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An integrated model of demography, patch dynamics and seed dispersal in a woodland herb, *Primula vulgaris*

Teresa Valverde and Jonathan Silvertown

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Primula vulgaris is a woodland herb often associated with canopy gaps. The canopy regeneration cycle results in a permanently changing environment which confers a dynamic character to the overall system of *P. vulgaris* populations inhabiting a forest. In order to describe the dynamics of this spatially structured population, we built a matrix model that incorporates both the spatio-temporal variation in its population dynamics and the dynamics of the forest habitat given by the opening and closure of canopy gaps. To build the model, we combined empirical data on 1) the demography of populations in various forest patches and 2) canopy closure rate. We then used the model to test the effect of disturbance rate and long-distance (i.e., off-patch) seed dispersal on overall population dynamics. Simulation results suggest that overall population growth rate of *P. vulgaris* would be enhanced by high gap opening rates, as this would increase the relative frequency of clearings, where population growth rate is maximal. Our analysis also predicts a negative effect of long-distance seed dispersal on overall population dynamics, since seeds dispersing out of occupied patches would have a high probability of landing in closed canopy patches. These results are an example of the costs of long-distance seed dispersal on overall population dynamics. Finally, the potential role of long-distance seed dispersal in the colonization of newly opened gaps is discussed.

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Most plant populations are patchily distributed at one scale or another, often reflecting habitat heterogeneity in relation to, for instance, spatial patterns of disturbance and recruitment (White and Pickett 1985, Husband and Barrett 1996). This is the case for many forest understorey herbs which are frequently associated with canopy gaps. Such clearings provide favourable conditions for their establishment and growth (Bierzychudek 1982, Collins et al. 1985, Barkham 1992); however, gaps disappear as the canopy closes, thus affecting the demography of plant populations associated with these forest micro-habitats (Alvarez-Buylla and García-Barríos 1993). Woodland herbs exist within this perma-

nently changing environment, which confers a dynamic character to the overall system at a larger scale. There are two ways in which these larger-scale systems can be conceived and analysed: 1) they can be thought of as metapopulations in which occupied patches are local populations interconnected through seed dispersal (Levins 1970, Hanski 1991, Husband and Barrett 1996); the dynamics of such systems would be described by the foundation and extinction of local populations. Alternatively, they can be conceived as 2) patchy or spatially structured populations in which the group of occupied patches within a forest is viewed as a single large extinction-resistant population (Harrison 1991); at a

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large scale, the dynamics of such systems (i.e., what we define here as 'overall population dynamics') should be analysed through the change in the number of individual plants in the forest as a whole and the way in which this number is affected by canopy dynamics.

Whether a particular system should be regarded as 1) a metapopulation, or 2) a spatially structured population depends upon the degree of interconnection among patches, the extent to which seed dispersal determines the foundation of new populations, and the importance of local population extinction (Harrison 1991, Silvertown and Lovett Doust 1993). Here we study the system formed by a gap-colonizing woodland herb, *Primula vulgaris* Huds., and its forest habitat based on the assumption that it forms spatially structured populations; in this case, the demography of occupied forest patches varies according to canopy cover, and canopy cover in turn changes as the forest regeneration cycle proceeds. Any detailed analysis of the temporal dynamics of such spatially structured populations requires both demographic data across the range of woodland conditions in which the species occurs, as well as careful monitoring of the forest mosaic (Alvarez-Buylla and García-Barrios 1993). In this study we build a 'population-and-patch dynamics' model for *P. vulgaris* by incorporating empirical data on both its demography in patches under different canopy openness and the dynamics of the forest canopy.

Two important ecological processes may dramatically affect the internal dynamics of this *P. vulgaris* system: gap opening rate (which affects the proportion of *P. vulgaris* patches in clearings vs closed canopy conditions) and long-distance (i.e., off-patch) seed dispersal (which determines the degree of interconnection among patches and therefore its spatial structure); thus, we use our 'population-and-patch dynamics' model to investigate the theoretical effect of canopy dynamics and long-distance seed dispersal on overall population dynamics (Horvitz and Schemske 1986). It is important to bare in mind that our analysis is based on the assumption that *P. vulgaris* forms spatially structured populations, since the role and importance of various ecological processes may differ depending on the system's spatial structure. In particular, the adaptive value of seed dispersal, and thus, the expected action of natural selection on dispersal traits, may strongly depend upon spatial structure (Cohen and Levin 1991). In a complementary study we investigate the effect of these same variables (i.e., gap opening rate and seed dispersal), but this time assuming that *P. vulgaris* forms real metapopulations; there, we analyse the change in the number of local populations within the forest given by colonizations and extinctions (Valverde and Silvertown, 1997a), which is a subject that we do not address in the present paper.

An increasing number of demographic studies have started to recognize that plant populations often exist

within non-static environments in which the disturbance/regeneration cycles inherent to particular community types play a major role. Thus, the analysis of demographic patterns in nature is necessarily turning towards the understanding of these larger-scale processes and their effects at the population level. The study of systems of population patches within heterogeneous environments and their interaction with their permanently changing habitat matrix, may indeed aid in the understanding of the factors that determine long-term population dynamics, which still remains a central issue in ecology (Horvitz and Schemske 1995).

In this context, Horvitz and Schemske (1986) developed a model of 'population-and-patch dynamics' for a tropical forest herb, *Calathea ovandensis*, and used it to project the effect of three kinds of seed dispersal on mean population fitness (i.e., overall population growth rate). This kind of model has also been applied to other species with different life histories and population structures (Cipollini et al. 1993, 1994). However, these studies extrapolated population behaviour in different forest patches from empirical data collected in a limited number of forest conditions. Similar approaches, involving detailed field surveys and various underlying theoretical questions, have been developed for some tropical trees (Martínez-Ramos et al. 1985, 1988, 1989, Alvarez-Buylla and García-Barrios 1991, Alvarez-Buylla 1994). Yet, the difficulty in generalizing these kinds of population-and-patch dynamics models, results from the relatively few complete empirical data sets describing the demographic behaviour of species along the range of environmental conditions in which they naturally occur (Horvitz and Schemske 1995). Direct field estimates are important because the demographic response of some species to succession may be complex and vary among different life-stages (Alvarez-Buylla and García-Barrios 1993). Moreover, some empirical knowledge of the patch dynamics processes of the habitat in question should add an element of objectivity in the construction of such models, thus making it possible to answer relevant theoretical questions.

The model we present here is based on a) a complete demographic study of *P. vulgaris* populations across a range of light conditions given by different levels of canopy cover, and b) a survey of canopy dynamics through the analysis of canopy closure rate. We combined empirical data at these two levels to build a population-and-patch dynamics model for *P. vulgaris* following a similar approach to the one developed by Horvitz and Schemske (1986). Our aim was to explore the theoretical effect of both the forest disturbance rate and long-distance seed dispersal between *P. vulgaris* patches, on overall population dynamics. These two processes must play a major role in determining overall population growth rate, and thus in shaping particular life-history traits in this species. The frequency of gap

formation in the canopy affects forest structure, which in turn defines the proportion of *P. vulgaris* patches along different stages of the canopy regeneration cycle. Additionally, the environmental patchiness resulting from canopy dynamics determines, to some extent, the hazards involved in long-distance seed dispersal (e.g., the probability of landing in favourable or unfavourable patches), which may act as a significant selective pressure on the evolution of seed dispersal traits by shaping particular seedling mortality patterns (Gadgil 1971, Hamilton and May 1977, Venable and Brown 1993). Little is known regarding seed dispersal patterns for this species (see below); thus, the use of a modelling tool like the one presented in this paper is of special relevance in allowing us to explore its theoretical effect on overall population dynamics.

Methods

The species

P. vulgaris is a perennial herbaceous rosette plant, characteristic of temperate moist, partly shaded habitats in northern Europe. In Britain, it is common in deciduous woodlands where it usually shows a patchy distribution. This distribution pattern appears to be a result of its limited dispersal ability (Richards 1993 – see below) and the fact that the establishment of populations is often associated with the opening of gaps in the forest canopy. Vegetative spread occurs only within very short distances through the production of lateral rosettes. Flowers are distylous and appear towards the beginning of March. Seed dispersal takes place during early summer. An elaiosome makes seeds attractive to ants and small mammals, which actively harvest them and may act as dispersers (Keith-Lucas 1968, Cahalan and Gliddon 1985, Richards 1993). Ants remove only a low proportion of seeds (around 10% – Valverde and Silvertown 1995) and it is unlikely that they transport them more than a few metres from the source (Keith-Lucas 1968, Cahalan and Gliddon 1985). Small mammals (e.g., rodents) appear to be primarily responsible for the large amount of seed loss (i.e., 50–60%) observed in some populations (Valverde and Silvertown 1995). Although these animals are mainly thought of as seed predators, they may store between one fifth and one third of their harvest (Price and Jenkins 1986), which suggests that they could potentially play an important role as long-distance (i.e., off-patch) seed dispersers. However, no detailed information is currently available on dispersal distances or post-dispersal seed fates for this species.

Study sites

We studied eight *P. vulgaris* populations along a range of light conditions in three different forests. Six populations were in Dancers End Nature Reserve, in Buckinghamshire, UK (Grid Reference SP902096). This area is mainly a *Fagus sylvatica* (beech) and *Fraxinus excelsior* (ash) forest on a chalky soil (National Vegetation Classification W8, with some stands closer to W12 – Rodwell 1991). It has traditionally been managed through coppice cycles of 5 to 10 yr, the coppiced species being *Corylus avellana* (hazel) and *Crataegus monogyna* (hawthorn). Two additional populations were studied: one in Woburn Wood, a *Quercus robur* (oak) and *Castanea sativa* (chestnut) forest in Bedfordshire (Grid Reference SP927325), and another one in Salcey Forest, a *Quercus robur* and *Fraxinus excelsior* forest in Northamptonshire (Grid Reference SP814508).

Canopy dynamics

While studying the demography of the eight *P. vulgaris* populations mentioned above, we also measured the degree of canopy openness at each patch through hemispherical photography (Mitchell and Whitmore 1993) in summer 1992, 1993 and 1994. By comparing photographs taken in exactly the same points in consecutive years we were able to calculate the rate of canopy closure, which occurs exponentially through time (Valverde and Silvertown 1997b); this implies that changes in canopy openness in one year were small in closed canopy patches compared to those in brighter patches (note the change in % canopy openness per patch in Table 2). Using this information we built a Markovian model of canopy dynamics. This involved the classification of forest patches into types according to % canopy openness (Table 1), and the calculation of the probability of each patch type advancing to the following patch type in one year's time. These probabilities were obtained from the exponential canopy closure rate measured: our data indicated that each patch type takes 3 yr to become the following patch type (i.e., the time required to go from one centre of patch-type category to another), therefore, we assume that an average of 1/3 type-*x* patches become type-*x* + 1 each year. The probability of a type-*x* patch becoming a

Table 1. Classification of forest patches into types according to their level of canopy openness. Categories' upper boundaries are inclusive.

Patch type	% canopy openness	General description
1	8.1–16	Large gap
2	4.1–8	Small gap
3	2.1–4	Closing canopy
4	1–2	Closed canopy

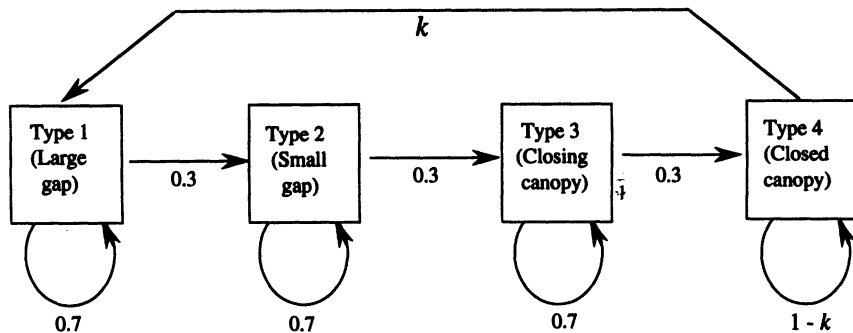


Fig. 1. Canopy dynamics model. The boxes represent different forest patch types and the arrows are the transitions among patch types from one year to the next. The probability of each transition is given below each arrow. k = disturbance rate (probability of gap opening).

type- $x + 1$ patch in one year is thus $1/3 = 0.3$. The transition probabilities among patch types obtained in this way are shown in Fig. 1. We gave different values to the disturbance rate, k (i.e., the probability of gap opening measured as the proportion of the forest area opened to gaps each year) spanning the range reported in the literature for other temperate forests (Runkle 1985, Runkle and Yetter 1987). For the sake of simplicity, our model assumes that gap formation occurs only in type-4 patches. This is a significant assumption since it determines important features of the model; however, it may not be far from reality since type-4 patches are the most frequent in the environment, thus the probability of gap formation in other forest patches may be negligible. On the other hand, gap formation can occur through both natural disturbances or coppicing; according to traditional practices this later activity is carried out mainly in closed canopy patches.

The canopy dynamics model is represented by a generalized $n \times n$ Lefkovich matrix, P , where n is the number of forest patch types. Each matrix entry, p_{ij} , represents the transition probability from a type- j patch to a type- i patch after one year. Let f_t be a vector representing the relative frequency of each patch type in the forest at time t . The structure of the forest after one year can be described by a vector, f_{t+1} , where

$$f_{t+1} = P \times f_t \quad (1)$$

The column eigen-vector of matrix P , f^* , associated with the dominant eigen-value ($\lambda = 1.00$) is proportional to the distribution of patch types in the forest at equilibrium, or 'stable patch-type distribution'. A detailed description of the construction of the canopy dynamics model may be found in Valverde and Silvertown (1997b).

Patch-specific demography of *P. vulgaris*

We studied the demography of each of the eight *P. vulgaris* populations in different light conditions mentioned in previous sections. In each population a random sample of approximately 350 plants was marked in

spring 1992. These plants were followed for two growing seasons until the summer of 1994 and their population dynamics were modelled using stage-based population projection matrices (Caswell 1989). To build the projection matrices, we defined five plant categories based on plant stage and area: seedlings, juveniles, adults 1, adults 2 and adults 3 (the 'seed' category was omitted, since most *P. vulgaris* seeds either die or germinate during the spring following seed shed; they do not remain viable in the soil for long periods of time - Boyd et al. 1990, Valverde and Silvertown 1995).

From the eight *P. vulgaris* populations sampled, in most cases there were two populations in the range of canopy openness corresponding to each of the four patch types defined in the previous section (Table 1). We pooled the demographic data for pairs of populations with similar levels of canopy openness to obtain a description of patch-specific population dynamics (Table 2). Thus, we built a total of eight patch-specific population projection matrices, i.e. one per patch type for each of the two growth periods studied. For each patch type, population growth rate, λ , was calculated as the dominant eigen-value of these projection matrices. As population dynamics varied greatly between the two years studied (i.e., 1992-93 and 1993-94), apparently as a result of weather conditions, we decided to treat the results of different years separately in order to explore the effect of 'bad years' and 'good years' on overall population dynamics. An alternative approach, which we did not explore, would be to explicitly incorporate these changes in population dynamics (caused by 'random' changes in environmental conditions) into the temporal sequence of patch transition matrices (see below) to include the effect of environmental stochasticity on overall population dynamics.

A more detailed analysis of the demography of *P. vulgaris* populations in different light conditions can be found in Valverde (1995).

Overall population dynamics including the effect of the forest regeneration cycle

To describe overall population dynamics (i.e., the changes in the number of *P. vulgaris* individuals in the

Table 2. Classification of the *P. vulgaris* populations studied in four patch types according to % canopy openness (see Table 1). Numbers in parentheses are the standard deviations and the number of hemispherical photographs from which mean % canopy openness was obtained in each case. In most cases the empirical data from two populations were pooled to build patch-specific projection matrices from which the λ values were calculated. Populations from Dancers End are referred to by number (DE2, DE3, etc.); populations from Woburn Wood and Salcey Forest are referred to as WW and SF, respectively.

	Patch type	Population	Mean % canopy openness	(SD, n)	Pooled Pop. growth rate (λ)
1992-93	1	DE2	12.01	(2.2, 8)	1.98
		DE5	5.95	(2.1, 7)	1.44
	3	WW	5.65	(2.9, 15)	1.05
		SF	3.09	(1.3, 11)	
	4	DE3	2.67	(1.4, 8)	1.19
		DE4	2.03	(0.7, 7)	
		DE6	1.57	(0.8, 7)	
1993-94	1	DE7	13.21	(4.4, 7)	1.09
		DE2	9.12	(1.7, 8)	
	2	DE5	4.88	(1.5, 7)	0.97
		WW	4.78	(3.1, 15)	
	3	SF	3.08	(1.7, 11)	0.94
		DE4	2.09	(0.6, 7)	
	4	DE3	1.87	(0.9, 8)	0.88

forest as a whole) including the effect of forest secondary succession, we combined the patch-specific population projection matrices with the Markovian model of canopy dynamics. First, we developed a matrix model representing the existence of spatial heterogeneity. Then, in the same fashion as in Horvitz and Schemske (1986), we incorporated the canopy regeneration cycle into the model to look at the effect of canopy dynamics on overall population growth rate.

The overall *P. vulgaris* population in a forest at time t can be described by a vector, n_t , with a dimension equal to the product of the number of plant stage-categories (i.e., 5) and the number of patch types (i.e., 4). All possible transitions among plant stages, as well as among patch types can be included in a 20×20 matrix, M , such that:

$$n_{t+1} = M_{abij} \times n_t \quad (2)$$

Each individual matrix entry, m_{abij} , represents the probability that an individual in stage category b in a type- j patch contributes to or becomes stage category a in a type- i patch in one year. M consists of 16 sub-matrices. Sub-indices a and b denote rows and columns, respectively, within sub-matrices, whereas sub-indices i and j correspond to rows and columns, respectively, among sub-matrices. Non-zero sub-matrices are present only along the diagonal; these correspond to the patch-specific projection matrices, T_x , describing the demography of *P. vulgaris* in each patch type (Horvitz and Schemske 1986).

To include the effect of the forest regeneration cycle, we modified matrix M and built a new matrix, R , that incorporated the temporal transitions among patch types in the forest. Matrix R is similar to M but contains non-zero sub-matrices along the leading diago-

nal, the sub-diagonal and in the upper right hand corner, corresponding to the non-zero probabilities of patches changing categories in time (Fig. 2).

The new sub-matrices in R , $SubR$, are given by

$$SubR_{ij} = (p_{ij}) \times (T_{ij}) \quad (3)$$

where p_{ij} is the probability of a type- j patch becoming a type- i patch in one year (as shown in Fig. 1). The sub-matrices in R are defined by three main elements: 1) patch-specific demographies, 2) forest patch dynamics and 3) the timing of gap formation relative to the

$0.7 \times T_1$	○	○	$(1-k) \times T_1$
$0.3 \times T_2$	$0.7 \times T_2$	○	○
○	$0.3 \times T_3$	$0.7 \times T_3$	○
○	○	$0.3 \times T_4$	$(k) \times T_4$

Fig. 2. Structure of matrix R (which includes the effect of the canopy Regeneration cycle). T_x sub-matrices correspond to patch-specific population projection matrices and k is the disturbance rate. The probability of patches changing types over one year was incorporated from the canopy dynamics model (Fig. 1).

timing of the annual population census. The latter refers to whether individuals in a type- j patch at time t will undergo the demographic transitions of type- j patches for most of the year, or if instead they will behave according to the demographic transitions expected for a type- i patch for most of the year (Horvitz and Schemske 1986). In this study we assumed that canopy gaps are created (due to either coppicing or natural disturbances) immediately following the population census, during late summer or early autumn. Thus, T_{ij} matrices in eq. (3) were actually T_{ii} , as represented in Fig. 2.

The dominant eigen-value of matrix R was obtained using MATLAB (The MathWorks 1992); this value represents a measure of overall population growth rate, λ_R , including the effect of the forest regeneration cycle. The associated column eigen-vector corresponds to the 'stable category \times patch type distribution', i.e., the relative frequency of individuals of different categories in each patch type at the dynamic equilibrium. The effect of different gap formation rates on overall population dynamics was analysed by giving k different values (ranging from 0.5 to 5%).

Effect of seed dispersal on overall population growth rate

To model the effect of seed dispersal we built a matrix D , which incorporated the transitions of individuals among patches given by migration. Matrix D is composed of 16 sub-matrices. Each 5×5 sub-matrix is comprised mostly of zeros; the only non-zero entries are those directly affected by seed dispersal (fecundity elements, d_{13ij} , d_{14ij} , and d_{15ij}). Although migrating diaspores are seeds, the fecundity elements of population projection matrices are given in terms of the number of seedlings emerging per adult in the population (see Results, Table 4). Thus, seed migration was analysed here indirectly, through its effect on seedling emergence (i.e., migration is referred to as 'seedling' dispersal).

To calculate the entries in matrix D , we used a slightly different approach to the one proposed by Horvitz and Schemske (1986) in their study of *Calathea ovandensis*. They estimated the probability of seeds arriving at a particular patch type as a function of only 1) the frequency of that patch type in the environment, and 2) the fraction of seeds dispersing out of populations. In this study we introduced two new terms to incorporate 3) the number of 'seedlings' typically produced in the source patch type (r_{bbij}), and 4) the frequency of both the 'seedling' source (f_j^*) and 'seedling' recipient (f_i^*) patch types in the forest. Including all these parameters results in a more realistic description of the spatial dynamics of 'seedling' dispersal for the *P. vulgaris* system (see Discussion for a more thorough analysis of this point).

Thus, non-zero elements in matrix D , d_{abij} , are given by the number of 'seedlings' arriving in each patch type (immigration) minus the number of 'seedlings' leaving it (emigration) as follows:

$$d_{abij} = (r_{bbij})(p_d)(f_i^*)(f_j^*) - (p_d)(r_{abij}) \quad (4)$$

where r_{abij} are the fecundity elements of the submatrices in matrix R defined above, i.e., the number of 'seedlings' typically produced in each patch type; p_d is the proportion of 'seedlings' dispersing away from the patch, which will be assumed constant for all patch types; and f_j^* and f_i^* are the relative frequencies of type- j (i.e., 'seedling' source) and type- i (i.e., 'seedling' recipient) patches in the forest. The relative frequency of each patch type at equilibrium is given by vector f^* , the dominant right eigen-vector of the gap dynamics model represented by matrix P . Note that eq. (4) distinguishes r_{bbij} (i.e., the fecundity elements of the 'seedling' source patch) from r_{abij} (i.e., the fecundity elements of the 'seedling' recipient patch).

To incorporate the effect of seed dispersal among patch types into the overall population dynamics model, we combined the dispersal matrix, D , with the previous model that already included the patch-specific demographics and the effect of canopy dynamics (i.e., matrix R) to obtain a new matrix, E , as follows:

$$D + R = E \quad (5)$$

Thus, matrix E describes overall population dynamics including the effects of both the canopy regeneration cycle and seed dispersal. The structure of E is similar to R ; the only differences lie in the fecundity elements in the top row of each sub-matrix, which have been modified by the addition of D to include the effect of seed dispersal. The dominant eigen-value of E , λ_E , represents the overall population growth rate taking into account both canopy dynamics and seed dispersal. λ_E was obtained using MATLAB (The MathWorks 1992) for several values of k (0.5, 1, 2, 3 and 5%) and p_d (0, 20, 40, 60, 80 and 100%), to project the effect of disturbance rate and seed dispersal on overall population dynamics.

Results

Canopy dynamics

The structure of the forest, in terms of the proportion of patches of each type, depends on both gap opening rate and canopy closure rate. Our results regarding canopy closure predict that the approximate time to full canopy closure after gap formation would be around 9 yr. We incorporated these data on canopy closure rate into our canopy dynamics model and projected forest

Table 3. Projected proportion of the forest area in different phases of the forest regeneration cycle (defined as type-1, -2, -3 and -4 patches) with various disturbance rate values (k), and resulting turnover rates (calculated as the reciprocal of the proportion of the forest in the gap phase multiplied by 3 – the time step for patch-type transition).

Patch type	Disturbance regime (k)		
	1%	2%	5%
Gap (1)	0.029	0.054	0.108
Successional (2 and 3)	0.058	0.108	0.216
Closed canopy (4)	0.913	0.838	0.676
Turnover rate (yr)	113.78	61.12	30.56

structure at equilibrium under different gap formation rates (Table 3). When $k = 1\%$, 91.3% of the forest corresponded to closed canopy patches; increasing k to 5% reduced the expected forest area in closed canopy conditions to 67.7%. The proportion of the forest area in the gap phase increased proportionally with gap opening rate, which yielded a dramatic variation in turnover rate (i.e., the mean time between successive gap formations at any one point in the forest, calculated as the reciprocal of the forest area in gaps multiplied by 3, the time needed for a type-1 patch to become a type-2 patch – Table 3).

Patch-specific demography

The patch-specific projection matrices for the four patch types and the two growth periods studied are shown in Table 4. Several demographic parameters varied in relation to the level of canopy openness in the *P. vulgaris* populations studied, which resulted in higher population growth rates in patches in brighter conditions compared to patches under the closed canopy. No further demographic analysis is presented here as our aim was not to give a detailed description of the demography of these populations; instead, our purpose was simply to provide realistic elements to construct the overall population-and-patch dynamics model. A detailed demographic analysis of these populations can be found elsewhere (Valverde 1995).

Overall population dynamics including the effect of the forest regeneration cycle

The model represented by matrix R describes overall population dynamics of *P. vulgaris*, taking into account that the demography of populations differs between patch types, and that patches change in time due to canopy dynamics. According to the model, increasing the disturbance rate should have a positive effect on overall population growth rate, λ_R (Fig. 3). Note that the λ_R derived from the overall

population dynamics model is different from a simple arithmetic or geometric mean of the individual λ values in different patches obtained by weighting the λ of each patch-type by its relative frequency in the habitat (Horvitz and Schemske 1986). For example, the weighted arithmetic and geometric means for the 1992–93 data set when $k = 1\%$ were 1.23 and 1.17 respectively, whereas the model predicts a λ_R value of 1.41 for the same conditions. The arithmetic and geometric means underestimate the overall population growth rate given by the dynamic model as they do not take into account transitions among patch types in time.

The λ_R values obtained fell into a relatively restricted range (1.39 to 1.48 in 1992–93 and 0.90 to 0.94 in 1993–94) considering that the disturbance rates tested varied by an order of magnitude (0.5–5%). In fact, the yearly variation in patch-specific demography had a more dramatic effect on λ_R than did the disturbance rate (Fig. 3).

Effect of seed dispersal on overall population dynamics

Seed dispersal is the process by which individual *P. vulgaris* patches remain interconnected, functioning as a unique system with its own overall dynamics. Thus, in addition to patch-specific demographies and canopy dynamics, the model given by matrix E also incorporated the effect of long-distance (off-patch) seed dispersal on overall population dynamics. The results of this model show that higher disturbance rates were again associated with greater λ_E values (Fig. 4). However, λ_E decreased with increasing proportion of seeds dispersing out of patches. The sensitivity of overall population growth rate to changes in the proportion of seeds dispersing out of patches was greater under higher disturbance rates (shown in Fig. 4 by the slightly greater slopes of the lines representing higher disturbance rates).

Overall population growth was always positive (i.e., > 1) in 1992–93 and negative in 1993–94 for all combinations of seed dispersal and disturbance rates tested. The range of variation in λ_E was smaller for the second period (0.884–0.945) than for the first period (1.145–1.476). Again, the variation in overall population growth rate, λ_E , between the two periods studied was greater than the effect of either the disturbance rate or seed dispersal.

Note that in the graph representing the 1992–93 conditions there is a point in which the lines cross (Fig. 4a); this point represents a seed-dispersal value for which the overall population growth rate would be approximately constant regardless of the disturbance rate.

Table 4. Patch-specific projection matrices, stable stage distributions (SSD) and stage-specific mortalities (Q_x) for the two periods studied. Patch types and λ values are given above each matrix. Plant categories are S = seedlings, J = juveniles, A1 = small adults, A2 = intermediate adults, A3 = large adults.

	1992-93						1993-94					
	S	J	A1	A2	A3	SSD	S	J	A1	A2	A3	SSD
1	$\lambda = 1.98$						$\lambda = 1.09$					
S	0	0	4.47	22.90	44.90	0.63	0	0	0.30	3.22	6.33	0.46
J	0.59	0.42	0.03	0	0	0.24	0.28	0.44	0.09	0.04	0	0.23
A1	0.02	0.45	0.56	0.12	0	0.09	0.02	0.26	0.58	0.20	0.10	0.18
A2	0	0.02	0.38	0.78	0.63	0.03	0	0.01	0.22	0.65	0.42	0.11
A3	0	0	0	0.10	0.33	0	0	0	0	0.09	0.48	0.02
Q_x	0.39	0.10	0.04	0	0.04		0.70	0.29	0.11	0.03	0	
2	$\lambda = 1.44$						$\lambda = 0.97$					
S	0	0	0.93	2.20	7.98	0.47	0	0	0.05	0.17	0.48	0.12
J	0.44	0.30	0.04	0.01	0	0.19	0.33	0.41	0.11	0.01	0	0.14
A1	0.12	0.51	0.50	0.22	0	0.19	0.05	0.33	0.59	0.25	0.04	0.34
A2	0	0.10	0.37	0.63	0.40	0.12	0	0.01	0.22	0.62	0.34	0.31
A3	0	0	0.05	0.13	0.58	0.03	0	0	0	0.11	0.60	0.09
Q_x	0.44	0.10	0.05	0.01	0.02		0.62	0.24	0.08	0.02	0.02	
3	$\lambda = 1.05$						$\lambda = 0.95$					
S	0	0	0.01	0.9	0.24	0.12	0	0	0.01	0.09	0.18	0.10
J	0.33	0.29	0.02	0	0	0.06	0.15	0.21	0.07	0.01	0	0.04
A1	0.10	0.54	0.38	0.05	0.03	0.10	0.02	0.28	0.49	0.10	0.05	0.15
A2	0	0.14	0.50	0.59	0.20	0.31	0	0.07	0.21	0.66	0.30	0.42
A3	0	0	0.07	0.35	0.77	0.41	0	0	0.01	0.21	0.64	0.29
Q_x	0.57	0.04	0.03	0.01	0.01		0.84	0.45	0.22	0.02	0.02	
4	$\lambda = 1.19$						$\lambda = 0.88$					
S	0	0	0.21	0.38	0.83	0.26	0	0	0.02	0.19	0.52	0.14
J	0.33	0.33	0.01	0.01	0	0.10	0.09	0.40	0.13	0.02	0	0.12
A1	0.29	0.54	0.42	0.13	0.01	0.21	0	0.20	0.55	0.22	0.05	0.31
A2	0	0.08	0.38	0.54	0.24	0.21	0	0	0.13	0.66	0.36	0.34
A3	0	0.02	0.15	0.32	0.73	0.22	0	0	0.03	0.06	0.60	0.10
Q_x	0.38	0.03	0.04	0.01	0.02		0.91	0.40	0.17	0.05	0	

Discussion

In this study, we have used empirical data on canopy closure rate and on the demographic variation of *P. vulgaris* patches along the forest regeneration cycle to characterize this spatially structured population within its dynamic forest habitat. We built a model that allowed us to test the theoretical effect of other variables on the system, i.e., disturbance rate and seed dispersal. Our canopy dynamics model, based on the results on canopy closure rate suggested that the approximate time to full canopy closure after gap formation is 9 yr. How realistic this estimate is will ultimately depend, among other things, on the size and type of disturbance and on the species involved in the regeneration. Comparable estimates have been obtained for both temperate and tropical forests (Runkle 1982, Brokaw 1985, Horvitz and Schemske 1986, Cipollini et al. 1993, 1994). Thus, our results based on empirical data on canopy closure appear reasonable (see Valverde and Silvertown 1997b for a thorough analysis of this point).

Regarding the variation in the demography of *P. vulgaris* populations, we collected empirical demographic data for eight populations along a range of light conditions during two consecutive growth periods. Thus, we did not need to infer or extrapolate the demographic behaviour of populations in patches with

different canopy openness. The range of environmental conditions and demographic variation covered provided a rather complete demographic data set in which to base a realistic population-and-patch dynamics model that described the dynamics of the whole system at a larger scale. According to our results, population growth rate is higher in type-1 patches (i.e., gaps). By definition, higher disturbance rates result in a larger proportion of the forest in gap conditions; hence, overall *P. vulgaris* numbers in the forest would be expected to increase with increasing disturbance rate, which is what the model predicts. Horvitz and Schemske (1986) and Cipollini et al. (1994) obtained equivalent results for *Calathea ovandensis* and *Lindera benzoin*, respectively. These results have important implications for forest management, as the opening of new gaps in a forest occurs through both natural disturbances and coppicing. The gradual loss of traditional coppicing practices in a great number of ancient woodlands in Britain could lead to a decrease in the abundance of understorey species such as *P. vulgaris* (Barkham 1992).

Our model predicts that overall population growth rate will increase with increasing forest disturbance rate. This appears to suggest that *P. vulgaris* populations would perform better in highly disturbed habitats, which is clearly not the case. Competition with other species characteristic of more open habitats seem to

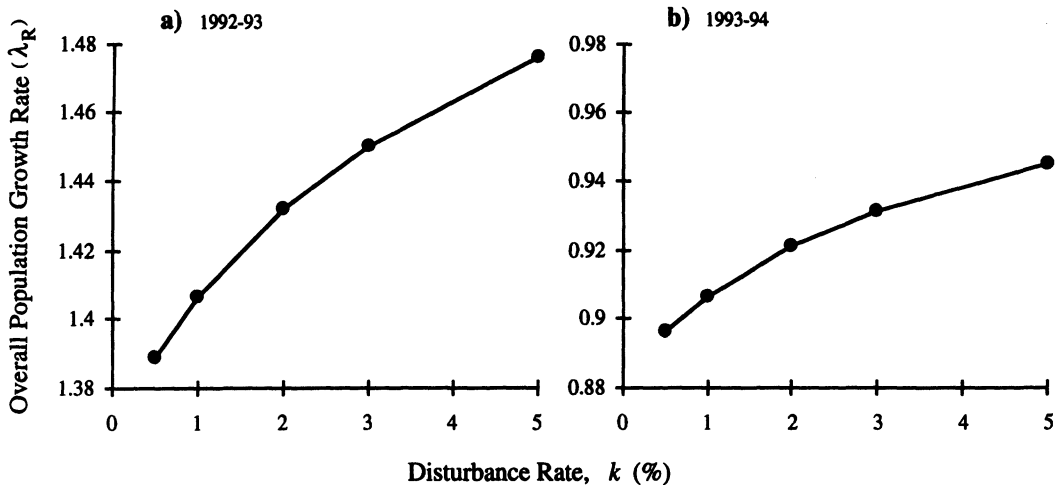


Fig. 3. Overall population growth rate (λ_R) under different disturbance rates taking into account the forest regeneration cycle for a) a model assuming 'good' years (from 1992–93 data) and b) a model assuming 'bad' years (from 1993–94 data). Note the different scale in the y axis of a) and b).

prevent the successful establishment of *P. vulgaris* populations in such conditions. Note that our model, as most of the population-and-patch dynamics models referred to here, do not include the effect of competition or density-dependence (but see Alvarez-Buylla 1994). In natural conditions there must be an upper threshold disturbance rate value above which overall population growth rate decreases.

With regards to seed dispersal, our results predict that the higher the proportion of seeds being dispersed out of occupied patches, the lower the resulting overall population growth rate. According to the model, one of the consequences of seed dispersal is that it results in an increased presence of dispersing 'seedlings' in closed canopy patches (since they are the most frequent kind in the environment), where population growth rate is lowest. These results are in agreement with those obtained by Horvitz and Schemske (1986) and Cipollini et al. (1994) despite the fact that these authors used a slightly different approach to incorporate the effect of seed dispersal in the model.

The difference between our approach to incorporate the effect of seed dispersal in the model (i.e., eq. 4) and that proposed by Horvitz and Schemske (1986) deserves particular attention. In general, the effect of including the new elements in the equation (i.e., the number of 'seedlings' produced in the source patch and the frequency of both 'seedling' source and recipient patches) was small when type-1, -2 and -3 patches (with low relative frequencies at equilibrium) were involved; however, when type-4 patches (which show the highest relative frequency in the forest at equilibrium) were either the 'seedling' source or recipient patches we observed a decrease in the resulting d_{abij} values compared to those obtained using Horvitz and Schemske's (1986) equation. The main consequence of these

changes was that, in our model, adding net seed dispersal (i.e., entries in matrix D , calculated from eq. 4) to matrix R resulted in a reduction of non-zero fecundity elements in most cases, i.e., in general, long-distance seed dispersal implied seed loss. This feature intended to reflect the high risk involved in long-distance seed dispersal in which the number of 'seedlings' leaving a patch was assumed to be higher than the number arriving at it as part of the seed rain. The amount of emigration may significantly exceed that of immigration, especially in spatially structured populations where occupied patches are embedded in a system primarily composed of patches unsuitable for germination and establishment (Horvitz and Schemske 1986, Cipollini et al. 1993, 1994, Olivieri et al. 1995). Additionally, migrants must incur some mortality during transit, especially in this study system where most long-distance seed dispersal appears to be carried out by rodents (Richards 1993, Valverde and Silvertown 1995), which are preferably seed predators.

According to these results, we could expect selection to act *against* long-distance seed dispersal in this species, since it decreases the average fitness of the overall population, i.e., it has a negative effect on overall λ (Horvitz and Schemske 1986, Murray 1986, Venable and Brown 1993). However, as other authors have emphasized, there appears to be various selective forces acting simultaneously on the dispersal rate of gap colonizing species such as *P. vulgaris* (Olivieri et al. 1995). There may be some conditions in which long-distance seed dispersal might be favoured, depending on the species' life-history response to gaps and the patch types generated during canopy closure. Additionally, there are at least two processes – not addressed in this paper – involving long-distance seed dispersal which could have a positive effect on the *P. vulgaris* system at

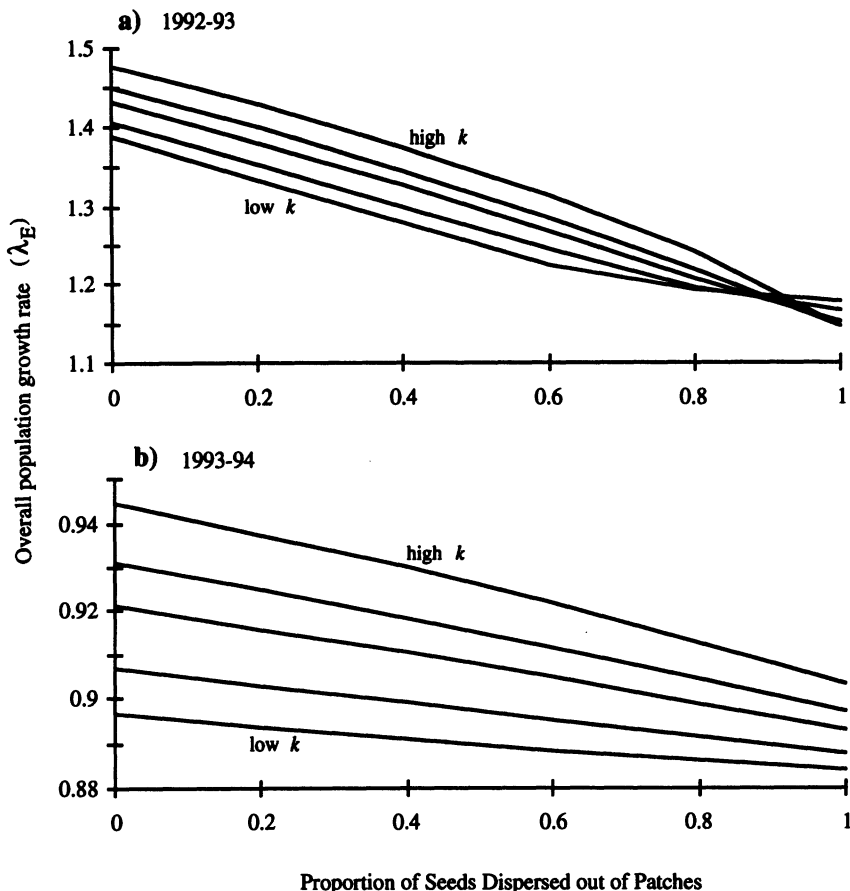


Fig. 4. Effect of seed dispersal on overall population growth rate (λ_E) for a) a model assuming 'good' years (from 1992-93 data) and b) a model assuming 'bad' years (from 1993-94 data). The different lines in each graph correspond to disturbance rate values (i.e., gap opening probabilities) of 5, 3, 2, 1 and 0.5% (from top to bottom). Note the different scale in the y axis of a) and b).

one scale or another: 1) there could be a reduction of density-dependent seedling mortality within occupied patches as a result of long-distance seed dispersal (Murray 1986), which could counteract the effect of the high seed mortality resulting from landing in unfavourable patches; and 2) if the system is structured as a metapopulation and canopy closure results in local population extinction, then long-distance seed dispersal would play a fundamental role in allowing the arrival of seeds at potentially colonizable patches (i.e., gaps), which would ultimately determine the long-term persistence of the species at a site. This idea is supported by the results of a further paper in which we have assumed that *P. vulgaris* forms real metapopulations where colonizations and extinctions of local populations are constantly occurring; given this particular spatial structure, long-distance seed dispersal becomes a key process in the colonization of gaps and therefore in the long-term persistence of metapopulations (Valverde and Silvertown 1997a).

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