

## DISPERSAL IN TIME AND SPACE: A COMBINED ANALYTICAL-EXPERIMENTAL APPROACH

RONEN KADMON

### Abstract

Many plants disperse their seeds in both space (via dispersal) and time (via dormancy). Theoretical models indicate that seed dispersal and between-year dormancy are alternative mechanisms that may contribute to the stabilization of populations in fluctuating environments, to the coexistence of competing species, to species diversity, and to the maintenance of populations in unfavorable habitats where local reproduction is insufficient to balance mortality. Unfortunately, most of these models contain variables and parameters which are extremely difficult to measure. As a consequence, there has been virtually no experimental calibration of these models, or tests of their predictions in natural plant populations. In an attempt to bridge this gap, a new approach combining a theoretical model and an experimental procedure has been developed for quantifying population dynamic functions of seed dispersal and dormancy. The approach is based on the identification of three potential sources of recruitment to plant populations: (1) input from local reproduction in the previous year, (2) input from the soil seed bank, and (3) input from dispersal. The quantitative relationships among these three sources of recruitment determine the contribution of seed dispersal and between-year dormancy to population density. The approach developed allows one to derive mathematical expressions for the three sources of recruitment, and to estimate their values in natural plant populations. Results from a field study based on this approach indicate that input of seeds produced in relatively favorable habitats may interact with seed dormancy in promoting the persistence of annual plant populations in less favorable habitats.

### Theoretical considerations

Results from theoretical models suggest that between-year dormancy and seed dispersal are alternative mechanisms enabling plants to reduce the risk of extinction in randomly fluctuating and unpredictable environments (COHEN, 1966; DEN-BOER, 1981; COHEN & LEVIN, 1985; VENABLE & BROWN, 1988). Between-year dormancy may serve as a hedge against extinction since it permits temporal averaging of the reproductive success (COHEN, 1966; ELLNER, 1985; BROWN & VENABLE, 1986). Dispersal is an analogous mechanism which enables a plant to spread the risk of extinction over space (DEN BOER, 1968, 1981; MOTRO, 1982; LEVIN & al. 1984; COHEN & LEVIN, 1985; KLINKHAMER & al. 1987). Both traits allow escape from spatially or temporally unfavorable conditions, and, on the average, to exploit more favorable ones.

Other models have indicated that seed dormancy and dispersal may function as important mechanisms for species coexistence in variable and unpredictable environments (COMINS & NOBLE, 1985; PACALA, 1986, 1987; CHESSON & HUNTLEY, 1989). Dispersal may contribute to coexistence because it may cause species to occur in habitats where they would otherwise be competitively excluded (SHMIDA & ELLNER,



1984). Between-year seed dormancy may lead to non-equilibrium coexistence so long as each species has the advantage in some years (SHMIDA & ELLNER, 1984; CHESSON & HUNTLEY, 1989). These theories have indicated that immigration of seeds produced in refuge habitats and/or temporal input of seeds produced in refuge years can contribute substantially to the diversity of plant communities in spatially heterogeneous and randomly fluctuating environments.

Further interest in the population dynamic functions of seed dispersal has been arisen from models of 'source-sink' population dynamics (SHMIDA & ELLNER, 1984; PULLIAM, 1988). Such models have shown that natural populations may be structured in such a way that a large fraction of the individuals occur in 'sink' habitats where within-habitat reproduction is insufficient to balance mortality. Populations may persist in such habitats because of immigration from neighboring 'source' habitats where reproduction exceeds mortality. The results of such models have indicated that the dynamics of populations in a given habitat may be determined to a large degree by conditions in other, neighboring habitats.

### A combined analytical-Experimental approach

The usefulness of theoretical models depends, in large part, on the extent to which the required variables and parameters can be measured in the field. Unfortunately, most of the models that have been used to explore the evolutionary and demographic consequences of between-year dormancy and dispersal (e.g., LEVIN & al., 1984; COHEN & LEVIN, 1985; KLINKHAMER & al., 1987; VENABLE & BROWN, 1988) contain variables and parameters which are extremely difficult to measure. A typical form of such models can be constructed as follows. Consider a system composed of  $L$  distinct patches ( $i = 1, \dots, L$ ) each occupying an area  $A_i$ . Let the density of the seeds in patch  $i$  in year  $t$  be  $S_i(t)$ . A proportion  $G$  of the seeds germinate with an expected seed yield  $Y_i(t)$ . A proportion  $D$  of the seeds disperse out of the parental patch and are spread uniformly over the entire area. A fraction  $(1-V)$  of the newly produced seeds are lost or die leaving the residual fraction  $V$  available for germination in year  $t+1$ . The seeds that did not germinate have survival  $U$  in the between-year seed bank. The discrete recursive growth formula for an annual plant with dispersal and dormancy under the above assumptions is:

$$\text{Eq. I} \quad S_i(t+1) = S_i(t)GY_i(t)(1-D)V + S_i(t)(1-G)U + GDV \left[ \sum_{i=1}^L A_i \right]^{-1} \sum_{j=1}^L S_j(t)Y_j(t)A_j$$

While models of this form have a number of desirable heuristic properties, from a practical point of view it is not very easy to census seeds in the soil. With field applications in mind, KADMON & SHMIDA (1989) rewrote this recursion equation in terms of the much more readily censused seedling densities. To do this, the whole equation is multiplied by  $G$  and then  $N_i(t) = S_i(t)G$  and  $N_i(t+1) = S_i(t+1)G$  are substituted, where  $N_i(t)$  and  $N_i(t+1)$  are seedling densities in patch  $i$  in year  $t$  and  $t+1$  respectively. Also, for practical purposes, dispersal is removed from the first term by separating the  $(1-D)$  term into two components and combining the '-D portion' with



the other dispersal term into a new third term. Finally, while the original heuristic models are defined in terms of 'patches', KADMON and SHMIDA (1989) formulated their model in terms of 'habitat types'. When defined in this way the  $N_i$ 's and  $Y_i$ 's become habitat averages rather than patch averages. A two-habitat version of this modified model can be written as the sum of three components:

$$\text{Eq. II } N_i(t+1) = \underbrace{N_i(t)Y_i(t)VG}_{\text{Component I}} + \underbrace{N_i(t)(1-G)U}_{\text{Component II}} + \underbrace{GDVA_j[N_j(t)Y_j(t) - N_i(t)Y_i(t)]}_{\text{Component III}} / (A_i + A_j)$$

where (i) and (j) are the two habitat types available in the system.

In this form of the model, seedling density of a given habitat,  $i$ , in a given year,  $t+1$ , is expressed as the sum of three demographic components, each representing a different spatio-temporal source of recruitment. Component I expresses the density of seedlings expected for the habitat if neither dispersal, nor dormancy contributes to its population (i.e., the density expected from within-habitat reproduction in year  $t$ ). Component II expresses the contribution to the seedling density from the between-year seed bank (i.e., from those seeds that were in the soil and did not germinate in year  $t$ ). Component III expresses the net contribution from dispersal (i.e., dispersal into the habitat minus dispersal out of the habitat). By comparing the values of these components with each other and with  $N_i(t+1)$  it is possible to determine the absolute and relative contribution of between-year dormancy and between-habitat dispersal to the maintenance of the relevant population.

Practically, Component I is quantified as the product of the mean seedling density in year  $t$ , the mean seed production per seedling, and the fraction of newly-produced seeds that germinate in the following year,  $t+1$ . Component II is calculated using seed-bank experiments and Component III is determined by subtracting the sum of the first two components from the actual seedling density measured in year  $t+1$  (see KADMON & SHMIDA, 1989 for a detailed description of these demographic measurements and experiments). Using such an approach, the population dynamic functions of seed dormancy and dispersal can be investigated without having to measure all of the model parameters. Moreover, since  $VG$ ,  $A_i$ ,  $N_i(t)$  and  $Y_i(t)$  are directly measured for each habitat type, Component III can be solved for  $D$ , the between-habitat dispersal fraction.

### A case study

The applicability of the approach described above was evaluated in a system of the annual grass species *Stipa capensis*. This species is common in the desert and semi-desert regions of the Middle East and northern Africa. The study was conducted about 20 km east of Jerusalem, an area receiving an annual average of 100 mm rainfall. The typical landscape consists of very gentle slopes dissected by small wadis. Height differences between the wadi bottoms and the surrounding slopes are at the order of 1-2 meters. Measurements of soil moisture and biomass indicated the habitat conditions in the wadis are much more favorable than those of the slope areas (KADMON, 1995; KADMON & SHMIDA, 1990).



Table 1 shows the results of demographic measurements and experiments that were conducted in the two types of habitats during two successive years, 1986 and 1987. Density and seed production per germinating plant were higher in the wadis than on the slopes. In contrast, the germination fraction was very similar in the two types of habitats (the germination fraction indicates the probability of a seed produced in 1986 to survive and germinate in 1987, i.e., it represents the combined parameters VG of equation II). The number of plants germinating from the seed bank was higher in the wadi habitat. Based on these data, the three demographic components of equation II can be calculated for each type of habitat. Such a calculation demonstrate the following trends (Table 2): (1) Local reproduction was the main source of recruitment for populations inhabiting the wadi habitat. (2) Dispersal was the main source of recruitment for slope populations. (3) The contribution of the soil seed bank was relatively small for both types of habitats. The results further indicate that within-habitat reproduction in the wadi was more than sufficient to balance local mortality, and that there was a net flow of seeds from the wadi into the slopes. In contrast, on the slopes, local reproduction was insufficient to balance mortality during the study period. Nevertheless, there was an increase in the density of slope populations during the study period due to a large input of seeds from the wadis.

	Slopes	Wadis
Density in 1986 (no. seedlings/1m <sup>2</sup> )	2	7,707
Reproduction in 1986 (no. seeds/seedling)	1.2	13.2
Germination fraction in 1987	0.18	0.17
Density in 1987 (no. seedlings/1m <sup>2</sup> )	22	15,813
Seed-bank contribution (no. seedlings/1m <sup>2</sup> )	1.6	1,440

Table 1. Results of demographic measurements conducted during two successive years in populations of *Stipa capensis* inhabiting two types of habitats in an area receiving an annual rainfall amount of 100 mm.

	Absolute Contribution (mean no. of seedlings per 1m <sup>2</sup> )		Percentage Contribution (% from N(t+1))	
	Slopes	Wadis	Slopes	Wadis
Component I (local recruitment)	0.44	17,371	2.0	109.9
Component II (seed bank)	1.60	1,440	7.3	9.1
Component III (net dispersal)	19.96	-2,998	90.7	-19.0

Table 2. Demographic data of slope and wadi populations of *Stipa capensis* calculated from Table 1, and expressed in terms of the three components of equation II.



## Conclusions

The results of the case study suggest that the demographic approach developed by KADMON & SHMIDA, (1989) may be valuable in determining the role of seed dispersal and seed dormancy in the population dynamics of annual plants. This approach may be particularly useful in studying "source-sink" population dynamic systems (PULLIAM, 1988). A source population may be defined as one in which births exceeds deaths, and immigration is less than emigration. A sink population is one in which births are fewer than deaths, and immigration exceeds emigration. Thus, source populations may maintain sink populations that would not be viable otherwise (PULLIAM 1988). The results obtained for *Stipa capensis* suggest that the studied populations might represent such a source-sink population dynamic system.

## References

- BROWN, J. V. & D. L. VENABLE (1986). Evolutionary ecology of seed bank annuals in temporally varying environments. *Am. Nat.* **127**: 31-47.
- CHESSON, P. L. & N. HUNTLEY (1989). Short-term instabilities and long-term community dynamics. *TREE* **4**: 293-298.
- COHEN, D. (1966). Optimizing reproduction in a randomly varying environment. *J. Theor. Biol.* **12**: 119-129.
- & S. A. LEVIN (1985). The interaction between dispersal and dormancy strategies in varying and heterogeneous environments. In E. TEROMATO & M. YOMAGUTI (eds.), *Mathematical topics in population biology, morphogenesis and neurosciences: 110-122. Proceed. Internat. Symp. Kyoto, 1985.*
- COMINS, H. N. & I. R. NOBLE (1985). Dispersal, variability, and transient niches: species coexistence in a uniformly variable environment. *Am. Nat.* **126**: 706-723.
- DEN-BOER, P. G. (1968). Spreading of risk and stabilization of animal numbers. *Acta Bioth.* **18**: 165-194.
- (1981). On the survival of populations in a heterogeneous and variable environment. *Oecologia (Ber.)* **50**: 39-53.
- ELLNER, S. (1985). ESS germination strategies in randomly varying environments I. Logistic-type models. *Theor. Popul. Biol.* **28**: 59-79.
- KADMON, R. (1995). Plant competition along soil-moisture gradients: a field experiment with the desert annual *Stipa capensis*. *Journ. Ecology* **82**: 253-262.
- & A. SHMIDA (1989). Spatio-temporal demographic processes in plant populations: an approach and a case study. *Am. Nat.* **135**: 382-397.
- KLINKHAMER, P. G. L., T. J. DE JONG, J. A. J. METZ & J. VAL (1987). Life history tactics of annual organisms: the joint effects of dispersal and delayed germination. *Theor. Popul. Biol.* **32**: 127-156.
- LEVIN, S. A., D. COHEN & A. HASTINGS (1984). Dispersal strategies in patchy environments. *Theor. Popul. Biol.* **26**: 165-191.
- MOTRO, U. (1982). Optimal rates of dispersion and migration in biological populations. *Theor. Popul. Biol.* **21**: 394-411.
- PACALA, S. W. (1986). Neighborhood models of plant population dynamics. IV. Single- and multi-species models of annuals with dormant seeds. *Am. Nat.* **128**: 859-878.



- (1987). Neighborhood models of plant population dynamics 3. Models with Spatial heterogeneity in the physical environment. *Theor. Popul. Biol.* **31**: 359-392.
- PULLIAM, H. R. (1988). Sources, sinks, and population regulation. *Am. Nat.* **132**: 652-661.
- SHMIDA, A. & S. ELLNER (1984). Coexistence of plant species with similar niches. *Vegetatio* **58**: 20-55.
- VENABLE, D. L. & J. S. BROWN (1988). The selective interactions of dispersal, dormancy, and seed size as adaptations for reducing risk in variable environments. *Am. Nat.* **131**: 360-384.

**Address of the author:**

Dr. R. Kadmon, Department of Evolution, Systematics & Ecology, Institute of Life Sciences, The Hebrew University of Jerusalem, Givat-Ram, 91904, Jerusalem, Israel.