) SL-seedling survival probabilities (q), and its lower left submatrix contains (on the first diagonal) EL-seedling probabilities of survival and recruitment to the SL-seedling stage ($r(d)$). The last column of the transition matrix contains the fecundities ($f(d)$), and the adult survival probability (1).

$$A = \left[\begin{array}{cc:cc:c} p(0.5) & 0 & & & f(0.5)\\ & \ddots & & 0 & \vdots\\ 0 & p(9.5) & & & f(9.5)\\ \hdashline r(0.5) & 0 & q & 0 & 0\\ & \ddots & & \ddots & \vdots\\ 0 & r(9.5) & 0 & q & 0\\ \hdashline 0\cdots & \cdots 0 & 0\cdots & \cdots 0 & 1 \end{array}\right]$$

At the first iteration, before the first year of reproduction, there was in every case no seedling and 1 adult ($u_0 = (0,\ldots,0,1)$). Each model was run for 60 yr since females are likely to produce fruits during about 60 yr.

All parameters were estimated with field data. Parameters for $s(d)$ were estimated by a nonlinear regression on the percentage of fruits collected in each distance class ($\alpha = -1.1202$, $\beta = -0.6225$, $\gamma = 1.0877$). Parameters for $p(d)$ and $r(d)$ were estimated through the same logistic regression models as presented in Table 2, but with no effect of the number of seedling leaves ($ap = -1.2178$, $ar = 4.6654$, $bp = br = -0.3498$). q and F were estimated with the same demographic data (999 EL-seedlings, $q = 0.9$; 6 females, $F = 15$).

We first used this matrix model where both survival and recruitment of EL-seedlings depended on distance. We also used two other versions of the model where only EL-seedling survival or recruitment depended on distance. All matrix model analyses were performed with the ULM software (Legendre and Clobert 1995).

Results

Field data

About 75% of the fruits fell within 3 m (and 95% within 6 m) of females (Fig. 2). A clear relative outward shift (away from mother palms) was observed between the four studied immature stages (Fig. 2). This shift was significant for every pair of successive stage: fruits/EL-seedlings, EL-seedlings/SL-seedlings, and SL-seedlings/juveniles (log likelihood ratio test, Table 1a).

There was also, within the EL- and SL-seedlings stages, relative outward shifts of seedling distributions with increasing age classes of mother palms (the older a female is, the further its EL-seedlings are) (Fig. 4). This shift was significant for EL-seedlings (Table 1b). For SL-seedlings samples were too small to use the G test (too many expected frequencies smaller than five) (Sokal and Rohlf), so that we used the Kolmogorov-Smirnov test. The outward shift was significant between SL-seedlings of young females, and SL-seedlings of middle-aged females ($D = 0.3794$, $n_1 = 23$, $n_2 = 99$, $P < 0.05$). There was also an outward shift between EL-seedlings of the younger females and fruits of all females (Table 1b).

Seedlings were censused during the wet season when no seedling death was recorded. Since fire burns the leaves of seedlings at the end of the dry season, seedlings probably mostly die during the dry season or after the fire before setting new leaves. Fire is unlikely to kill seedlings directly (Miranda et al. 1993) because bulbs (that contain the reserves) and terminal buds of seedlings are about 50 cm deep below ground. No predator was observed.

When seedlings of all females were pooled together both distance and number of seedling leaves had a global effect on the fate of EL-seedlings (Table 2). The proportional odds ratio test showed that they had the same significant effect on both P_d and P_{d+p} probabilities (same slope in the linear functions f_p and f_r; i.e. b_p is not significantly different from b_r and same slopes for the effect of seedling number of leaves; cf. model description). That means that distance to the mother palm and seedling number of leaves had a significant effect on both survival without recruitment ($P_{d+p} - P_d$) and recruitment ($1 - P_d$). The slopes estimated by the logistic regression model (b_p and b_r of the f_p and f_r functions as defined for the matrix model, and also the two slopes estimated for the effect of number of leaves) for the effects of distance and seedling number of leaves were negative. As a consequence, survival without recruitment and recruitment probabilities increase with distance and number of leaves. For the model including the effect of EL-seedling density, density had no effect on the fate of EL-seedlings (Table 2). This points out that distance had a clear common effect on survival and recruitment of EL-seedlings for all studied females, whereas density did not affect either survival or recruitment.

To test whether EL-seedling density had an effect that would not be contained in the effect of distance, we incorporated both distance to the mother palm and density of EL-seedlings (residuals of the regression of density against ln(distance)) in the same logistic regression model for the six females. Again, only the effect of distance was significant (Table 2, last row). There was no effect of density on the fate of EL-seedlings.

Model

As the matrix A was neither primitive nor irreducible it was not possible to use the Perron-Frobenius theorem (Caswell 1989) to investigate the behaviour of the seedling population model. Nevertheless, this matrix was found to have a dominant eigenvalue λ_1 equal to 1. The other eigenvalues were real and strictly inferior to 1 (they were in fact equal to the survival probabilities $p(d)$ and q). Thus the model necessarily displayed a stable stage distribution (Caswell 1989): percentages of EL-seedlings and SL-seedlings in each distance class converged towards finite values. Furthermore, since λ_1 was equal to 1, absolute numbers of seedlings did not increase exponentially, but since there was initially no seedling (at $t = 0$ the mother palm had never reproduced), they increased and converged towards finite values (this is the transient behaviour of the model). In every case, after 60 yr of simulation and when mother palms are supposed to stop reproducing and die, populations of seedlings were still in the transient phase of the model. They had not reached the stable stage distribution, and absolute numbers of individuals had not converged to their final values. That means that seedling recruitment curves (in percentages) changed from year to year all through the reproductive part of the life of their mother palms.

The model overestimates absolute numbers of SL-seedlings by a factor three. This discrepancy may be due to many uncontrolled factors of variability. Some of the model parameters (particularly fecundity, and survival of seedlings) vary from year to year whereas we only use here a first estimation of these parameters based on one year of data. In the same way, numbers of SL-seedlings are likely to be overestimated, since the model focuses on the first two stages of the *B. aethiopum* life cycle and SL-seedlings were not allowed to recruit to the juvenile stage. Therefore, we only use the model results qualitatively, to analyse the mechanisms of recruitment curve dynamics and not to investigate thoroughly the case of *B. aethiopum*.

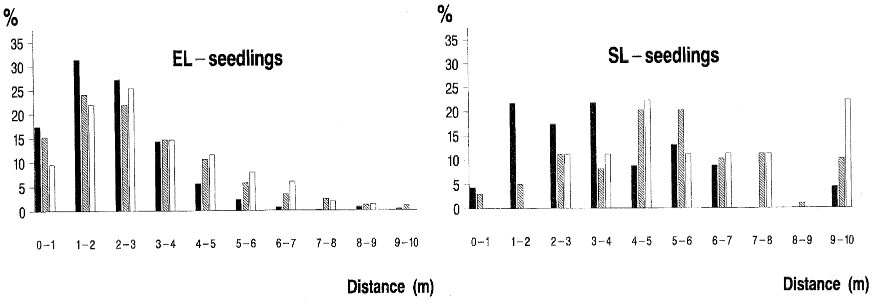


Fig. 4. Distribution of EL- and SL-seedlings in 1-m-wide concentric bands around females of three age classes (respectively 574, 1845, and 315 EL-seedlings; respectively 23, 99 and 9 SL-seedlings): young females ■, middle-aged females ▧, senescent females □.

Table 2. Logistic regression for the fate of EL-seedlings used as an ordinal response (death < survival in the same stage < survival and recruitment to the SL-seedling stage) as a function of distance to the female or seedling density. The logit link function was used. ES, estimated slope; $W\chi^2$, Wald chi-square; nt, not tested in the model; ***, $P<0.0005$. The score test (χ^2) for the proportional odds assumption was used to test whether independent variables had the same effect on P_d and P_{d+p} probabilities (P_d is the probability of death, and P_{d+p} is the probability of death or survival without recruitment to the EL-seedling stage as defined for the cumulative logit link function; cf. model description). Models were analysed for all the EL-seedlings of the six females pooled together (999 EL-seedlings). For the distance and density model, the residuals of the regression of the density of EL-seedlings against the logarithm of distance was used instead of the density.

	Distance to the female		Seedling density		Number of leaves		Model global assessment		Proportional odds ratio	
	ES	$W\chi^2$	ES	$W\chi^2$	PE	$W\chi^2$	$-2 \ln L$	P	χ^2	P
Distance model	−0.33	23.6***	nt		−1.04	25.0***	56.78	0.0001	0.442	0.8018
Density model	nt		0.06	1.20	−1.06	23.9***	28.02	0.0001	0.412	0.8138
Distance and density model	−0.34	22.3***	−0.09	0.32	−1.04	24.2***	57.01	0.0001	4.004	0.2610

The model displays qualitatively the same features (Fig. 5) as the field data: an outward shift of the SL-seedlings in comparison with the EL-seedlings (the modal distance class of the distributions shifts from 1–2 m to 2–3 m), and an outward shift of both EL- and SL-seedlings according to the number of years of reproduction. Outward shifts seem to be less important in the model than in the observed distributions; this may be due mainly to a possible positive effect of distance on the survival of SL-seedlings, even though such an effect was not statistically detected in this study.

When only survival of EL-seedlings depended on distance (Fig. 6) there was a temporal outward shift of the distributions according to the number of years of reproduction (age of the female), but no discordance between EL- and SL-seedling distribution. When only recruitment of EL-seedlings depended on distance (Fig. 6) there was only a relative outward shift between EL- and SL-seedling distributions: there was no temporal evolution of the distributions according to the age of the female.

Discussion

We found that most fruits were dispersed very close to the mother palms. This result is not surprising for heavy fruits dispersed by barochory. We have shown that the difference between EL- and SL-seedling distributions must be due to distance-dependent rather than to density-dependent survival and recruitment. Thus two mechanisms are possible: (1) action of some distance-dependent seed predators or seed pathogens on EL-seedlings, or (2) competition with the mother palm. No seedling predator is known for the leaves or the roots (Vuattoux 1965) and both roots and leaves contain much silica that is likely to deter at least invertebrate herbivores (Vicary and Bazely 1993). We have looked for below- and aboveground pathogens but none were found. Nevertheless, an inconspicuous underground attack, such as the attack of a root-eating nematode, may have remained undetected. Competition with the mother palm for water or nutrients is very likely according to the high root density found around adult palms (very high density within 3 m) (Mordelet et al. 1996). Competition between mother palms and their seedlings would lead to distance-dependent recruitment and survival of SL-seedlings. The advantage of this competition hypothesis is that it is parsimonious since competition could also be responsible for the observed outward shift between SL-seedlings and juveniles. On the contrary, a pathogen such as a root-eating nematode or a fungus is more likely to be able to kill seeds or young seedlings than well established SL-seedlings that are on average 15 yr old, and even EL-seedlings that are on the average 9 yr old (ages estimated through a matrix population model, unpubl. results).

The transition between seeds and EL-seedlings is currently being studied. The slight but significant difference between the distributions of fruits and EL-seedlings (or even between the distributions of fruits and EL-seedlings of the young females) may be due either to spatial variations in germination rates, due to some predator or pathogen, or to the observed distance dependence for early EL-seedling survival. As opposed to seedlings, some seed predators are known for seeds (especially some Bostrichideae) (Vuattoux 1965) and may be distance or density dependent.

A former study (Barot et al. 1999) of the spatial pattern, on the scale of a few hectares, of *B. aethiopum* confirms the present smaller-scale study. SL-seedlings were found to be strongly associated with females, whereas there was no association between juveniles and female palms.

We showed that the dynamics of PRCs (relative outward shifts between distributions of offspring stages, and increasing temporal outward shifts of the distributions of offspring stages along the reproductive life of parent trees) may only be due to the cumulative effect of distance-dependent survival and recruitment events concerning individuals of stages that last more than one year as for the transition between EL- and SL-seedlings in *B. aethiopum*. This simple mechanism leads to relatively complicated dynamics of PRCs during the reproductive life of a tree. Real PRC dynamics must be much more complicated than the one we have modelled with our matrix population model. (1) Fecundity is not constant. (2) The distance or density effects are likely to change over years; for example, if the density of predators is not constant or if climate variations lead to variations in the intensity of competition between seedlings, or between seedlings and parents. (3) PRC dynamics are likely to change after the death of the focal reproductive trees. These dynamics will be very different according to the mechanism of the initial outward shift of the PRCs. For example, if this outward shift is due to competition with parent trees, the outward shift is likely to stop. That is not necessarily the case if the outward shift is due to some predator or pathogen. Populations matrix models could help exploring the consequences of the three issues above.

The fact that both seedling survival and recruitment into a later stage are distance dependent is informative about the underlying process. Unless we suppose that two different processes are responsible for this distance dependence, that means that this process probably weakens EL-seedlings leading to a low recruitment probability into the SL-seedling stage (case of lightly weakened EL-seedlings), and to a lower survival probability (case of strongly weakened EL-seedlings); i.e. this process is continuous and does not act like seed or seedling predators that kill an attacked seed or seedling. Competition with the mother palm could have such an effect, yet it cannot be excluded that some pathogen is able to weaken seedlings with various intensities and with a probability depending on the distance to the mother palm.

Both dynamic data and model results, taken into account qualitatively, showed here that the observed El- and SL-seedling PRC distributions around mother palms (relative outward shift of distributions of individuals of successive stages, and temporal outward shift of distributions of individuals of a given stage along the reproductive life of parent trees) can only be explained by both distance-dependent survival and recruitment. For example, model results pointed out that, for the transition between two stages, spatial variations of survival rates were responsible for the temporal outward shift of the distributions of both stages but not for the discrepancy between the distributions of the two stages (Fig. 6). Can such results be generalised?

On the one hand, survival and recruitment rates were distance dependent in our model, simply because field data proved that it was the case for *B. aethiopum*, but a model incorporating density dependence displayed qualitatively the same pattern of PRC dynamics (the model is not presented here), with the same respective role for spatial variations in survival and recruitment rates. Density-dependent processes could lead to the

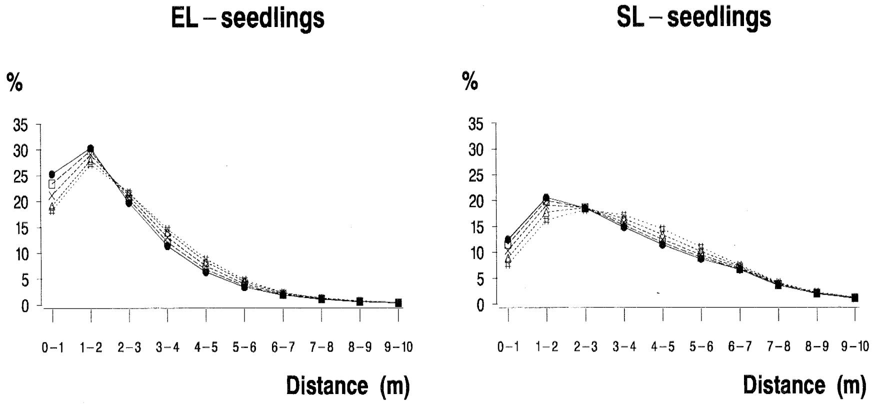


Fig. 5. Simulated distributions of EL- and SL-seedlings in 1-m-wide concentric bands around a female after 2 ●, 5 □, 10 X, 20 △ and 60 ⌗ yr of reproduction.

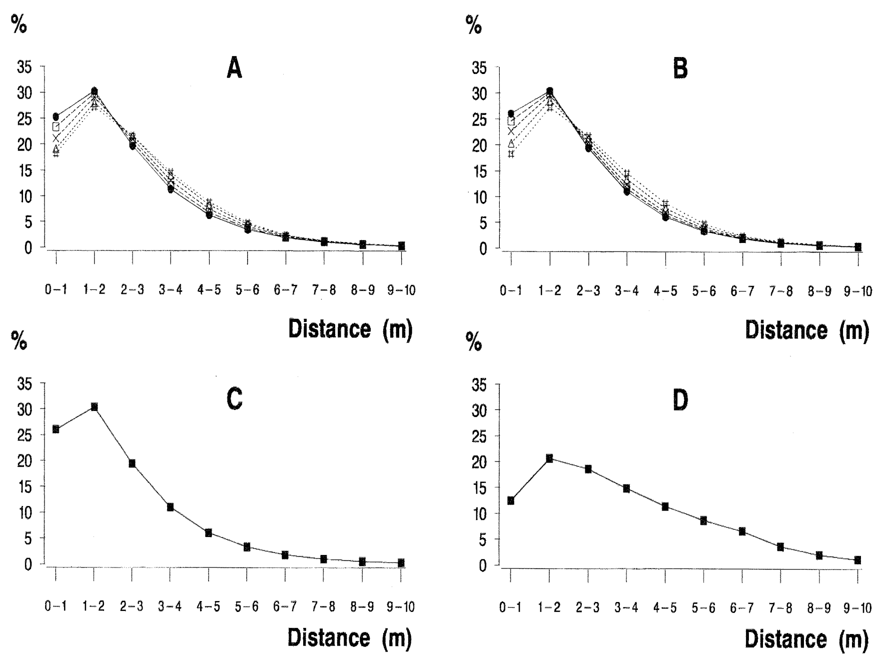


Fig. 6. Simulated distributions of EL- and SL-seedlings in 1-m-wide concentric bands around a female after 2, 5, 10, 20 and 60 yr (same legend as Fig. 5) of reproduction: only survival of EL-seedlings depends on distance, (A) EL-seedlings, (B) SL-seedlings; only recruitment of EL-seedlings depends on distance, (C) EL-seedlings, (D) SL-seedlings.

same PRC dynamics. On the other hand, PRCs of > 1-year-old seedlings have been rarely studied (Clark and Clark 1984, Condit et al. 1992). Most studies focus on seeds and young seedlings (Janzen 1971a, 1972b, Augspurger 1983a, b, 1984, Clark and Clark 1981, Howe et al. 1985, Schupp 1988, Chapman and Chapman 1996, Cintra 1997, Peres et al. 1997). Furthermore, most of these studies measured distributions of cohorts (individuals resulting from the seeds produced at a given time), and did not measure distributions of stages that incorporate individuals belonging to many cohorts, so that measuring recruitment rates between two discrete stages was not possible. Here, demographic data are available for one year, but studied EL-seedlings and SL-seedlings are on average 9-yr-old, and 14-yr-old, respectively (unpubl. matrix population model). This explains why no study has emphasised both a relative outward shift between successive stages (on average, the older a seedling is, the farther it is from the parent tree), and a temporal outward shift of the distributions of individuals of a given stage along the reproductive life of parent trees (the older a reproductive tree is, the farther are its offspring). Anyway, the patterns observed for *B. aethiopum* should be expected if seedling and sapling stages last several years. *B. aethiopum* display morphologically distinct immature stages, but recruitment between "stages" defined by size classes may be distance or density dependent so that any tree species may display the same PRCs dynamics as *B. aethiopum*. In this way, if seedling or sapling growth is reduced close to the parent tree as in Hubbell et al. (1990), the same offspring distribution as in *B. aethiopum* could be detected. The pattern observed for *B. aethiopum* may be much more conspicuous than for studied trees of tropical forests for two reasons. (1) It is a savanna palm tree so that tree cover is not closed as in forests and *B. aethiopum* seedling distribution is probably not significantly influenced by interspecific competition. (2) The low dispersal distance and the adult spatial pattern (females and also males grow on average about 15 m away from each other) permit to determine easily which are the seedlings of a given female, and reduce the possibility of interaction between seedling and other adult palms than their mother.

Whatever the process leading to the outward shift of the PRC, it results in the death of most seeds and seedlings produced during the life of *B. aethiopum* females. This death is not due to chance and harshness of environmental conditions but indirectly to the parent palms either as a source of predators (distance-dependent predation) or even directly to the negative action of parent palms on their offspring (which is the more likely for *B. aethiopum*). Females invest a lot of resources in the production of heavy fleshy fruits and heavy seeds that are very unlikely to reach the adult stage because seeds are not dispersed very far from their mothers. Thus, it seems that *B. aethiopum* should have evolved either towards more efficient seed dispersal, or towards a concentrated production of less seeds at the end of the life (or finally to semelparity) (Smith 1984). However, the opposite pattern has been found. *B. aethiopum* females produce fruits for many years and their fecundity starts to decrease soon after sexual maturity (Barot and Gignoux 1999).

In fact, abundant seed production can have evolved (1) so that seedling predators could be satiated (Janzen

1970, 1971b), or (2) for risk reduction (or bet hedging) (Howe and Smallwood 1982, Stearns 1992, Venable and Brown 1993) so that one seedling among the great quantity produced could reach a temporally and spatially favourable patch. For *B. aethiopum*, the former is possible but not very likely because no predator has been found for the seedlings. The latter is more likely but there is no dormancy, and the average dispersal distance seems to be too small to enable efficient escape of negative effects of mother palms or to colonise new favourable patches. *B. aethiopum* has probably evolved large fleshy fruits to attract seed dispersers that are no longer present in the Lamto reserve, such as baboons (Vuattoux pers. comm.) and elephants (Alexandre 1978) that were probably efficient dispersers for *B. aethiopum* seeds. These dispersers were likely to permit a few seeds to escape distance-dependent mortality. In this context, the Lamto savanna could constitute a large-scale field experimental test of the evolutionary importance of seed dispersal; we have to test whether *B. aethiopum* populations are presently stable or whether they are declining due to the impossibility of taking advantage of environmental spatial heterogeneity and escaping intraspecific competition.

We have demonstrated that a savanna palm verifies the first part of the Janzen-Connell hypothesis, i.e. recruitment distance of seedlings is greater than could be predicted from the seed dispersal curve. Thus, this hypothesis should not be tested only in tropical forests. However, the second part of this hypothesis, i.e. long recruitment distances favour coexistence and thus tree biodiversity, is questionable for *B. aethiopum*, and is still to be tested. Nevertheless, PRC dynamics should be studied in any ecosystem for the role it plays in tree dynamics and especially as a process linking tree demography, and tree spatial pattern. The consequences of an outward shift of PRC must be studied both for its consequences on other species than the focal tree species, and for its consequences on the dynamics of the focal tree species itself. We also emphasise that the PRC patterns found here, in a particular case – relative outward shifts between successive immature stages, and outward shift of the distributions of each immature stage according to the mother age – is potentially very common, and may only be due to the cumulative effect with time of small spatial differences in survival and recruitment rates.

Acknowledgements – We express our gratitude to the Université Nationale de Côte d'Ivoire, and to R. Vuattoux for their help in the field, and many personal communications. We thank Lamto technicians (Kouassi Kouassi Etienne, Kouame N'Guessan François, Konan Marcel and Savadogo Sadaré Prosper) for their practical assistance and sharing their knowledge of the field with us. We are grateful to S. Legendre for his help about matrix population models. The work was supported by funding from the CNRS-ORSTOM SALT program (GCTE core research project).

References

Alexandre, D.-Y. 1978. Le rôle disseminateur des éléphants en forêt de Taï, Côte-d'Ivoire. – Terre Vie 32: 47–62.

Augspurger, C. K. 1983a. Offspring recruitment around tropical trees: changes in cohort distance with time. – Oikos 40: 189–196.

Augspurger, C. K. 1983b. Seed dispersal of the tropical tree, *Platypodium elegans*, and the escape of its seedlings from fungal pathogens. – J. Ecol. 71: 759–771.

Augspurger, C. K. 1984. Seedling survival of tropical tree species: interactions of dispersal distance, light-gaps, and pathogens. – Ecology 65: 1705–1712.

Barot, S. and Gignoux, J. 1999. Population structure and life cycle of *Borassus aethiopum* Mart.: evidence of senescence in a palm tree. – Biotropica in press.

Barot, S., Gignoux, J. and Menaut, J.-C. 1999. Demography of a savanna palm tree: predictions from comprehensive spatial pattern analyses. – Ecology in press.

Becker, P., Lee, L. W., Rothman, E. D. and Hamilton, W. D. 1985. Seed predation and the coexistence of tree species: Hubbell's models revisited. – Oikos 44: 382–390.

Caswell, H. 1989. Matrix population models. – Sinauer, Sunderland, MA.

Chapman, C. A. and Chapman, L. J. 1996. Frugivory and the fate of dispersed and non-dispersed seeds of six African tree species. – J. Trop. Ecol. 12: 491–504.

Cintra, R. 1997. A test of the Janzen-Connell model with two common tree species in Amazonian forest. – J. Trop. Ecol. 13: 641–658.

Clark, D. A. and Clark, D. B. 1981. Effects of seed dispersal by animals on the regeneration of *Bursera graveolens* (Burseraceae) on Santa Fe Island, Galapagos. – Oecologia 49: 73–75.

Clark, D. A. and Clark, D. B. 1984. Spacing dynamics of a tropical rain forest tree: evaluation of the Janzen-Connell model. – Am. Nat. 124: 769–788.

Condit, R., Hubbell, S. P. and Foster, R. B. 1992. Recruitment near conspecific adults and the maintenance of tree and shrub diversity in a neotropical forest. – Am. Nat. 140: 261–286.

Connell, J. H. 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. – In: Den Boer, P. J. and Gradwell, G. (eds), Dynamics of populations. PUDOC, Wageningen, pp. 298–312.

Connell, J. H., Tracey, J. G. and Webb, L. J. 1984. Compensatory recruitment, growth, and mortality as factors maintaining rain forest tree diversity. – Ecol. Monogr. 54: 141–164.

Coomes, D. A. and Grubb, P. J. 1998. Responses of juvenile tree to above- and belowground competition in nutrient-starved Amazonian rain forest. – Ecology 79: 768–7982.

Howe, H. F. and Smallwood, J. 1982. Ecology of seed dispersal. – Annu. Rev. Ecol. Syst. 13: 201–228.

Howe, H. F., Schupp, E. W. and Westley, L. C. 1985. Early consequences of seed dispersal for a neotropical tree (*Virola surinamensis*). – Ecology 66: 781–791.

Hubbell, S. P. 1980. Seed predation and the coexistence of tree species in tropical forests. – Oikos 35: 214–229.

Hubbell, S. P., Condit, R. and Foster, R. B. 1990. Presence and absence of density dependence in a neotropical tree community. – Philos. Trans. R. Soc. Lond. B 330: 269–281.

Janzen, D. H. 1970. Herbivores and the number of tree species in tropical forests. – Am. Nat. 104: 501–528.

Janzen, D. H. 1971a. Escape of juvenile *Dioclea megacarpa* (Leguminosae) vines from predators in a deciduous tropical forest. – Am. Nat. 105: 97–112.

Janzen, D. H. 1971b. Seed predation by animals. – Annu. Rev. Eco. Syst. 2: 465–492.

Janzen, D. H. 1972a. Association of a rainforest palm and seed-eating beetles in Puerto-Rico. – Ecology 53: 258–261.

Janzen, D. H. 1972b. Escape by *Sterculia apetala* seeds from the bug *Dysdercus fasciatus* in a Costa Rican deciduous forest. – Ecology 53: 350–361.

Janzen, D. H., Miller, G. A., Hackforth-Jones, J., Pond, C. M., Hooper, K. and Janos, D. P. 1976. Two costa rican bat-generated seed shadows of *Andira inermis* (Leguminosae). – Ecology 57: 1068–1075.

Legendre, S. and Clobert, J. 1995. ULM, a software for conservation and evolutionnary biologists. – J. Appl Stat. 22: 817–834.

McCanny, S. J. 1985. Alternatives in parent-offspring relationships in plants. – Oikos 45: 148–149.

Menaut, J.-C. 1983. The vegetation of African savannas. – In: Bourlière, F. (ed.), Tropical savannas. Elsevier, Amsterdam, pp. 109–149.

Menaut, J.-C. and César, J. 1979. Structure and primary productivity of Lamto savannas, Ivory Coast. – Ecology 60: 1197–1210.

Miranda, A. C., Miranda, H. S., de Fatima Oliveira Dias, I. and Ferreira de Souza Dias, B. 1993. Soil and air temperatures during prescribed cerrado fires in Central Brazil. – J. Trop. Ecol. 9: 313–320.

Monod, T. 1957. Les grandes divisions chorologiques de l'Afrique. – C.S.A. C.C.T.A. Publ. 24: 1–147.

Mordelet, P., Barot, S. and Abbadie, L. 1996. Root foraging strategies and soil patchiness in a humid savanna. – Plant Soil 182: 171–176.

Peres, C. A., Schiesari, L. C. and Dias-Leme, C. L. 1997. Vertebrate predation of Brazil-nuts (*Bertholletia excelsa*, Lecythidaceae), an agouti-dispersed Amazonian seed crop: a test of the escape hypothesis. – J. Trop. Ecol. 13: 69–79.

Portnoy, S. and Willson, M. F. 1993. Seed dispersal curves: behavior of the tail of the distribution. – Evol. Ecol. 7: 25–44.

SAS 1989. SAS/STAT User's Guide, Ver. 6, 4th ed. – SAS Inst., Inc., Cary, NC.

Schupp, E. W. 1988. Seed and early seedling predation in the forest understory and in treefall gaps. – Oikos 51: 71–78.

Smith, A. 1984. Postdispersal parent-offspring conflict in plants: antecedent and hypothesis from the Andes. – Am. Nat. 123: 354–370.

Sokal, R. R. and Rohlf, F. J. 1981. Biometry. – Freeman, New York.

Stearns, S. C. 1992. The evolution of life histories. – Oxford Univ. Press, Oxford.

Tomlinson, P. B. and Jeffrey, E. C. 1990. The structural biology of palms. – Clarendon Press, Oxford.

Venable, D. L. and Brown, J. S. 1993. The population-dynamic functions of seed dispersal. – Vegetatio 107/108: 31–55.

Vicary, M. and Bazely, D. R. 1993. Do grasses fight back? The case for antiherbivore defences. – Trends Ecol. Evol. 8: 137–142.

Vuattoux, R. 1965. Le peuplement du palmier Rônier (*Borassus aethiopum*) d'une savane de Côte d'Ivoire. – PhD thesis, Université de Paris, Paris.

Appendix

Life cycle graph corresponding to the matrix population model. EL-S i, entire-leaved seedlings of the *i*-th 1-m-wide concentric band; SL-S i, slit-leaved seedlings of the *i*-th 1-m-wide concentric band; *f*(*i*), number of new EL-seedlings produced yearly in the *i*-th band; *p*(*i*), survival probability of EL-seedlings in the *i*-th band; *r*(*i*), recruitment probability of EL-seedlings in the *i*-th band; *q*(*i*), survival probability of SL-seedlings in the *i*-th band (Fig. A1).

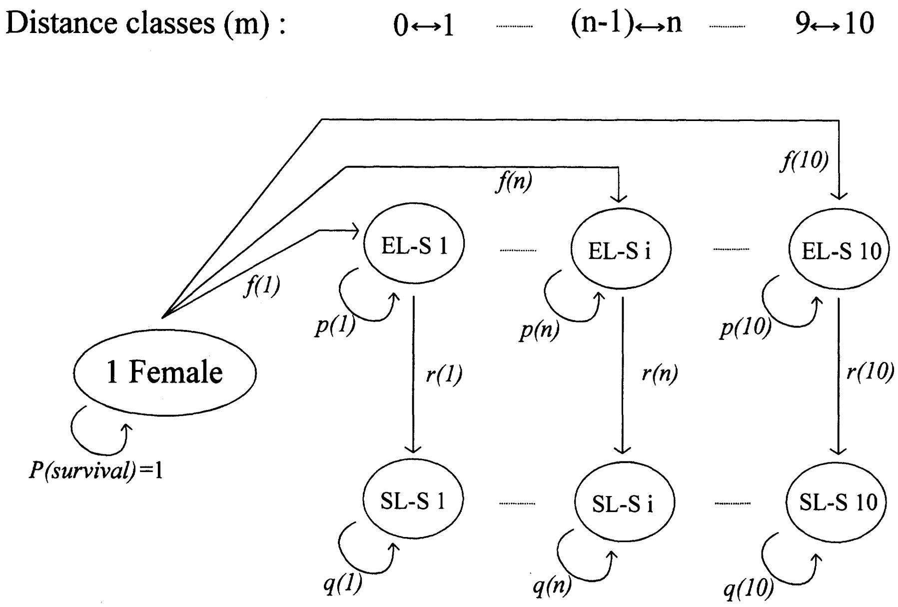


Fig. A1. Life cycle graph corresponding to the matrix population model.