Variation in the Demography of a Woodland Understorey Herb (Primula vulgaris) along the Forest Regeneration Cycle: Projection Matrix Analysis

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Variation in the demography of a woodland understorey herb (*Primula vulgaris*) along the forest regeneration cycle: projection matrix analysis

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Summary

1 Gaps in the forest canopy allow establishment of many understorey species. As gaps close, their demographic behaviour is affected by changing environmental conditions. A demographic analysis of *Primula vulgaris* populations in forest patches with varying canopy openness was carried out to investigate the effect of forest canopy dynamics on the demography of this forest understorey herb.

2 Eight *P. vulgaris* populations across a range of light conditions were studied in three deciduous temperate forests in Britain. Demographic data were collected in each population during summer 1992, 1993 and 1994, and stage-based population projection matrices were built to describe their demography for two growth periods (1992–93 and 1993–94).

3 Population growth rate (λ) varied from 0.97 to 1.98 in 1992–93, and from 0.88 to 1.23 in 1993–94. There was a significant positive correlation between λ and diffuse light for the two periods studied: generally, population growth rate was lower in darker patches, implying that populations decline as the canopy closes. Lower λ-values in 1993–94 were the result of increased mortality and decreased fecundity compared to 1992–93. In most cases the observed population structures were significantly different from the calculated stable-stage distributions.

4 Sensitivity analysis showed that λ was most sensitive to changes in matrix transitions that corresponded to growth from small to adult stages, especially those that implied fast growth. Elasticity analysis revealed that the contribution of fecundity elements to λ was small, but populations in brighter patches showed comparatively higher fecundity elasticities than populations under the closed canopy. High elasticities corresponded to the entries that implied growth (especially in brighter patches) or persistence in adult categories (predominantly in darker patches).

5 The observed variation in the demography of *P. vulgaris* in different patches along the forest regeneration cycle stresses the importance of studying the variation in plant population dynamics across the range of habitat patches in which the plant naturally occurs.

Keywords: canopy gaps, demographic change, gap-dependent species, population dynamics, sensitivity and elasticity analysis

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Introduction

The opening of canopy gaps due to natural disturbances is a recurring source of environmental heterogeneity in forest habitats; this process creates a mosaic of regenerating phases of different sizes and ages occurring simultaneously at a site (Brokaw 1985; Martínez-Ramos *et al.* 1985; Pickett & White 1985; Runkle & Yetter 1987). The resulting habitat heterogeneity favours the co-existence of species with different life histories and ecological requirements, which contributes to the maintenance of community

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diversity (Barkham 1992a). In particular, the opening of canopy gaps allows the establishment of many understorey herbs; however, gaps close as canopy regeneration proceeds. To understand how forest herbs persist in such dynamic conditions, we need to consider ecological processes at two different spatial and temporal scales: (i) at the level of the demography of local populations occupying individual forest patches, and (ii) at the level of the forest as a whole, understood as a metapopulation formed by a set of local populations in which colonizations and extinctions occur constantly. This paper addresses the first of these levels and concentrates on the demography of local populations of a forest herb, *Primula vulgaris* Huds. (Primulaceae); we use the demographic analysis of populations in patches with different levels of canopy openness to infer the effect of canopy closure on the demography of this species. The second level of analysis referred to above, i.e. the metapopulation dynamics, is discussed elsewhere (Valverde & Silvertown 1997b).

Many woodland herbs, including *P. vulgaris*, colonize the clearings produced by the opening of canopy gaps. The demography of such species has been much studied (Bierzychudek 1982a, 1982b; Collins *et al.* 1985; Kawano *et al.* 1987; Barkham 1992b; Damman & Cain 1998). However, the ephemeral character of their habitat patches, determined by gap closure through the growth of adjacent vegetation, has seldom been considered in demographic studies. Relatively little is known about the effect of the environmental changes brought about by canopy closure on the demography of herb populations.

Horvitz & Schemske's (1986) paper on the demography of the tropical forest herb *Calathea ovandensis* was one of the first to address the effect of forest succession on the demography of herb populations. Their model of the demographic changes that would occur due to canopy closure was based on empirical data on the demography of a *C. ovandensis* population under relatively open conditions and on observations of other populations under the closed canopy (Horvitz & Schemske 1986). Cipollini *et al.* (1993, 1994) published similar analyses for the understorey plants *Cynoglossum virginianum* and *Lindera benzoin*. In these studies, projection matrices were built for hypothetical populations along the forest regeneration cycle, as actual data were available for only a limited number of forest conditions. Although attention is being paid to the spatiotemporal variation in the demography of some herb populations (e.g. Horvitz & Schemske 1995), little is known about their response to forest secondary succession in particular. Other studies on this issue have mainly concentrated on tropical trees (i.e. *Cecropia obtusifolia* and *Astrocaryum mexicanum*; Martínez-Ramos *et al.* 1985; Alvarez-Buylla & García-Barrios 1991; Alvarez-Buylla 1994), but no complete demographic data set on woodland herb populations in different stages

along the forest regeneration cycle has been published. The coupling of the population dynamics of woodland herbs with the forest regeneration cycle ultimately determines the long-term prospects for such species. In this context, the demographic analysis of populations in patches with varying canopy openness would throw light on the mechanisms that determine the persistence of woodland herbs in the dynamic conditions imposed by their environment.

In the present study we analysed the demography of eight *P. vulgaris* populations located along a gradient of light conditions (given by varying canopy openness) and asked: (i) How does population dynamics vary among patches with different canopy openness? (ii) Are differences between populations correlated with light environment? (3) Which demographic parameters are most affected by the variation in canopy cover? To address these questions we built population projection matrices from which several demographic parameters were derived (i.e. population growth rate, stable-stage distributions, reproductive values, stage-specific mortalities, and the relative contribution of matrix elements to λ) and compared among the eight populations studied. In a complementary study we have used the demographic information obtained from these analyses to build a population-and-patch dynamics model for *P. vulgaris* that incorporates both the patch-specific demography and the dynamics of the forest mosaic (Valverde & Silvertown 1997c); the latter model is used to address the effect of seed dispersal and gap-formation rate on overall population dynamics, which is a subject that we do not address in the present paper.

Methods

THE SPECIES

Primula vulgaris is a perennial herb characteristic of moist shaded habitats, with a North Atlantic and Mediterranean distribution. In Britain, it is common in temperate deciduous woodlands on soils ranging from heavy and slightly acidic to basic (Richards 1989). It grows through the production of leaves in basal rosettes; vegetative spread occurs within very short distances through the production of lateral rosettes. Although most rosettes die off each year, individual plants are relatively long-lived (10–30 years; Boyd *et al.* 1990). In Britain, rosettes lose old leaves during the autumn and the production of new leaves occurs in late winter (February–March) and is immediately followed by flowering. Flowers are distylous, pale yellow and borne on separate stalks. The peak of the flowering period is in April and capsules ripen and open around the middle of June, when seed dispersal takes place. Seeds have an elaiosome that attracts ants and small mammals (Richards 1993; Valverde & Silvertown 1995). Within a forest, *P. vul-*

garis usually shows a patchy distribution, with dense populations surrounded by entirely unoccupied areas. This distribution pattern appears to be a result of its limited dispersal ability and the fact that the establishment of populations is often associated with the opening of gaps in the forest canopy.

STUDY SITES

Most of the field work was conducted at 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, *Fraxinus excelsior–Acer campestre–Mercurialis perennis* woodland, with some stands closer to W12, *Fagus sylvatica–Mercurialis perennis* woodland; Rodwell 1991). It has traditionally been managed through coppice cycles of 5–10 years, the coppiced species being mainly *Corylus avellana* (hazel) and *Crataegus monogyna* (hawthorn). Important elements of the ground flora include *P. vulgaris*, *Mercurialis perennis*, *Rubus fruticosus* and *Hyacinthoides nonscripta*. Six forest populations (DE2–DE7) were chosen to represent the range of light conditions at this site.

Two additional populations, close to Dancers End Nature Reserve, were also studied: one in Woburn Wood (WW), a *Quercus robur* (oak) and *Castanea sativa* (chestnut) forest in Bedfordshire (grid reference SP927325), and another one in Salcey Forest (SF), a *Quercus robur* and *Fraxinus excelsior* forest in Northamptonshire (grid reference SP814508).

LIGHT MEASUREMENT

The diffuse site factor (i.e. a measure of diffuse light), which other authors have used to evaluate gap size (Kennedy & Swaine 1992), was used in this study to describe the light environment of each population (Anderson 1964; Mitchell & Whitmore 1993). It was evaluated through the computer image analysis of hemispherical photographs taken during summer 1992, 1993 and 1994. Photographs were taken along a transect in each patch, during the same time period and at exactly the same points each year. Digitized images were analysed using the program Solarcalc 5.41 (Mac), which calculates diffuse light as a percentage of open sky in the hemispherical photograph (Chazdon & Field 1987). Each year the mean value for diffuse light estimated from seven to 15 photographs (depending on the size of the patch and the variation in light conditions) was used to characterize the light environment of each population (see Valverde & Silvertown 1997a for details). No actual light measurements were taken since the variable used to characterize forest patches was percentage canopy

openness, which may be derived directly from hemispherical photographs.

POPULATION SAMPLING

Demographic data were obtained from samples of approximately 350 plants per population, followed from 1992 until 1994. In May 1992 we set permanent 1-m^2 quadrats regularly spaced along a transect passing through the centre of each population. The number of quadrats per population ranged from eight to 32, depending on the density of *P. vulgaris* plants. The four corners of each quadrat were marked by plastic pipes sunk into the ground. Each plant was relocated each year to record its demographic attributes. To avoid damage, plants were not tagged individually; instead, they were located through x and y coordinates (in cm) along the horizontal and vertical axis of the grid formed by sampling quadrats. This method proved efficient even in the densest quadrats.

Populations were sampled between the end of May and the beginning of July in 1992, 1993 and 1994, at the time when plants had developed to their full size and their capsules were ripening (plants produce their leaves in a single flush at the start of the season and reach their maximum size around the beginning of May). Each year all plants in the quadrats were recorded, their leaves, rosettes and capsules counted and their area estimated as an ellipse, based on their longest radius, a, and a perpendicular radius, b (area = πab).

All new seedlings observed in the quadrats were counted and their positions recorded each year. They were marked with small straw rings for relocation the following year. In quadrats with high seedling emergence, only the seedlings within a randomly chosen 20 × 20 cm subquadrat were marked to be recounted and measured the following year.

These records gave detailed information about the fate of each individual plant in the sample from one year to the next, from which we built population projection matrices for two growth periods: 1992–93 and 1993–94.

POPULATION PROJECTION MATRICES

Most recent demographic studies have used Lefkovitch matrices to describe the demography of plant populations (see, for instance, Horvitz & Schemske 1995 for a recent, detailed example). The Lefkovitch matrix is based on the classification of plants into size or stage categories and has been used to analyse the demography of species with complex life cycles (Caswell 1989). The basic matrix model is given by:

$$n_{(t+1)} = An_{(t)} \qquad (1)$$

where $n_{(t)}$ and $n_{(t+1)}$ are vectors whose elements, a_i,

are the number of individuals that belong to the i-th category at time t and $t + 1$, respectively; and A is a non-negative square matrix, whose elements, a_{ij}, represent the transitions or contributions from individuals in the j-th category to the i-th category after one time step. These are given by the survivorship, growth and fecundity of individuals in the population between t and $t + 1$ (Caswell 1989).

We used the power method to calculate the main demographic parameters of each population from the projection matrices: the dominant right eigenvector of the matrix and its associated eigenvalue correspond with the stable-stage distribution and the finite rate of increase (λ) of the population, respectively, whereas the left eigenvector represents the stage-specific reproductive values (Caswell 1989).

Sensitivity and elasticity analyses were performed on projection matrices to study the relative importance of different phases of the life cycle on population dynamics (de Kroon *et al.* 1986; van Groenendael *et al.* 1988; Caswell 1989). The sensitivity of matrix entries ($s_{ij} = \delta\lambda/\delta a_{ij}$) measures the impact on λ of a small change in each particular matrix element, relative to changes of the same absolute magnitude in other matrix elements. A measure of proportional sensitivity is given by the elasticity ($e_{ij} = a_{ij}/\lambda \times s_{ij}$), which calculates the proportional contribution of each matrix element, a_{ij}, to λ. The sum of all the elasticities of a matrix equals unity, which allows for comparisons between different species or populations of the same species (de Kroon *et al.* 1986; Caswell 1989).

Sensitivity and elasticity matrices, along with other demographic results (i.e. population growth rate, stable-stage distributions and reproductive values) were calculated using a Pascal program for matrix analysis written by Elena Alvarez-Buylla. In the following sections we provide a brief description of the way in which projection matrices were built.

Stage categories

Plants were classified into categories to build projection matrices. In *P. vulgaris*, survival, growth and fecundity are clearly stage- or size-dependent (Boyd 1986), as is the case for most plants (Werner & Caswell 1977). We defined stage categories based on size and other biological attributes, according to our knowledge of the species' natural history. The choice of the number of categories is not a simple one since it may affect the results of the sensitivity and elasticity analyses. However, when various populations of the same species are being compared, the use of a fixed number of categories is recommended in order to allow for valid comparisons among them (Enright *et al.* 1995); therefore, we decided not to use Moloney's (1986) algorithm to establish these categories, with the aim of avoiding differences in the categorization of each

population (Enright *et al.* 1995). Five categories that reflect natural stages and apparent threshold size values for reproduction were determined (Table 1). The subdivision of reproductive plants into categories was done by setting arbitrary threshold size values that represented, on average, small, medium and large rosettes. The sample sizes within categories were large enough (i.e. each containing a minimum of 10 individuals) to allow satisfactory estimates of transition probabilities between categories for the period studied.

The various potential fates of *P. vulgaris* plants in different stages are shown in the life-cycle graph (Fig. 1), in which arrows represent transition probabilities between stages from one year to the next. We did not include a seed category as most *P. vulgaris* seeds either die or germinate during the spring following seed shed (Boyd *et al.* 1990; Valverde & Silvertown 1995).

Transition probabilities and fecundity

For each population, transition probabilities were obtained by calculating the proportion of individuals in each category experiencing each particular fate from one year to the next.

Fecundity, the mean number of offspring per reproductive plant at a given time that joins the population the following growth season, was calculated as follows. First, we estimated the proportional contribution of each adult category to total reproductive effort, measured as total number of capsules. Secondly, the total number of seedlings counted the following year in the sample quadrats was allocated to the different adult categories according to their proportional reproductive effort. Finally, the number of recruitments per category was divided by the total number of individuals in each category to obtain the mean fecundity per category.

STATISTICAL TREATMENT OF MATRIX RESULTS

Differences between population structures (i.e. observed vs. calculated stable-stage distributions,

Table 1 Stage categories used to describe the population dynamics of *Primula vulgaris*

Category	Plant size (area in cm²)	Stage
Seedling	0.5–5	Cotyledons present
Juvenile	5.1–35	Non-reproductive
Adult 1	35.1–200	Potentially reproductive
Adult 2	200.1–600	Potentially reproductive
Adult 3	Larger than 600	Potentially reproductive

Stage at time t

$$
\begin{array}{c c}
& \begin{array}{ccccc} \textbf{Sd} & \textbf{J} & \textbf{A1} & \textbf{A2} & \textbf{A3} \end{array} \\
\begin{array}{c} \textbf{Sd} \\ \textbf{J} \\ \textbf{A1} \\ \textbf{A2} \\ \textbf{A3} \end{array} &
\left(
\begin{array}{ccccc}
0 & 0 & F_{13} & F_{14} & F_{15} \\
G_{21} & S_{22} & S_{23} & S_{24} & 0 \\
0 & G_{32} & S_{33} & S_{34} & S_{35} \\
0 & G_{42} & G_{43} & S_{44} & S_{45} \\
0 & 0 & G_{53} & G_{54} & S_{55}
\end{array}
\right)
\end{array}
$$

Stage at time $t+1$

Fig. 1 Life-cycle graph of *P. vulgaris* and its correspondence with the basic population projection matrix. Circles correspond to plant stages, arrows represent the possible transitions between stages, and letters show the connection between each transition and its corresponding matrix entry. Matrix entries are subdivided into fecundity (F, i.e. seed production), growth (G, i.e. transition to larger categories, pictured above relevant arrows) and survival (S, i.e. remaining in the same or shrinking to smaller categories, pictured below relevant arrows).

observed population structures in different years, and calculated stable-stage distributions in different years) were evaluated using the log likelihood ratio, *G*, which is a more robust test than χ^2 to evaluate goodness-of-fit (Sokal & Rohlf 1981; Zar 1984).

Demographic differences between populations in different patches or at different times may be ascertained by comparing entire transition matrices using log-linear analysis of contingency tables to evaluate the degree of interdependence between the explanatory and the response factors involved (Caswell 1989; Silva *et al.* 1990; Ehrlen 1995; Horvitz & Schemske 1995). Here we determined the significance of time (years) and forest patch (population) on observed population structure and transition matrices.

A log-linear analysis of a three-way contingency table was performed to compare the observed structure among all populations for the three periods studied (1992, 1993 and 1994). Explanatory factors were patch and year; the observed frequency of individuals per category was the response factor. A log-linear analysis of a four-way contingency table was done to compare entire transition matrices using year, patch and initial category as explanatory variables, and the fate of individuals as the response variable.

Estimation of individual matrix entries from field data necessarily implies errors and uncertainty associated with the estimate of λ. However, there appears to be no general formula describing the distribution of λ in terms of the a_{ij}, nor an expression for the variance of λ as a function of the variance of the a_{ij}. Two approaches have been developed to address this

matter: (i) an analytical method uses the sensitivity formula and the variance of individual matrix entries to estimate an approximate variance of λ, from which confidence intervals may be calculated assuming a normal distribution; (ii) computer resampling methods (i.e. bootstrap and jack-knife) may be used to estimate non-parametric confidence intervals by repeatedly calculating λ from subsamples of the original data set (Caswell 1989; Alvarez-Buylla & Slatkin 1991). For the sake of simplicity, here we applied the analytical method to calculate approximate confidence intervals for λ. This method also incorporates the covariance between pairs of transitions from the same initial category to any other category (a_{ij} and a_{kj}). The analytical method is reliable provided that the coefficients of variation for matrix entries to which λ is very sensitive are sufficiently low (less that 50%; Alvarez-Buylla & Slatkin 1993, 1994).

The variance of fecundity entries was calculated using the information on the natural variability in this parameter obtained directly from the empirical demographic data collected in different populations (Lande 1988; Alvarez-Buylla & Slatkin 1991). The variance of transition probabilities was calculated assuming a binomial distribution, and the sampling covariances between pairs of transitions from the same initial category were estimated according to the multinomial distribution (Alvarez-Buylla & Slatkin 1991). The standard error (σ), given by the square root of the variance of λ, was used to calculate approximate 95% confidence intervals (i.e. $\lambda \pm 2\sigma$).

Results

LIGHT MEASUREMENT

The woodland patches studied covered the full range of light conditions in which *P. vulgaris* populations usually occur, from a large gap in the canopy (13.21% canopy openness) to completely closed canopy conditions (1.57% canopy openness) (Table 2). This measure of diffuse light changed from year to year in each patch. In general, light decrease (due to canopy closure) was more noticeable in brighter patches, whereas the light conditions in darker patches remained approximately constant (see Valverde & Silvertown 1997a for a detailed analysis of this subject).

POPULATION PROJECTION MATRICES

In this section we present the main results of the analysis of population projection matrices (λ, stable-stage distributions and reproductive values) for the periods 1992–93 and 1993–94 and compare the results obtained in populations in forest patches with different levels of canopy openness. These elements are later used in the discussion to speculate about the effect of the forest regeneration cycle on the demographic behaviour of *P. vulgaris*. Projection matrices for the populations studied and the main results of matrix analysis are presented in order of decreasing diffuse light in Table 3. Population DE6 was only studied from 1992 to 1993 because the forest was cut down in that area at the end of 1993. Population DE7 was studied only during the second period.

Population dynamics

Population growth rates (λ) were higher in 1992–93 than in 1993–94 (Table 3). In general, high λ-values were obtained in populations in brighter patches, whereas lower λ were observed in populations under relatively darker conditions. Percentage canopy openness correlated significantly with population growth rate (Fig. 2; $R^2 = 0.788$, $P = 0.01$, and $R^2 = 0.884$, $P = 0.005$, for the first and second period, respectively). The general pattern of the relationship between λ and light was similar for the two periods studied. Note, however, that two populations were excluded from the linear regressions shown in Fig. 2: WW in 1992–93, in which severe deer and rodent over-grazing produced atypically high adult mortality and low fecundity, and DE7 in 1993–94, which suffered from a slug plague that resulted in a dramatic increase in adult mortality and a decrease in seedling establishment. In both cases the levels of herbivory were quite extreme in relation to what was observed in other populations, which resulted in extremely low λ-values. Nevertheless, the purpose of the graph in Fig. 2 was to show that there is, in fact, a relationship between λ and light; as in the latter two cases the λ-values were strongly affected by non-light-related factors, we decided to exclude them from this particular analysis. (Including WW in the 1992–93 correlation resulted in $R^2 = 0.59$, $P = 0.04$; and including DE7 in the 1993–94 correlation gave $R^2 = 0.04$, $P = 0.64$).

The differences between the λ for the two periods studied were determined mainly by yearly variations in mortality and fecundity (i.e. capsule production and seedling recruitment). Mortality was higher in 1993–94 than in 1992–93, and darker patches gen-

Table 2 Results of the light measurements for *P. vulgaris* populations at Dancers End (DE), Woburn Wood (WW) and Salcey Forest (SF). Populations are listed in order of decreasing diffuse light according to the 1992 measurements. The mean diffuse light (and standard deviations) were calculated from a varying number (*n*) of hemispherical photographs per population

| Population | Diffuse light (% canopy openness) | | | *n* |
	1992	1993	1994	
DE7	NM	13.21 (4.44)	11.16 (3.14)	7
DE2	12.01 (2.20)	9.12 (1.73)	7.31 (2.82)	8
DE5	5.95 (2.09)	4.88 (1.53)	3.16 (1.75)	7
WW	5.65 (2.92)	4.78 (3.13)	4.05 (2.48)	15
SF	3.09 (1.28)	3.08 (1.73)	1.90 (1.00)	11
DE3	2.67 (1.36)	1.87 (0.88)	1.84 (0.60)	8
DE4	2.03 (0.71)	1.95 (0.58)	1.46 (0.72)	7
DE6	1.57 (0.79)	1.97 (0.81)	NM	7

NM, not measured, but DE7 placed highest because values were highest in the other 2 years.

Table 3 Population projection matrices and main demographic results of the matrix analysis for the eight *P. vulgaris* populations studied during the periods (a) 1992–93 and (b) 1993–94. The first column indicates the λ of each population

		Seedling	Juvenile	Adult 1	Adult 2	Adult 3	n_t+1	Stable-stage distribution	Reproductive value
(a)	**1992–93**								
DE2	Seedling	0.000	0.000	4.469	22.904	44.898	0.900	0.634	0.014
$\lambda = 1.976$	Juvenile	0.588	0.423	0.025	0.000	0.000	0.033	0.241	0.042
	Adult 1	0.021	0.454	0.562	0.120	0.000	0.032	0.089	0.128
	Adult 2	0.000	0.021	0.375	0.780	0.630	0.029	0.033	0.318
	Adult 3	0.000	0.000	0.000	0.100	0.333	0.005	0.002	0.498
	n	*97*	*97*	*80*	*50*	*27*			
DE5	Seedling	0.000	0.000	2.136	5.463	13.140	0.811	0.598	0.031
$\lambda = 1.794$	Juvenile	0.444	0.328	0.030	0.000	0.000	0.028	0.183	0.080
	Adult 1	0.111	0.492	0.310	0.025	0.000	0.042	0.107	0.177
	Adult 2	0.000	0.115	0.570	0.658	0.317	0.077	0.081	0.270
	Adult 3	0.000	0.000	0.090	0.304	0.682	0.042	0.031	0.441
	n	*18*	*61*	*100*	*79*	*63*			
WW	Seedling	0.000	0.000	0.026	0.092	0.303	0.080	0.055	0.104
$\lambda = 0.974$	Juvenile	0.429	0.273	0.040	0.007	0.000	0.056	0.066	0.171
	Adult 1	0.143	0.545	0.661	0.326	0.000	0.415	0.503	0.199
	Adult 2	0.000	0.045	0.210	0.619	0.540	0.390	0.348	0.241
	Adult 3	0.000	0.000	0.008	0.034	0.405	0.059	0.028	0.285
	n	*10*	*22*	*124*	*147*	*37*			
SF	Seedling	0.000	0.000	0.015	0.063	0.189	0.072	0.107	0.090
$\lambda = 1.035$	Juvenile	0.294	0.250	0.000	0.000	0.000	0.050	0.041	0.188
	Adult 1	0.176	0.350	0.385	0.059	0.012	0.143	0.086	0.216
	Adult 2	0.000	0.300	0.461	0.568	0.171	0.377	0.287	0.241
	Adult 3	0.000	0.000	0.108	0.356	0.805	0.358	0.482	0.264
	n	*17*	*20*	*65*	*118*	*82*			
DE3	Seedling	0.000	0.000	0.037	0.144	0.231	0.096	0.128	0.071
$\lambda = 1.055$	Juvenile	0.385	0.305	0.041	0.000	0.000	0.071	0.072	0.195
	Adult 1	0.000	0.639	0.377	0.037	0.046	0.200	0.111	0.227
	Adult 2	0.000	0.055	0.531	0.626	0.231	0.387	0.333	0.248
	Adult 3	0.000	0.000	0.041	0.336	0.723	0.246	0.356	0.258
	n	*13*	*36*	*98*	*107*	*65*			
DE4	Seedling	0.000	0.000	0.332	0.514	1.020	0.316	0.318	0.092
$\lambda = 1.267$	Juvenile	0.200	0.167	0.039	0.000	0.000	0.038	0.065	0.166
	Adult 1	0.400	0.474	0.364	0.079	0.000	0.152	0.191	0.210
	Adult 2	0.000	0.278	0.351	0.476	0.264	0.229	0.187	0.243
	Adult 3	0.000	0.055	0.234	0.444	0.717	0.265	0.239	0.288
	n	*10*	*18*	*77*	*63*	*53*			
DE6	Seedling	0.000	0.000	0.121	0.297	0.620	0.194	0.202	0.097
$\lambda = 1.133$	Juvenile	0.375	0.400	0.009	0.012	0.000	0.071	0.110	0.156
	Adult 1	0.250	0.556	0.459	0.165	0.019	0.260	0.233	0.205
	Adult 2	0.000	0.000	0.396	0.588	0.211	0.287	0.249	0.241
	Adult 3	0.000	0.000	0.099	0.223	0.750	0.188	0.205	0.300
	n	*16*	*45*	*111*	*85*	*52*			
(b)	**1993–94**								
DE7	Seedling	0.000	0.000	0.035	0.230	1.073	0.201	0.133	0.050
$\lambda = 0.868$	Juvenile	0.441	0.340	0.092	0.060	0.000	0.187	0.204	0.078
	Adult 1	0.051	0.245	0.494	0.298	0.139	0.293	0.369	0.169
	Adult 2	0.000	0.000	0.195	0.500	0.500	0.253	0.252	0.277
	Adult 3	0.000	0.000	0.000	0.083	0.361	0.066	0.041	0.425
	n	*59*	*53*	*87*	*84*	*36*			
DE2	Seedling	0.000	0.000	0.543	6.480	18.610	0.747	0.625	0.009
$\lambda = 1.229$	Juvenile	0.200	0.490	0.082	0.011	0.000	0.070	0.182	0.052
	Adult 1	0.008	0.270	0.660	0.112	0.000	0.086	0.109	0.132
	Adult 2	0.000	0.010	0.237	0.787	0.214	0.081	0.069	0.279
	Adult 3	0.000	0.000	0.000	0.090	0.786	0.016	0.014	0.527
	n	*125*	*100*	*97*	*89*	*14*			
DE5	Seedling	0.000	0.000	0.049	0.209	0.623	0.185	0.175	0.050
$\lambda = 1.019$	Juvenile	0.349	0.440	0.105	0.000	0.000	0.137	0.140	0.111
	Adult 1	0.058	0.280	0.474	0.164	0.000	0.178	0.191	0.210
	Adult 2	0.000	0.020	0.355	0.650	0.325	0.329	0.333	0.283
	Adult 3	0.000	0.000	0.000	0.171	0.662	0.171	0.160	0.345
	n	*86*	*50*	*76*	*140*	*77*			

Table 3 *(Continued)*

		Seedling	Juvenile	Adult 1	Adult 2	Adult 3	n_t+1	Stable-stage distribution	Reproductive value
WW	Seedling	0.000	0.000	**0.033**	**0.103**	**0.185**	0.068	0.052	0.054
$\lambda = 0.934$	Juvenile	0.250	0.350	0.116	0.022	0.000	0.101	0.136	0.171
	Adult 1	0.036	0.450	0.646	0.326	0.190	0.457	0.529	0.222
	Adult 2	0.000	0.000	0.156	0.580	0.381	0.329	0.259	0.271
	Adult 3	0.000	0.000	0.000	0.051	0.381	0.044	0.024	0.281
	n	*28*	*20*	*147*	*138*	*21*			
SF	Seedling	0.000	0.000	**0.014**	**0.093**	**0.192**	0.107	0.100	0.019
$\lambda = 0.951$	Juvenile	0.130	0.188	0.087	0.000	0.000	0.032	0.037	0.142
	Adult 1	0.000	0.375	0.500	0.116	0.061	0.158	0.172	0.183
	Adult 2	0.000	0.125	0.196	0.636	0.304	0.388	0.401	0.318
	Adult 3	0.000	0.000	0.022	0.231	0.617	0.315	0.289	0.336
	n	*23*	*16*	*46*	*121*	*115*			
DE3	Seedling	0.000	0.000	**0.019**	**0.185**	**0.521**	0.197	0.137	0.008
$\lambda = 0.879$	Juvenile	0.088	0.400	0.127	0.015	0.000	0.066	0.117	0.076
	Adult 1	0.000	0.200	0.549	0.219	0.046	0.213	0.308	0.183
	Adult 2	0.000	0.000	0.127	0.657	0.356	0.355	0.337	0.304
	Adult 3	0.000	0.000	0.028	0.058	0.598	0.169	0.101	0.429
	n	*34*	*25*	*71*	*137*	*87*			
DE4	Seedling	0.000	0.000	**0.016**	**0.044**	**0.155**	0.089	0.073	0.010
$\lambda = 0.933$	Juvenile	0.152	0.231	0.056	0.025	0.000	0.094	0.042	0.040
	Adult 1	0.019	0.154	0.481	0.086	0.032	0.155	0.127	0.183
	Adult 2	0.000	0.000	0.222	0.691	0.287	0.368	0.465	0.361
	Adult 3	0.000	0.000	0.000	0.173	0.660	0.294	0.293	0.406
	n	*105*	*13*	*54*	*81*	*94*			

n_{t+1} refers to the observed population structure in (a) 1993 and (b) 1994. *n* refers to the number of individuals from which transitions were calculated. Diagonal matrix elements are underlined and fecundity entries are in bold to facilitate reading.
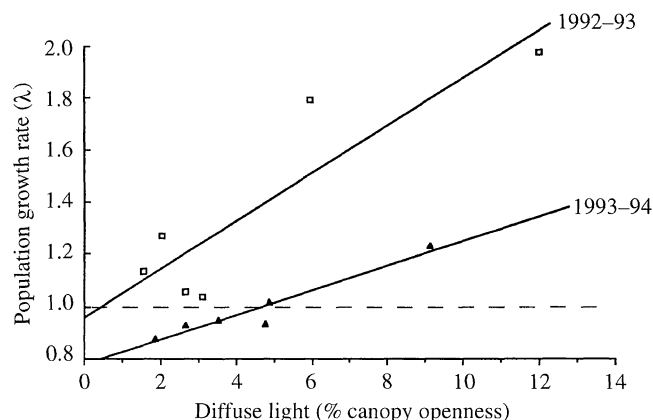

Fig. 2 Relationship between population growth rate (λ) and diffuse light (% canopy openness) for six *P. vulgaris* populations during the periods 1992–93 (squares) and 1993–94 (triangles). Diffuse light averages for summer 1992 and 1993 were used to plot the λ-values obtained for the 1992–93 and 1993–94 periods, respectively.

erally showed higher mortality than brighter patches. Mortality risk was higher among smaller categories and decreased with increasing plant size in both periods. Fecundity values were higher in 1992–93 than in 1993–94; in both periods fecundity decreased with decreasing diffuse light. Also, larger plants showed higher fecundity values (Table 3).

The λ of any two populations were considered to be statistically indistinguishable if the λ of one population fell within the confidence interval of the other (Fig. 3). In 1992–93 the two populations under the brightest conditions (DE2 and DE5) showed higher λ than the populations under darker conditions, with the only exception of DE4, which did not differ significantly from DE5 (Fig. 3). Note that, for this period, only the λ-values of DE2 and DE5 were sig-
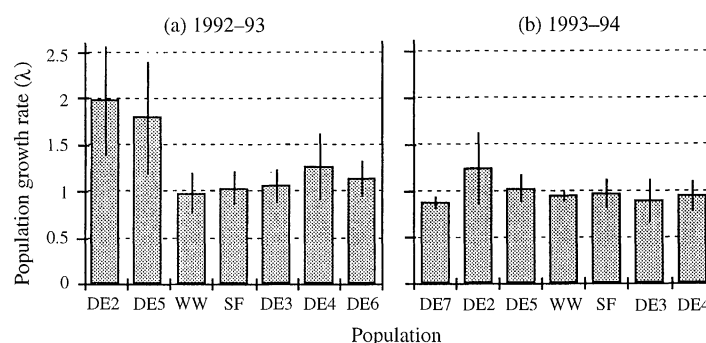
Fig. 3 Population growth rate (λ) with approximate 95% confidence intervals ($\pm 2\sigma$) for the *P. vulgaris* populations studied during (a) 1992–93 and (b) 1993–94. Populations are arranged from left to right in order of decreasing diffuse light.

nificantly higher than unity. For the 1993–94 period, the λ-values did not differ significantly from each other. Only DE7 and WW were significantly lower than unity. Comparing between years, only DE2 and DE5 had significantly higher λ in 1992–93 than in 1993–94. In general, lower λ-values had narrower confidence intervals (Fig. 3).

Although the analysis of the confidence intervals of λ suggests little difference between populations, the log-linear analysis of entire transition matrices indicated that the effect of population (i.e. patch) and of year were both significant ($P < 0.05$). Moreover, the two factors interacted in their effect on the fate of individuals, conditional on their initial category, i.e. the explanatory factors (year, patch and initial category) were not independent of each other in their effect on the fate of individuals (the three–way interaction term was significant; Table 4). In such cases, it is interesting to look at the interaction between two of the factors within each level of a third one (Sokal & Rohlf 1981). Therefore, we tested the effect of initial category and patch on the fate of individuals for each of the two periods studied (1992–93 and 1993–94), as well as the effect of year and patch on the fate of individuals within each initial category.

The log-linear analyses performed with the transition matrices of each period revealed that both initial category and patch had a significant effect on the fate of individuals in both years ($P < 0.05$). However, the interaction of these two factors was statistically significant only for the 1993–94 matrices (Table 5).

The log-linear analysis testing the effect of patch and year on the fate of individuals from each initial category showed that both factors had a significant effect on the fate of individuals coming from all categories. However, year and patch significantly interacted in their effect on fate only in individuals coming from categories adult 1 and adult 2, reflecting yearly differences in the effect of patch on the fate of individuals in those categories (Table 6).

Population structure and stable-stage distributions

Observed population structures and calculated stable-stage distributions (Table 3) were compared for each population and each of the two periods studied. The results indicate that the observed population structures differed significantly from the calculated stable-stage distributions in most cases (Table 7). The only

Table 4 Results of the log-linear analysis for the models built with entire transition matrices from eight *P. vulgaris* populations, for the periods 1992–93 and 1993–94. Frequency matrices (including death as a fate and excluding fecundities) were used for the analysis. Structural zeros were included in some cells in populations DE6 and DE7 (data from these populations were available for only one growth period). A constant 0.5 was added to all cells prior to analysis (Silva *et al*. 1990). The explanatory variables are P = patch (DE2, DE5, etc.) and Y = year (1992–93 and 1993–94); and the response variable is F = fate (death, juvenile, adult 1, etc.), conditional on I = initial category (seedling, juvenile, adult 1, etc.). The significance of each factor is analysed by examining the reduction in χ^2 (i.e. $\Delta\chi^2$) when each factor is added to a model that excludes it

Model	Efect	d.f.	χ^2	$\Delta\chi^2$	P
IPY, FI		272	1119.39		<0.001
IPY, FIY		252	834.80		<0.001
	Year	20		284.59	<0.001
IPY, FIP		112	407.25		<0.001
	Patch	160		712.14	<0.001
IPY, FIY, FIP	Year × patch	92	196.43		<0.001

Table 5 Results of the log-linear analysis for the models built with entire transition matrices from seven *P. vulgaris* populations, for 1992–93 and 1993–94. Frequency matrices (including death as a fate and exclunding fecundities) were used for the analysis. A constant 0.5 was added to all cells prior to analysis (Silva *et al.* 1990). The explanatory variables are P = patch (DE2, DE5, etc.) and I = initial category (seedling, juvenile, adult 1, etc.); and the response variable is F = fate (death, juvenile, adult 1, etc.). The significance of each factor is analysed by examining the reduction in χ^2 (i.e. $\Delta\chi^2$) when each factor is added to a model that excludes it

Model	Effect	d.f.	1992–93			1993–94		
			χ^2	$\Delta\chi^2$	P	χ^2	$\Delta\chi^2$	P
PI, F		147	2576.58		<0.001	3433.55		<0.001
PI, FP		119	1916.57		<0.001	2928.83		<0.001
	Patch	28		660.01	<0.001		504.72	<0.001
PI, FI		131	479.28		<0.001	315.90		<0.001
	Initial category	16		209.73	<0.001		3117.65	<0.001
PI, FP, FI	Patch × initial category	103	118.72		0.138	137.92		0.012

two exceptions were DE5 and SF in 1993–94. Also, observed population structures differed significantly between years in most populations, with the only exception of SF, and stable-stage distributions were significantly different for the two periods studied in all populations except for DE2 and WW (Table 7).

Figure 4 shows an example of the observed structure of three populations for 1993 and 1994, along with the calculated stable-stage distributions for 1992–93 and 1993–94. Only three populations along the light gradient were included in the figure to facilitate visual comparison. In general, the relative frequency of large individuals increased with decreasing diffuse light. The log-linear analysis performed to test the effect of patch and year on population structure indicated that both factors, as well as the interaction between them, significantly affected the frequency of individuals in each category (Table 8).

Reproductive values

The reproductive values obtained from the analysis of projection matrices are given in the last column of Table 3. As with stable-stage distributions, they have been normalized to unity. Note that higher reproductive values were associated with larger plant categories. For the period 1992–93, the seedlings of populations under brighter conditions (DE2 and DE5) had particularly low reproductive values. The three reproductive categories (adult 1, 2 and 3) showed quite similar reproductive values in patches in darker conditions, whereas in populations under brighter conditions the difference between categories was more noticeable. This pattern was also present, although not as clear, in the results of the 1993–94 period.

SENSITIVITY AND ELASTICITY ANALYSIS

In this section we present the sensitivity and elasticity matrices for the two periods studied (Table 9). From

the analysis of these matrices it is possible to detect the life-cycle stages that are most important in relation to their contribution to population growth rate and the way in which these vary among patches with different light conditions. The differences in the sensitivity and elasticity matrices of populations in forest patches along the forest regeneration cycle may be interpreted as changes in the way in which natural selection operates on these populations as canopy closure proceeds.

In the populations in brighter patches the highest sensitivities often corresponded to growth transitions from young to adult (i.e. reproductive) stages. In some cases, entries that implied fast growth, by skipping one category, were particularly high. For populations in darker patches high sensitivities corresponded to the growth of adults to larger categories or their persistence in the same category (i.e. towards the bottom, right-hand corner of the matrix). The highest sensitivity values were almost always less than 25% of the total sensitivity, and this percentage decreased in populations under darker conditions. Most fecundity elements had low sensitivities, especially for populations in brighter patches. The lowest sensitivity value was almost always below 1% of the total sensitivity. These patterns were similar for both periods studied.

The sensitivity index (i.e. the square root of the total sensitivity) measures the sensitivity of λ to changes in the entire life cycle (Caswell 1978). In this study sensitivity indices varied from 1.615 to 2.695 and were quite similar in both years, although in most cases they were smaller in 1993–94. In the first year, populations under brighter conditions (DE2, DE5 and WW) showed higher sensitivity indices than populations in closed canopy patches. However, this pattern was not maintained in 1993–94.

Matrix entries with highest sensitivity rarely coincided with those of highest elasticity (Table 9). In general, the elasticity of fecundity elements was low; the lowest elasticity value of eight out of the 14 matrices in Table 9 was a fecundity element. As a general

Table 6 Results of the log-linear analyses, corresponding to each of the initial categories, for the models built with entire transition matrices from eight *P. vulgaris* populations for 1992–93 and 1993–94. Other details of the analyses as in Table 5. The explanatory variables are P = patch (DE2, DE5, etc.) and Y = year (1992–93 and 1993–94); and the response variable is F = fate (death, juvenile, adult 1, etc.)

Model	Effect	d.f.	Seedlings χ^2	$\Delta\chi^2$	P	Juveniles χ^2	$\Delta\chi^2$	P	Adult 1 χ^2	$\Delta\chi^2$	P	Adult 2 χ^2	$\Delta\chi^2$	P	Adult 3 χ^2	$\Delta\chi^2$	P
PY, F		56	229.4		<0.001	188.4		<0.001	385.0		<0.001	271.7		<0.001	84.8		<0.001
PY, FY		52	168.1		<0.001	106.4		<0.001	279.8		<0.001	228.2		<0.001	74.1		<0.001
	Year	4		61.3	<0.001		82.0	<0.001		105.2	<0.001		43.5	<0.001		10.72	<0.05
PY, FP		24	75.5		<0.001	80.1		<0.001	153.5		<0.001	92.1		<0.001	27.3		<0.001
	Patch	32		153.9	<0.001		108.3	<0.001		231.5	<0.001		179.6	<0.001		57.51	<0.005
PY, FY, FP	Year × Patch	20	30.5		0.062	18.6		0.545	86.4		<0.001	50.4		0.001	19.8		0.071

trend, populations in brighter patches showed higher fecundity elasticities. High elasticity values tended to concentrate in the entries that corresponded to young/small individuals growing to larger categories in populations under brighter conditions (middle left-hand side of the matrices). On the other hand, for populations in darker patches high elasticities were found in the entries that corresponded to large adults remaining in the same category or growing to the next one (towards the bottom, right-hand side of the matrices). This pattern was more noticeable in the 1992–93 period.

The contribution of different parts of the life cycle to population growth rate can be studied through the analysis of the elasticity values of matrix elements that correspond to different life-cycle components (Silvertown *et al.* 1993). Total elasticities for particular elements of the life cycle can be calculated by adding together all the elasticity values involved in specific transitions. Thus, total elasticity for fecundity elements (contribution to the first category through the production of seeds), survival (remaining in the same category or shrinking to smaller categories) and growth (progressing to larger categories) can be plotted on a triangular diagram with each axis corresponding to one of these three basic elements of the life-cycle graph (Silvertown *et al.* 1993). In this way, the relative importance of these life-cycle components may be evaluated while the restraints imposed by the particular stage-categorization used are reduced (Enright *et al.* 1995).

Following this methodology we used the data in the elasticity matrices in Table 9 to generate a triangular diagram in which each population was represented (Fig. 5). Populations are concentrated towards the bottom, right-hand part of the triangle. This pattern corresponds to high elasticities for survival elements and low elasticities for fecundity elements. The triangular plot for 1992–93 shows higher elasticities for growth and fecundity elements and lower elasticities for survival elements relative to the one in 1993–94 (i.e. points are distributed closer to the bottom, right-hand corner of the triangle in 1993–94). Note that, in general, populations with higher λ-values had relatively higher fecundity and growth elasticities (i.e. they fell closer to the centre of the triangle) than populations with lower λ-values, which in turn showed high survival elasticities (i.e. they fell closer to the survival (L) axis of the triangle). Also, populations with higher diffuse light showed a tendency towards higher fecundity and growth elasticities compared to populations with low diffuse light (Fig. 5).

Discussion

Our results show that the demography of *P. vulgaris* populations varied spatially according to the light conditions of the specific forest patch they occupied.

Table 7 Statistical results of the comparison of population structures

	Observed in 1993 vs. stable 1992–93	Observed in 1994 vs. stable 1993–94	Observed in 1993 vs. observed in 1994	Stable 1992–93 vs. stable 1993–1994
DE7	–	19.06	–	–
DE2	1315.07	146.62	476.56	6.09
DE5	600.31	1.89	3352.82	111.29
WW	20.63	86.94	16.44	7.42
SF	32.51	2.33	9.35	20.48
DE3	40.21	44.65	34.80	57.51
DE4	12.21	19.79	161.81	71.05
DE6	10.21	–	–	–

The table gives the G (log likelihood ratio) values obtained in each comparison. Comparisons that were not significant are underlined. d.f. = 4 in all cases. DE6 was followed only from 1992 to 1993 and DE7 only from 1993 to 1994.
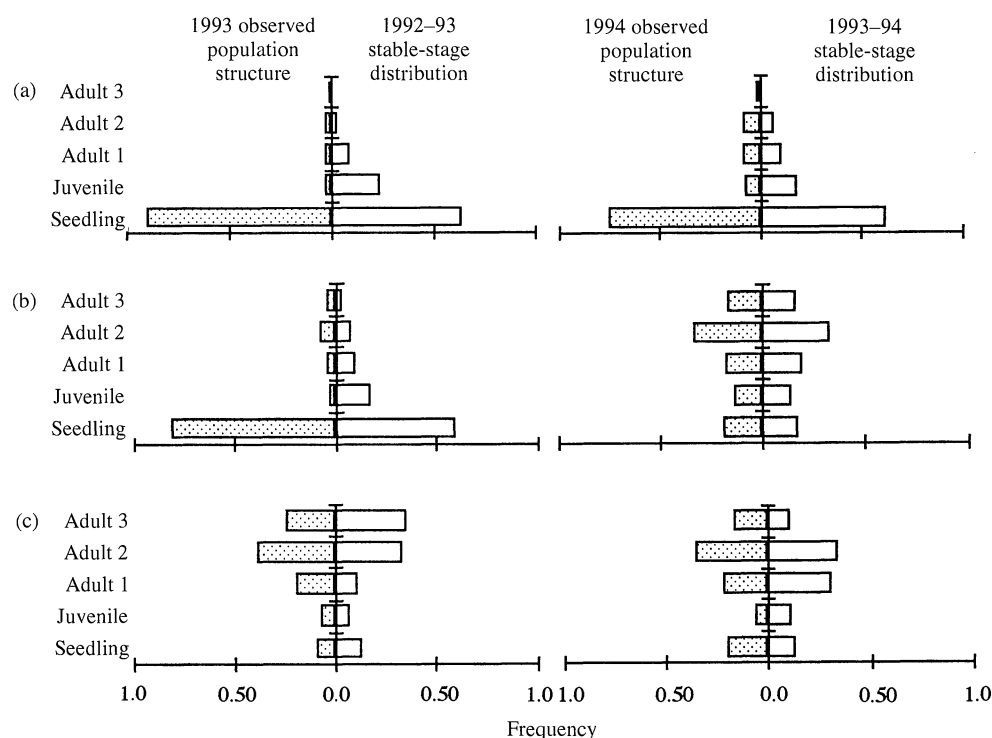
Fig. 4 Population structures recorded in 1993 and 1994 and calculated stable-stage distributions for the periods 1992–93 and 1993–94 for (a) a population in a large gap (DE2), (b) a population in a small gap (DE5), and (c) a population under closed canopy conditions (DE3).

Table 8 Results of the log-linear analysis for the models of observed population structures (frequency of individuals in each category) for three years in eight *P. vulgaris* populations. Structural zeros were included in some cells in populations DE6 and DE7 (data were available for only two years in this population). A constant 0.5 was added to all cells prior to analysis (Silva *et al.* 1990). The explanatory variables are P = patch (DE2, DE5, DE3, etc.) and Y = year (1992, 1993 and 1994); and the response variable is C = category (seedling, juvenile, adult 1, adult 2 and adult 3). The significance of each factor is analysed by examining the reduction in χ^2 (i.e. $\Delta\chi^2$) when each factor is added to a model that excludes it

Model	Effect	d.f.	χ^2	$\Delta\chi^2$	P
PY, C		91	1133.76		<0.001
PY, CY		83	905.39		<0.001
	Year	8		228.37	<0.001
PY, CP		59	412.33		<0.001
	Patch	32		721.43	<0.001
PY, CP, CY	Year × patch	51	112.74		<0.001

Table 9 Sensitivity and elasticity matrices for eight *P. vulgaris* populations for the periods (a) 1992–93 and (b) 1993–94. The two highest values are bold and the smallest value is underlined in each matrix. The first column shows the λ-values, the total sensitivity (TS) and sensitivity indices (SI) for each population

		Sensitivity					Elasticity				
		Seedling	Juvenile	Adult 1	Adult 2	Adult 3	Seedling	Juvenile	Adult 1	Adult 2	Adult 3
(a)											
DE2	Seedling	0	0	0.029	0.011	0.001	0	0	0.066	0.127	0.015
λ = 1.976	Juvenile	0.632	0.240	0.089	0	0	**0.188**	0.051	0.001	0	0
TS = 7.26	Adult 1	**1.946**	0.740	0.275	0.102	0	0.020	**0.170**	0.078	0.006	0
SI = 2.69	Adult 2	0	**1.831**	0.679	0.252	0.015	0	0.019	0.129	0.099	0.005
	Adult 3	0	0	0	0.395	0.024	0	0	0	0.020	0.004
DE5	Seedling	0	0	0.038	0.028	0.011	0	0	0.045	0.087	0.079
λ = 1.794	Juvenile	0.550	0.169	0.098	0	0	**0.136**	0.031	0.002	0	0
TS = 5.19	Adult 1	**1.208**	0.370	0.216	0.163	0	0.075	0.101	0.037	0.002	0
SI = 2.28	Adult 2	0	**0.566**	0.330	0.249	0.095	0	0.036	0.105	0.091	0.017
	Adult 3	0	0	0.539	0.407	0.155	0	0	0.027	0.069	0.059
WW	Seedling	0	0	0.251	0.174	0.014	0	0	0.006	0.016	0.004
λ = 0.974	Juvenile	0.045	0.054	0.411	0.284	0	0.020	0.015	0.017	0.002	0
TS = 4.44	Adult 1	0.052	0.063	0.480	0.332	0	0.008	0.035	**0.326**	0.111	0
SI = 2.11	Adult 2	0	0.076	**0.579**	0.401	0.032	0	0.003	0.125	**0.255**	0.018
	Adult 3	0	0	**0.685**	0.474	0.038	0	0	0.006	0.016	0.016
SF	Seedling	0	0	0.033	0.112	0.188	0	0	0.001	0.007	0.034
λ = 1.035	Juvenile	0.087	0.032	0	0	0	0.025	0.008	0	0	0
TS = 3.28	Adult 1	0.100	0.037	0.080	0.267	0.450	0.017	0.013	0.029	0.015	0.005
SI = 1.81	Adult 2	0	0.041	0.089	0.297	**0.500**	0	0.012	0.039	**0.163**	0.082
	Adult 3	0	0	0.097	0.326	**0.549**	0	0	0.010	0.112	**0.427**
DE3	Seedling	0	0	0.038	0.115	0.122	0	0	0.001	0.016	0.027
λ = 1.055	Juvenile	0.120	0.067	0.104	0	0	0.044	0.019	0.004	0	0
TS = 3.33	Adult 1	0	0.072	0.111	0.339	0.358	0	0.044	0.040	0.012	0.016
SI = 1.82	Adult 2	0	0.079	0.121	0.371	**0.391**	0	0.004	0.061	**0.220**	0.086
	Adult 3	0	0	0.126	0.386	**0.407**	0	0	0.005	0.123	**0.279**
DE4	Seedling	0	0	0.091	0.089	0.113	0	0	0.024	0.036	0.091
λ = 1.267	Juvenile	0.272	0.055	0.163	0	0	0.043	0.007	0.005	0	0
TS = 3.46	Adult 1	**0.344**	0.070	0.206	0.202	0	0.108	0.026	0.059	0.013	0
SI = 1.87	Adult 2	0	0.081	0.238	0.233	0.298	0	0.018	0.066	0.088	0.062
	Adult 3	0	0.096	0.283	0.277	0.353	0	0.004	0.052	0.098	**0.200**
DE6	Seedling	0	0	0.109	0.117	0.096	0	0	0.012	0.031	0.053
λ = 1.133	Juvenile	0.153	0.083	0.176	0.188	0	0.051	0.029	0.001	0.002	0
TS = 3.72	Adult 1	0.201	0.110	0.232	0.248	0.204	0.044	0.054	0.094	0.036	0.003
SI = 1.93	Adult 2	0	0	0.272	0.291	0.240	0	0	0.095	**0.151**	0.045
	Adult 3	0	0	**0.339**	**0.362**	0.298	0	0	0.030	0.071	**0.198**
(b)											
DE7	Seedling	0	0	0.106	0.073	0.012	0	0	0.004	0.019	0.015
λ = 0.868	Juvenile	0.060	0.093	0.168	0.115	0	0.031	0.036	0.018	0.008	0
TS = 3.39	Adult 1	0.130	0.200	0.361	0.247	0.041	0.008	0.056	**0.206**	0.085	0.006
SI = 1.84	Adult 2	0	0	**0.592**	0.405	0.067	0	0	0.133	**0.234**	0.038
	Adult 3	0	0	0	**0.622**	0.102	0	0	0	0.060	0.043
DE2	Seedling	0	0	0.018	0.011	0.002	0	0	0.008	0.060	0.035
λ = 1.229	Juvenile	0.578	0.168	0.100	0.064	0	0.094	0.067	0.007	0.001	0
TS = 5.88	Adult 1	**1.474**	0.428	0.255	0.162	0	0.009	0.094	**0.137**	0.015	0
SI = 2.42	Adult 2	0	**0.900**	0.537	0.342	0.069	0	0.007	0.104	**0.218**	0.012
	Adult 3	0	0	0	0.646	0.131	0	0	0	0.047	0.084
DE5	Seedling	0	0	0.045	0.078	0.037	0	0	0.002	0.016	0.023
λ = 1.019	Juvenile	0.091	0.073	0.100	0	0	0.031	0.032	0.010	0	0
TS = 3.13	Adult 1	0.172	0.138	0.188	0.327	0	0.010	0.038	0.087	0.053	0
SI = 1.77	Adult 2	0	0.186	0.252	**0.439**	0.211	0	0.004	0.088	**0.280**	0.067
	Adult 3	0	0	0	**0.537**	0.258	0	0	0	0.090	**0.168**
WW	Seedling	0	0	0.130	0.064	0.006	0	0	0.005	0.007	0.001
λ = 0.934	Juvenile	0.040	0.106	0.410	0.201	0	0.011	0.039	0.051	0.005	0
TS = 3.32	Adult 1	0.052	0.138	**0.533**	0.261	0.024	0.002	0.066	**0.369**	0.091	0.005
SI = 1.82	Adult 2	0	0	**0.650**	0.318	0.029	0	0	0.109	**0.197**	0.012
	Adult 3	0	0	0	0.330	0.030	0	0	0	0.018	0.012

Table 9 (*Continued*)

|		Sensitivity					Elasticity				
		Seedling	Juvenile	Adult 1	Adult 2	Adult 3	Seedling	Juvenile	Adult 1	Adult 2	Adult 3
SF	Seedling	0	0	<u>0.013</u>	0.029	0.021	0	0	<u>0.0002</u>	0.003	0.004
$\lambda = 0.951$	Juvenile	0.054	0.020	0.093	0	0	0.007	0.004	0.008	0	0
TS = 3.04	Adult 1	0	0.025	0.120	0.278	0.200	0	0.010	0.063	0.034	0.013
SI = 1.74	Adult 2	0	0.044	0.209	**0.486**	0.350	0	0.006	0.043	0.325	0.112
	Adult 3	0	0	0.219	**0.510**	0.368	0	0	0.005	0.124	**0.239**
DE3	Seedling	0	0	0.011	0.012	<u>0.003</u>	0	0	<u>0.0002</u>	0.003	0.002
$\lambda = 0.879$	Juvenile	0.049	0.042	0.111	0.121	0	0.005	0.019	0.016	0.002	0
TS = 3.67	Adult 1	0	0.101	0.266	0.291	0.087	0	0.023	**0.166**	0.072	0.005
SI = 1.92	Adult 2	0	0	0.442	0.483	0.144	0	0	0.064	**0.361**	0.058
	Adult 3	0	0	**0.623**	0.681	0.203	0	0	0.020	0.045	0.138
DE4	Seedling	0	0	<u>0.004</u>	0.015	0.010	0	0	<u>0.0001</u>	0.001	0.002
$\lambda = 0.933$	Juvenile	0.009	0.005	0.016	0.059	0	0.001	0.001	0.001	0.001	0
TS = 2.61	Adult 1	0.042	0.025	0.074	0.272	0.172	0.001	0.004	0.038	0.025	0.006
SI = 1.61	Adult 2	0	0	0.047	**0.537**	0.339	0	0	0.035	**0.398**	0.104
	Adult 3	0	0	0	**0.603**	0.381	0	0	0	0.112	**0.269**
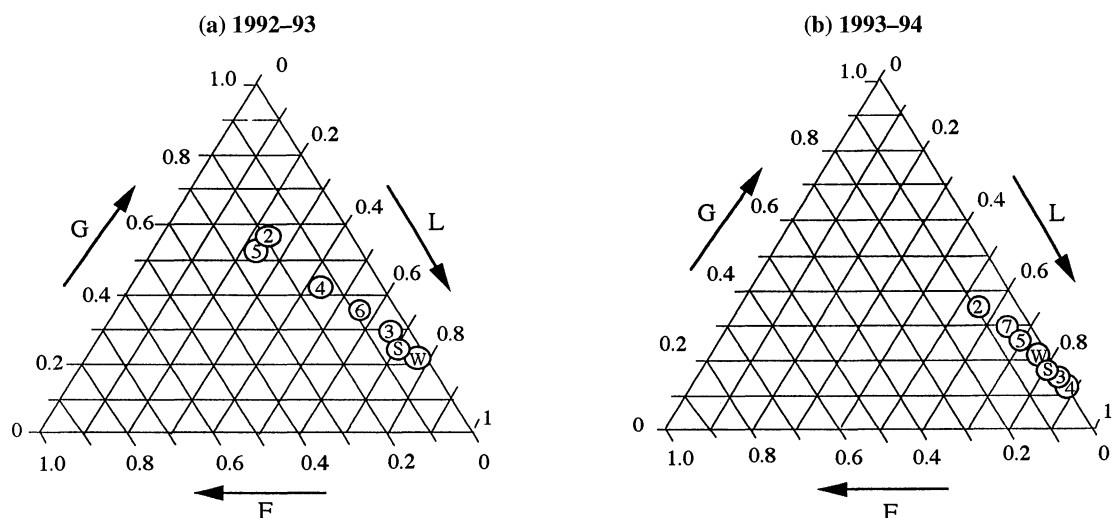
Fig. 5 Triangular graphs of fecundity (F), survival (L) and growth (G) elasticities for the periods (a) 1992–93 and (b) 1993–94 for the eight populations studied. Each circle in the graphs represents a population (Dancers End populations referred to by number, and Salcey Forest and Woburn Wood populations as S and W, respectively).

This suggests that, on a longer time-scale than the one used in this study, population dynamics may change as a result of natural changes in the forest canopy. Population growth rate tends to be lower in darker patches, implying that populations decline as the canopy closes. A similar demographic behaviour was inferred for *Calathea ovandensis* (Horvitz & Schemske 1986), *Cynoglossum virginianum* (Cipollini *et al.* 1993) and *Lindera benzoin* (Cipollini *et al.* 1994). In these studies, the authors assumed that the demography of these understorey plants varies in time, not only due to random environmental variation, but also as a

result of directional changes in light availability given by forest secondary succession. Although our study of *P. vulgaris* was not a long-term analysis of population dynamics during the whole process of gap opening and closure, our results support the idea that populations may decline as the canopy regeneration cycle proceeds. It appears that, as the canopy closes, population growth rate slows down; this makes populations in darker patches more vulnerable to bad years, which is evident in the lower-than-unity λ-values obtained in these populations in 1993–94. Lower λ-values in closed canopy patches were the

result of increased mortality (especially of small plants) and decreased fecundity compared to populations in brighter patches. These cannot be attributed to density-dependent effects (because density declined as canopy openness decreased) or to other intrinsic factors (e.g. no signs of plant senescence were apparent); thus, it appears that light-related differences in survival and reproduction patterns are responsible for an important part of the demographic variation observed among populations.

Given the results emphasized above, the question arises as to whether *P. vulgaris* populations may persist for long periods of time in closed canopy conditions. Our analysis does not allow a straightforward answer to this question given the limitations of our data set (i.e. we observed substantial yearly variation in demographic behaviour and only two growth periods were considered). However, we may expect that populations in brighter patches experience a demographic decline through time associated with canopy closure. Thus, the long-term success of this kind of gap-dependent species in a forest may depend upon the opening of canopy gaps, which would recreate the conditions adequate for population growth. These results have important implications in terms of forest management: the gradual cessation of traditional coppicing practices could lead to a decline in the abundance of understorey species such as *P. vulgaris* (Harrison 1991; Barkham 1992a).

The high yearly variation observed in the *P. vulgaris* populations studied deserves further comment. Population growth rate was substantially higher in 1992–93 than in 1993–94. Although the λ-values for 1992–93 might have been slightly overestimated due to a 2-week delay in the sampling dates in 1992 (i.e. we missed part of the period of typically heavy seedling mortality that occurs immediately after germination, which may have resulted in a slight overestimation of the seedling-to-juvenile transitions from 1992 to 1993), the difference in demographic behaviour between the two periods was mainly a result of both higher mortality (particularly in the smaller categories) and lower fecundities in most populations during 1993–94 compared to 1992–93. The differences in fecundity were given by a massive flower and capsule production in 1992 and consequently high seedling emergence in 1993. The variation in fecundity between the two periods studied could have been determined by several factors affecting reproductive success. In particular capsule production (and hence seed set) has been observed to vary greatly from year to year in natural populations of *P. vulgaris* (Valverde & Silvertown 1995), apparently related to pollinator availability (Piper *et al.* 1984; Boyd *et al.* 1990). The fact that fecundities varied from patch to patch along the light gradient, as well as in time, also suggests that there may be light-related differences in pollinator abundance within forest patches. Whether canopy openness affects pollinator availability is unknown;

however, the pattern observed in this study suggests that pollinator abundance might be higher in brighter patches compared to closed canopy patches (Valverde & Silvertown 1995).

In may be argued that the decrease in population growth rate in 1993–94 compared to 1992–93 could have been a result of canopy closure. However, this decrease was noticeable in all populations studied, including those in which canopy openness remained constant from one year to the next. This suggests that factors affecting all of them in a similar fashion (e.g. weather conditions – the 1993–94 period was dryer and warmer) were responsible for the yearly variation observed, and that perhaps our data set represents demographic behaviour during 'good' and 'bad' years. Moreover, yearly variation in the demography of forest herb populations seems to be more the rule than the exception (Barkham 1980; Bierzychudek 1982b; Horvitz & Schemske 1995; Damman & Cain 1998). The effect of this year-to-year demographic variation upon the long-term dynamics of the species remains to be investigated.

Given the wide confidence intervals for λ obtained in this study, few statistically significant differences between λ-values for different populations or different years were found. However, in addition to the analysis of population growth rate, spatiotemporal variation in population dynamics may be ascertained by comparing entire transition matrices (Ehrlen 1995). In this case, the log-linear analysis of transition matrices revealed that both patch and year (as well as the interaction of both factors) had a significant effect on transition matrices, i.e. the fate of individuals, conditional on their initial category, was not independent of patch or year, and the effect of patch was not the same for all years.

Similarly, population structure was affected by both patch and year (Table 8). Smaller/younger individuals of *P. vulgaris* made up a greater proportion of the population in brighter patches than in those under completely closed canopy conditions. The changes in population structure from brighter to darker patches suggest that seedling recruitment and juvenile survival are high in large gaps but may decline slowly as the canopy closes. Thus, populations in closed canopy patches might persist largely due to the survival of established individuals. This is also a common phenomenon among other forest understorey plants (Pitelka *et al.* 1985; Barkham 1992b; Cipollini *et al.* 1993, 1994; Hara & Wakahara 1994; Horvitz & Schemske 1994).

In this study, observed population structures were generally significantly different from stable-stage distributions. Natural populations are often not at their stable-stage distribution (Caswell 1989). However, the concept of stable-stage distribution itself, which relies on the assumption of demographic and environmental stasis, is particularly meaningless for species like *P. vulgaris* that live in dynamic environments.

Thus, it is not surprising that this species has population structures that differ from those expected at equilibrium; there is no such thing as 'equilibrium' for a population embedded in a constantly changing environment determined by the dynamics of the forest canopy.

The results of the elasticity analysis showed that decreasing canopy openness resulted in a directional change in the various demographic components of the life cycle. In general, fecundity and growth made a larger contribution to λ in patches in brighter conditions, where λ was highest, and survival became more important in populations under the closed canopy, where λ was lowest. This is shown by the trajectory followed by the dots in the triangular plots in Fig. 5, i.e. as diffuse light and λ decreased, populations were located further towards the bottom right-hand corner of the triangle, which corresponds to high elasticities for survival elements and low elasticities for fecundity and growth. The region of the 'demographic triangle' in which *P. vulgaris* populations in brighter patches were concentrated coincides with the pattern found by Silvertown *et al.* (1993) for iteroparous herbs of open habitats, whereas populations in darker patches were closer to the survival axis, which corresponds to the pattern observed for other perennial forest herbs. Thus, the patterns described in Silvertown *et al.* (1993) for different plant species appear to also hold for single plant species studied over a range of environmental conditions.

In *Cynoglossum virginianum*, another temperate forest herb, Cipollini *et al.* (1993) found that the contribution of the seed-to-seedling transition to the value of λ was more important in populations established in new gaps than in populations under closed canopy conditions. Silvertown & Franco (1993) and Silvertown *et al.* (1996) found that the contribution of fecundity to population growth rate in several species was higher during the early stages of colonization than later in the successional process. For *Plantago* populations living in variable habitats, seed production had higher elasticity compared to populations in more stable habitats, in which adult survival had relatively greater elasticities (van Groenendael & Slim 1988). Finally, Horvitz & Schemske (1995) observed that the elasticity of survival elements was high in *Calathea ovandensis* when low λ-values were recorded, whereas growth and fecundity became relatively more important in populations with higher λ-values; similar results were obtained for *Silene regia* by Menges & Dolan (1998). Our results coincide with these observations, which indicates that the demographic trends observed in different populations of *P. vulgaris* are not unique. These findings stress the importance of studying the variation in the dynamics of plant populations across the range of environmental conditions in which they naturally occur to obtain a more complete picture of demographic patterns in nature.

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