

Population responses of *Ulex* shrubs to fire in a lowland heath community

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Abstract.

Question: How does the frequency of heathland fire events affect population growth rates of two woody shrub species, *Ulex gallii* and *U. minor*?

Location: Dry heathland on the south coast of England, UK.

Methods: The population dynamics of *U. gallii* and *U. minor* were modelled at each phase of the heathland cycle – pioneer, building, mature and degenerate – using periodic matrix products to investigate the response to different fire regimes.

Results: Population growth rates of both *Ulex* species declined under annual burning. Initially, as the time between burns increased, population growth rate increased for both species. Maximum population growth rates for each *Ulex* species were achieved under a 16-yr fire return interval. Fire return intervals > 16 yr resulted in declining population growth rates.

Conclusions: A species-specific critical fire frequency can be predicted, the minimum fire return intervals permitting persistence were 4 yr for *U. minor* and 3 yr for *U. gallii*. These patterns are similar to those reported for a range of woody plant species within savanna environments.

Keywords: Dwarf shrub; Fire regime; Habitat-specific vital rate; Heathland vegetation cycle; Periodic matrix model; Woody plant.

Nomenclature: Stace (1997).

Introduction

Fire regimes have been shown to impact plant communities by altering stand structure (Zammit & Zedler 1993; Price & Bowman 1994; Peterson & Reich 2001), community composition (San José & Farinas 1983; Jacobs & Schloeder 2002), and the distribution and abundance of species (Segura et al. 1998; Ribeiro & Fernandes 2000). The impact of differing fire frequencies on plant growth and population dynamics has been particularly well studied in savanna systems (Watkinson et al. 1989; Silva et al. 1991; Hoffmann 1999; Roques et al. 2001).

Fire also has an important role in the dynamics of

Atlantic heathlands of northwestern Europe. These communities are dominated by ericaceous dwarf shrubs established on acidic nutrient-poor mineral soils. European heathlands were, in general, created by human activities such as forest clearance, and they have been maintained by management regimes such as burning, livestock-grazing, turf-stripping, and cutting of scrub and bracken (Gimingham 1972; Webb 1986; Bullock & Pakeman 1997). Management prevents tree and scrub colonization, halts the degeneration of the dwarf-shrub layer, and maintains low nutrient status (Webb & Haskins 1980). Historically, heathland was burnt on a 30 to 40 year cycle (Webb 1986). In recent years, there have been concerns over the potential impact of more frequent fires. The increased incidence of uncontrolled burning events can potentially damage heathland communities by destroying all above-ground vegetation; burning into the humus; killing roots, buds and seeds; causing excessive loss of nutrients; and destroying invertebrate and reptile populations (Hobbs & Gimingham 1987).

Demographic responses to fire include the size and growth of individuals, survivorship and reproductive output (Chapman et al. 1989; Warton & Wardle 2003). Within the context of a fire-prone environment, the range of fire frequencies which permits positive population growth rate will determine how well a species can cope with long-term changes in fire frequency. Hoffmann (1999) studied woody plants within a savanna ecosystem in Brazil, predicting that if each species was able to persist only under a narrow range of fire frequencies, one would expect large shifts in species composition in response to changes in fire frequency. Periodic matrix models predicted a decline in the majority of the woody species at high fire frequencies and an increase under infrequent burning.

The frequency of burning events on managed heathland is inter-linked with the cyclical processes occurring within heathland vegetation communities because prescribed management burns are restricted to areas of mature vegetation. When the population of the dominant

shrub species is uneven-aged, gaps appear irregularly in the canopy, caused either by the death of individuals or changes in plant structure. Community structure then takes the form of a mosaic of patches at different stages in the cycle (Watt 1947, 1955). Demographic rates within these different patches can show considerable variation because the structure of the vegetation alters environmental conditions, and therefore influences the favourability of growth conditions. Various matrix population modelling approaches have been proposed to represent both patch-specific demographic rates and patch dynamics (Horvitz & Schemske 1986; Alvarez-Buylla 1994; Cipollini et al. 1994; Valverde & Silvertown 1997, 1998). These approaches can be used when population matrices are available for several years or a variety of environmental conditions. The matrices are then multiplied together to estimate population growth in an environment which cycles among the observed environmental states.

This study investigates how fire frequency could impact two perennial dwarf shrubs, *Ulex gallii* and *U. minor*, within dry lowland heath communities of southern England. It builds on the study of Stokes et al. (2004), which described population dynamics of *Ulex* species across geographic gradients. The aim of this study is to quantify the impact of differing fire return intervals upon population growth rate of the two species. This is achieved through modelling population dynamics at each stage of the heathland cycle using periodic matrix products, enabling prediction of the range of fire frequencies that permits positive population growth rate.

Material and Methods

Study species

Ulex gallii and *U. minor* (*Fabaceae*) are perennial dwarf shrubs characteristic of acid, nutrient-poor soils. In Britain they are found most commonly on wet, dry and humid heaths (H1-H6 and H8 in the National Vegetation Classification; Rodwell 1991) but also occur in acid grasslands (U2, U3) and in drier parts of acid mire communities (M14, M16, M24). *Ulex gallii* and *U. minor* are described at length in Stokes et al. (2003), both species are long-lived; each forms a persistent seedbank and has the capacity to re-sprout following fire.

Study sites

The *Ulex* species were studied on heathland sites in Dorset on the south coast of England. At each site the *Ulex* species were sub-dominants in typical British lowland 'dry heath' communities comprising dwarf-shrub vegetation dominated by *Calluna vulgaris* and *Erica*

cinerea (both *Ericaceae*). In Dorset four mature heathland sites with similar management histories were identified for study: two *U. gallii* sites, Canford Heath (National Grid Reference: SZ 030 955) and Upton Heath (National Grid Reference: SY 985 945), and two *U. minor* sites, Arne Heath (National Grid Reference: SY 973 882) and Hartland Moor (National Grid Reference: SY 955 856). Detailed spatial records compiled by site managers (N. Gartshore & J. Martin unpubl.) existed for the burning history of one *U. gallii* site (Canford Heath) and one *U. minor* site (Stoborough Heath) in Dorset.

Field methods

At each of the four sites, 200 individuals in patches of mature heathland were selected during June and July 1999 to represent the full range of plant sizes at the site. Basal stem diameter of each individual was measured. Individuals were tagged with plastic-coated wire and re-censused one year later. A metal detector was used to relocate individuals. Plants were scored as alive or dead and the basal stem diameter of each surviving plant was re-measured. The patches of mature heathland at these sites were not burned during the duration of the study.

Historical records existed for Canford Heath and Stoborough Heath, enabling identification of populations which differed in the time elapsed since the last burning event. At these two sites basal stem diameter of 100 individuals was measured for each differently aged population.

Fecundity was estimated at Canford Heath (*U. gallii*) and Arne Heath (*U. minor*). At each site ten 2 m × 2 m quadrats were located within areas of the heath containing *Ulex* individuals of a range of sizes. Basal stem diameter, branch number and pod number of a representative branch were recorded for each plant. Samples of approximately 20 pods were removed from each individual and seed number per pod determined.

Seedbank density estimates were obtained at the same two sites. Sixteen soil samples of 25 cm × 25 cm were removed to a depth of 10 cm during October 2000. Samples were sieved in the laboratory and *Ulex* seeds were then counted.

Seed longevity in the seed bank was investigated through burial experiments. Seed of each species was collected from plants at all four sites during May 1999 and a sub-sample tested for viability using 2-3-5 tetrazolium chloride (see Courtney 1968). Viable seed was placed into muslin bags of 5 cm × 5 cm with 50 seeds per bag. Four bags of seed of each species were buried to a depth of approximately 20 cm during September 1999 at each site. This depth was chosen to reduce the probability of sample loss through predation. Bags were retrieved

after a 1-yr period and tested for viability.

To obtain information on demographic rates following burning mature heathland, sites in Dorset were burnt during March 1997, thus complying with the legal restrictions for seasonally prescribed fires (Gimingham 1992). Eight 5 × 10 m plots were burnt and three 1 m × 1 m quadrats were laid out in each plot. Each quadrat was divided into 100 squares. The location of squares in which a burnt *Ulex* stump was rooted and the number of individuals rooted per quadrat were recorded. Sites were re-surveyed and the proportion of *Ulex* individuals re-sprouting recorded 1 year after fire.

Seedling emergence was quantified in burnt and unburnt plots. Seedling densities were recorded in 50 25 cm × 25 cm quadrats located on burnt plots for one post-fire year. Proportional post-fire seedling emergence values were calculated by assuming seedbank densities to be equivalent to those measured in unburnt plots. This may slightly underestimate the true seedling emergence, as burning may have killed a proportion of seeds within the seedbank. However this proportion is likely to be small, laboratory tests have shown that temperatures of 100 °C or more sustained for at least 15 minutes are necessary to kill *U. europaeus* seeds (Zabkiewicz 1979). A sample of 40 emerging seedlings were tagged at each site and counted 1 yr later to establish the survival probability of seedlings.

Sowing experiments were conducted at the four sites to quantify seedling emergence and survival at a range of densities within unburnt degenerate heath. During October 2000 seed collected from all four sites was scatter-sown at a range of densities (160 ind.m⁻², 800, 1600, 3200, 4800 ind.m⁻²) into 25 cm × 25 cm plots in stands of 'degenerate' heath (see Table 1). Each planting density was replicated five times in a fully randomized design and plots were located randomly over an area of 50 m² at each site. Individual seedling demography was recorded once every 2 wk for a 1-yr period.

Matrix analysis

The heathland patch model

Heathland vegetation can be aged by the size and structure of the ericaceous dwarf shrubs (Watt 1947, 1955; Barclay-Estrup & Gimingham 1969). Thus, patches of vegetation can be classified according to the estimated time since disturbance. In this study, five patch types were designated (Table 1), classified by the structure (and therefore age) of the vegetation.

The heath cycle is driven by the ageing of the ericaceous shrubs, and the return to early phases occurs through death of senescent individuals in the degenerate phase or through disturbance. Disturbance occurs through burning of the vegetation by conservation managers (Fig. 1).

Demographic data were amalgamated from each pair of sites to construct a basic species-specific matrix population model for each *Ulex* species. Each basic matrix was then adapted to describe demography in the different patch types.

The basic matrix model

Populations were divided into stage categories using stem diameter to define the categories: the initial category represents a seed, stage category two, a seedling of stem diameter 2 mm or less. Stage categories ascend in size by 0.5 mm stem diameter for the majority of the stages but larger intervals were used for the larger plants. This represents a compromise between sampling error and distribution error (see Caswell 2001), the latter being substantial if larger size categories were used.

Parameter estimates obtained from the field methods described above enabled a matrix population model to be constructed, incorporating the probability of each species to re-sprout. An assumption is made that all individuals

Fig. 1. The heathland patch cycle.



Table 1. Definition of the heathland patch cycle based on age and size of constituent *Ulex* individuals.

Patch type	Age of individuals	Size of individuals (<i>U. gallii</i>)	Size of individuals (<i>U. minor</i>)	Gap status	Gap creation
Post-burn	0-1 yr	Seeds to < 2 mm stem diameter	Seeds to < 2 mm stem diameter	Gaps present	
Pioneer	1-5 yr	Seeds to 8.0 mm stem diameter	Seeds to 6.0 mm stem diameter	Gaps present	
Building	6-15 yr	Seeds to 11 mm stem diameter	Seeds to 10 mm stem diameter	Gaps present	
Mature	16-25 yr	2.5 mm to maximum stem diameter	2.5 mm to maximum stem diameter	No gaps	Cutting/burning management
Degenerate	25+ yr	Seeds to maximum stem diameter	Seeds to maximum stem diameter	Gaps present	Senescent adults

with a stem diameter of 2.5 mm or greater have the potential to re-sprout, as both *Ulex* species have sufficient resources to allocate to sexual reproduction and produce flowers at smaller sizes (Stokes et al. 2003). All re-sprouting individuals are classified as stage 3 individuals (2.5–3.0 mm), as the diameter of the re-sprouting stem rarely exceeded this dimension one year after a burning event (Fig. 2) and no relationship was observed between pre-burn stem diameter and re-sprout diameter. The probability of any individual from stage 3 or above re-sprouting to enter the matrix at stage 3 is entered along row 3, $F_{i,3}$. F_i is the annual seed production of an individual in size class i .

The basic projection matrix can thus be defined as:

$$A = \begin{bmatrix} P_{1,1} & F_2 & F_3 & F_4 & F_5 & F_6 & F_7 & \dots & F_{16} \\ G_{1,2} & P_{2,2} & 0 & 0 & 0 & 0 & 0 & \dots & 0 \\ 0 & G_{2,3} & P_{3,3} & F_{4,3} & F_{5,3} & F_{6,3} & F_{7,3} & \dots & F_{16,3} \\ 0 & G_{2,4} & G_{3,4} & P_{4,4} & 0 & 0 & 0 & \dots & 0 \\ 0 & 0 & G_{3,5} & G_{4,5} & P_{5,5} & 0 & 0 & \dots & 0 \\ 0 & 0 & G_{3,6} & G_{4,6} & G_{5,6} & P_{6,6} & 0 & \dots & 0 \\ 0 & 0 & 0 & G_{4,7} & G_{5,7} & G_{6,7} & P_{7,7} & \dots & 0 \\ 0 & 0 & 0 & 0 & G_{5,8} & G_{6,8} & G_{7,8} & \dots & 0 \\ 0 & 0 & 0 & 0 & G_{5,9} & G_{6,9} & G_{7,9} & \dots & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & \dots & 0 \\ \dots & \dots & \dots & \dots & \dots & \dots & \dots & \dots & \dots \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & \dots & P_{16,16} \end{bmatrix}$$

The probability of survival and remaining in the same size class (P_{ii}), is defined as the product of the probability of an individual in class i surviving for a year and the probability of remaining in the same size class. The probability of survival and growth to a larger size class (G_{ij}) was obtained by multiplying the survival probability by the probability of surviving individuals making the transition to class j .

Parameter estimates

Annual seedling emergence was calculated as the total number of individuals emerging as a proportion of the total planted. Sowing density had an effect on seedling emergence but for the purposes of this paper proportional seedling emergence was averaged across densities (density-dependent matrices have been analysed in Stokes et al. 2004). To obtain the annual probability of transition from seed (stage 1), to juvenile (stage 2 < 2 mm stem diameter), the probability of seedling emergence was multiplied by the probability of seedling survival. Annual survival within the seedbank was estimated from the number of buried seeds that survived 1 year. Stasis of seed within the seed bank was derived as:

1 – (probability of transition from stage 1 to stage 2 × probability of survival within the seed bank)

Seed production per plant was estimated as the product of branches per plant, pods per branch and seeds per

pod. This estimate was regressed against plant size (stem diameter), enabling an estimate of annual seed production per individual to be derived for each stage class in the matrix model (F_i).

Patch-specific matrices

One of the most critical parameters influencing population growth rate of *U. gallii* and *U. minor* is the transition from seed to size class 2. This transition ($G_{1,2}$) consistently had the highest elasticity value in site-specific matrices for each species (Stokes et al. 2004). Essentially it is this matrix transition, and by default the survival of seed within the seed bank, which changes between the pioneer, building, mature and degenerate matrices (Table 2). Therefore, patch-specific demographic rates corresponding to these two matrix elements were calculated separately for *U. gallii* and *U. minor*. The majority of the transitions between larger individuals remain the same.

Burning occurs at the beginning of the one year period simulated by the post-burn matrix, during which time re-sprouting takes place. Re-sprouting individuals are capable of producing seed within one year and the amount of seed produced is assumed to be equivalent to the fecundity of an individual in size class 3. This value is multiplied by the re-sprout probability to obtain the value of $F_{3,i}$. *Ulex* individuals are not capable of progressing beyond the second stage class within one year, thus all transition probabilities beyond stage 2 are entered as zero in the post-burn matrix (Table 2, Matrices **a** and **c**). It was assumed that re-sprouting of individuals occurs only in the year immediately following burning, and failure to re-sprout within this time interval indicated that the parent plant did not survive. Thus the pioneer matrix comprises transitions involving classes from seed to size class 12 for *U. gallii* and to size class 10 for *U. minor*, the maximum size that could be attained within the 5-yr pioneer period.

As seedlings cannot establish beneath a dense canopy, ($G_{1,2}$) is zero in the mature matrix (Table 3). Juvenile plants that establish in building vegetation may be present in mature vegetation patches and progress through the adult stages according to the probabilities of stasis and transition described by the basic matrix. Estimates of the probability of seedling emergence for the degenerate matrix were obtained from the sowing experiments in unburnt plots, and so differ from those used in the post-burn, pioneer and building matrices (Table 2, Matrices **b** and **d**).

Estimation of individual matrix entries from field data implies errors, which must be quantified by assigning confidence limits to estimates of λ . We used Taylor's series expansion (Alvarez-Buylla & Slatkin 1993, 1994) to estimate approximate 95% confidence intervals for λ .

Table 2. Patch specific matrices for *U. gallii* (a) post-burn matrix, (b) degenerate matrix and *U. minor*, (c) post-burn matrix and (d) degenerate matrix. The arrows represent size classes 3 to 16 for which all transition probabilities are zero in matrices (a) and (c).

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
(a)	.206	0.0	5.0	5.0	5.0	5.0	5.0	5.0	5.0	5.0	5.0	5.0	5.0	5.0	5.0	5.0
	.450	.450														
↓			.343	.343	.343	.343	.343	.343	.343	.343	.343	.343	.343	.343	.343	.343
16																
(b)	.367	0.0	0.0	0.0	19.5	21.8	24.2	26.5	28.8	31.0	33.2	37.6	44.0	50.3	56.4	66.4
	.022	.699														
		.143	.185													
		.143	.600	.118												
			.200	.333	.285											
				.533	.300	.085										
					.200	.300	.235									
					.100	.400	.500	.370								
					.100	.100	.250	.385	.485							
								.077	.500	.360						
										.125	.001					
								.154		.500	.984					
												.652				
												.250	.984			
												.083	.001	.235		
														.750	.001	
															.984	.985
(c)	.243	0.0	.475	.475	.475	.475	.475	.475	.475	.475	.475	.475	.475	.475	.475	.475
	.190	.190														
↓			.058	.058	.058	.058	.058	.058	.058	.058	.058	.058	.058	.058	.058	.058
16																
(d)	.296	0.0	8.19	11.0	14.1	17.4	21.1	24.9	29.1	33.4	38.0	42.9	47.9	64.2	95.2	131.0
	.012	.630														
		.310	.213													
		.034	.714	.443												
				.277	.430											
			.048	.213	.455	.581										
				.021	.091	.121	.618									
						.061	.357	.494								
								.222	.546							
								.259	.143	.740						
									.286	.118	.225					
											.250	.575				
										.059	.250	.400	.001			
											.250		.974			
														.974		
														.001	.974	
															.001	.975

Calculation of λ at periodic fire intervals

To investigate the impact of periodic burning the matrices were multiplied together using standard matrix multiplication methods within MATLAB (Anon.). Each patch-specific matrix describes the population dynamics for one year. Residence time in each phase was designated according to the time intervals set out in Table 1. In a periodic environment, population growth over one cycle length is given by the dominant eigenvalue of the product of the projection matrices for each phase in the cycle. Following Caswell (2001) and supposing that the phase-specific matrices are $\mathbf{B}^{(1)}, \mathbf{B}^{(2)}, \dots, \mathbf{B}^{(m)}$, where m is the cycle length in yr, then $n(t + m) = \mathbf{B}^{(m)} \dots \mathbf{B}^{(2)} \mathbf{B}^{(1)} n(t) = \mathbf{A} n(t)$.

Table 3. Alterations to $P_{1,1}$ and $G_{1,2}$ within the patch specific matrices for *U. gallii* and *U. minor*. $P_{1,1}$ is the probability of a seed surviving and remaining within the seedbank for one year and $G_{1,2}$ is the probability of survival and growth from the seed size class to size class 2.

	<i>U. gallii</i> ($P_{1,1}$)	<i>U. gallii</i> ($G_{1,2}$)	<i>U. minor</i> ($P_{1,1}$)	<i>U. minor</i> ($G_{1,2}$)
Post-burn [F]	.206	.450	.243	.190
Pioneer [P]	.206	.450	.243	.190
Building [B]	.206	.450	.243	.190
Mature [M]	.375	.000	.300	.000
Degenerate [D]	.367	.022	.296	.012

Population growth over an m -year cycle is given by the dominant eigenvalue, $\lambda^{(A)}$, of the product matrix \mathbf{A} . The mean annual growth rate is then given by:

$$= (\lambda^{(A)})^{\frac{1}{m}} \quad (1)$$

Under a constant fire return interval the population converges to a stable size distribution. The final estimation of population growth rate is calculated from the product matrix $[\mathbf{A}]$, as the T th root of the lambda value of $[\mathbf{A}]$, where T is equal to the number of years between fires, or the fire return interval (Hoffmann 1999). Population growth rates were estimated for fire return times of between 1 and 200 yr.

Results

Population size structure following fire

The development of a size-hierarchy of *Ulex* individuals in the heathland is clearly illustrated (Fig. 2). The size of individuals within previously burnt patches of vegetation tends to show a large amount of variation, illustrated by the high coefficient of variation both populations show one year after burning (Table 4). Some individuals will have been produced from seed and others will be re-sprouting plants. Immediately following burning, the size distribution of the *U. gallii* population is composed entirely of seedlings with a stem diameter of 0.5 mm or less. As the populations age one year after burning, 50% of *U. gallii* juveniles attain a stem diameter of 1 - 1.5 mm, whereas, within the *U. minor* population, 75% of individuals remain within the 0 - 0.5 mm size class (Fig. 2). The presence of re-sprouting individuals within both the *U. gallii* and *U. minor* populations can be seen within the larger size classes (> 2.0 - 2.5 mm) one year after fire.

Skewness measures the asymmetry of the distribution and kurtosis is a measure of the degree to which the size

distribution is more 'flat topped' (negative or platykurtosis), or more sharply pointed (positive or leptokurtosis) than a normal distribution (Weiner & Whigham 1988). All the populations are positively skewed and leptokurtic following fire (Fig. 2). Individuals show a broader distributional spread throughout the larger size classes as the populations age. However the mode of the *U. gallii* distribution exists within the 2 - 2.5 mm size class 4 yr after a burning event, whereas, in the case of *U. minor*, the mode is in the 1 - 1.5 mm size class 5 yr after burning and does not reach the 2 - 2.5 mm size category until 7 yr after burning. It is clear that the larger sizes achieved by *U. gallii* reflect, at least in part, a higher growth rate following burning.

Population growth rates of each heathland phase

U. gallii showed higher population growth rates than *U. minor* for each of the heathland phases (Table 5). However patterns of variation among matrices for different phases were very similar for the two *Ulex* species (Table 5). The immediate post-burn matrices had very low population growth rates (< 1) but the growth rates from matrices for other phases were either approximately equal to, or greater than, one. The growth rates were lower in the mature phase because no individuals progress from stage one to stage two beneath a mature *Ulex* canopy. Thus populations represented by the mature matrix decline at the rate of adult mortality. Estimates of λ for the degenerate matrices increased again because individuals enter the population through germination within the gaps created by senescent plants.

Effect of fire frequency on population growth rate

Both *Ulex* species were predicted to decline under annual burning. However as the time between burns increases, the population growth rate initially increases for each species (Fig. 3). The minimum fire return intervals permitting persistence ($\lambda > 1$) were 4 yr for *Ulex*

Table 4. Descriptive statistics for *Ulex* populations in Dorset differing in time elapsed since the last burning event. Size is measured by stem diameter (mm).

Time since last burn	Mean	Mode	Maximum	Minimum	Range	C.V.	Skewness	Kurtosis
<i>U. gallii</i>								
2 months	0.20	0.2	0.2	0.2	0.0	00.00	-	-
1 yr	1.14	1.0	4.0	0.2	3.8	66.83	1.60	2.66
2 yr	2.17	1.5	6.0	0.2	5.8	54.97	1.22	1.95
3 yr	3.05	3.0	6.0	1.0	5.0	33.26	0.50	0.28
4 yr	2.36	2.0	5.0	0.2	4.8	41.22	0.41	0.36
<i>U. minor</i>								
1 yr	0.49	0.2	2.5	0.2	2.3	124.40	2.06	3.04
5 yr	1.98	1.5	4.0	1.0	3.0	32.48	0.80	0.62
7 yr	1.89	2.0	4.0	1.0	3.0	30.43	0.86	2.01

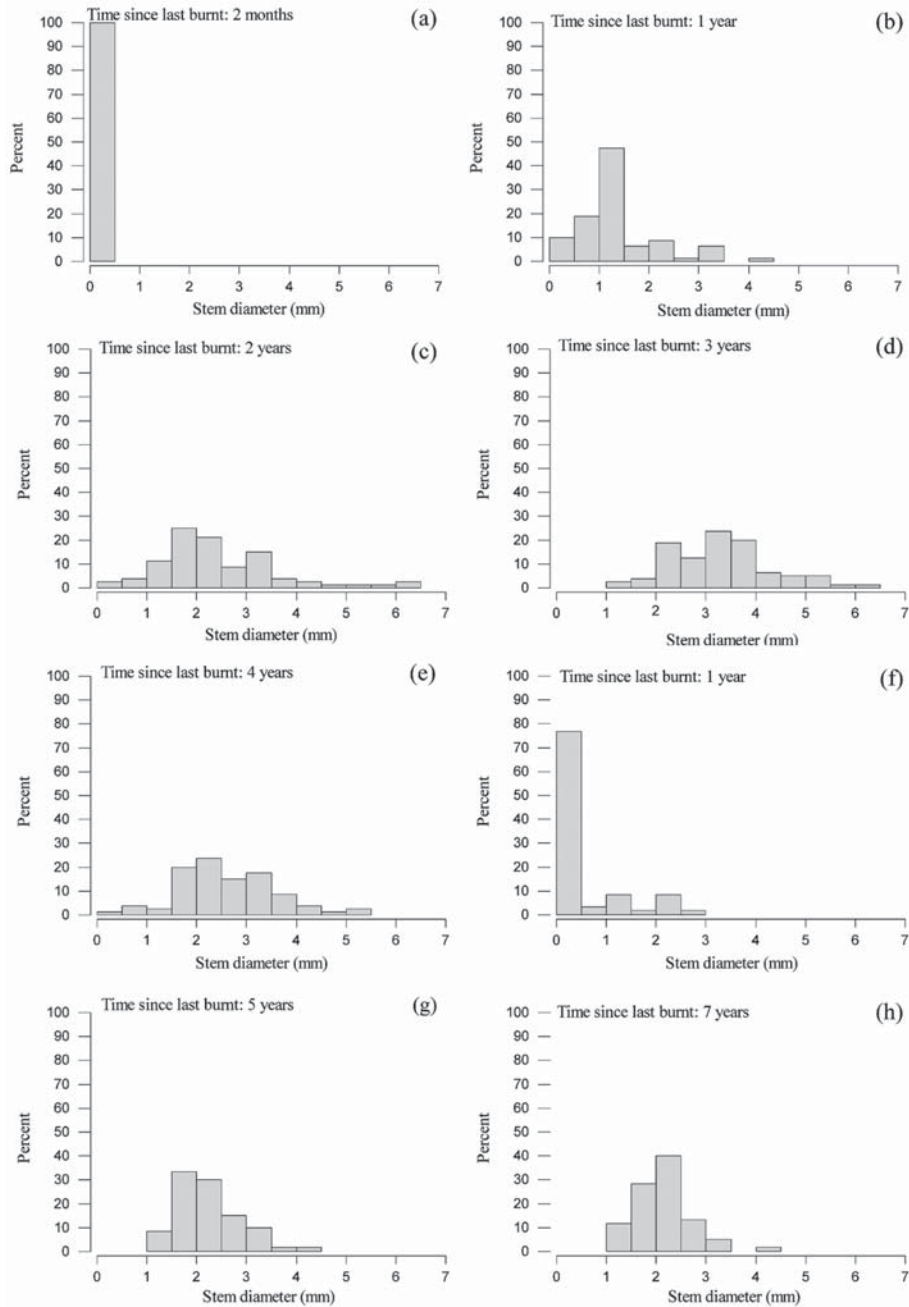


Fig. 2. The size distribution of *Ulex* populations in Dorset measured by stem diameter in relation to the length of time since the last burning event (*U. gallii*: **a-e**; *U. minor*: **f-h**)

minor and 3 yr for *U. gallii*. Maximum population growth rates for both species were achieved at the 16-yr fire return interval. For longer fire return intervals the population growth rates of both *Ulex* species declined and rapidly approached asymptotes (Fig. 3), representing the estimate of population growth rates for the degenerate matrices. This asymptotic rate of population increase was greater for *U. gallii*, as the degenerate matrix for *U. gallii* has the higher growth rate.

Table 5. Estimates of population growth rate (λ) and 95% confidence intervals for *U. gallii* and *U. minor* derived from the patch-specific matrices.

Heathland stage	λ (95% C.I.) <i>Ulex gallii</i>	λ (95% C.I.) <i>Ulex minor</i>
Post-burn	0.45 (0.408-0.492)	0.24 (0.208-0.272)
Pioneer	1.75 (1.697-1.803)	1.59 (1.533-1.647)
Building	1.76 (1.707-1.813)	1.59 (1.532-1.648)
Mature	0.98 (0.892-1.068)	0.97 (0.884-1.056)
Degenerate	1.24 (1.147-1.333)	1.16 (1.071-1.249)

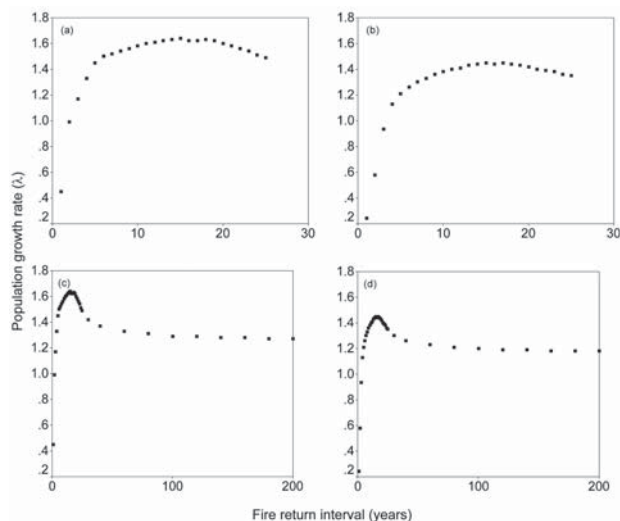


Fig. 3. The effect of fire return interval on population growth rate (λ) as simulated by the stage-specific matrix models for (a) *U. gallii* and (b) *U. minor* showing fire return intervals of up to 25 years and (c) *U. gallii* and (d) *U. minor* showing fire return intervals of up to 200 yr.

Discussion

The nature of population dynamics within a periodic fire environment presented here agrees with published studies of woody plants in savanna systems. Hoffmann (1999) carried out a similar study on woody shrubs in savannas of Brazil and found population growth rates were predicted to decline under annual burning, but, as the time between burns increased, population growth rate increased monotonically for each species. A species-specific critical fire frequency could be identified above which species were unable to persist. The range of fire frequencies permitting positive population growth rates for the *Ulex* species also corresponds with the study of Hoffmann (1999). The population growth rate of both species initially increased as the frequency of fires decreased and reached a maximum at 16 years. However, populations of *U. gallii* could persist (i.e. $\lambda > 1$) at higher frequencies of burning than *U. minor*. This probably reflects the greater re-sprouting probability exhibited by *U. gallii* (34.3%) compared to *U. minor* (5.8%).

Fire return intervals that maximize population growth rates for other shrub species are similar to that observed for the *Ulex* species. Serotinous *Proteaceae* in fynbos vegetation of South Africa show maximum recruitment after summer fires that occur at intervals of roughly 15 years (Bond 1980, 1984; van Wilgen & Viviers 1985). Gill & McMahon (1986) suggested that the minimum interval between fires in populations of the Australian shrub, *Banksia ornata*, should be 16 yr to allow the

population to replace itself, based on seed production, germination and survival of seedlings. Similar optimal fire frequencies may be found in other species of *Banksia*. Enright et al. (1996) used a deterministic model to prescribe a fire management strategy to maximize the finite rate of population increase of *B. hookeriana* and found it to be 15 - 18 yr. In *B. goodii* the optimal inter-fire interval of 16 yr was found to correspond to the maximum position in the seed storage curve (Drechsler et al. 1999). In *B. cuneata*, optimal inter-fire intervals are 15 - 25 yr, which corresponds to the generation time of the species (Burgman & Lamont 1992).

All of these examples relate to serotinous seeders, which are dependent on fire to release seeds. *Ulex* species do not require fire to release or germinate seed. However, it is highly probable that fire increases germination rates in *U. gallii* and *U. minor*, explaining the similarity of the optimal fire return interval with those of serotinous species. Increased germination following fire is well documented in the closely-related *U. europaeus*; temperatures below 100 °C stimulate germination and permit accelerated water intake equivalent to that achieved by scarification of the seed testa (Zabkiewicz & Gaskin 1978). Allchin (1998) found that burning of heath vegetation stimulated germination of *U. gallii* seeds. Hossaert-Palauqui (1980) studied heathlands in Brittany in France and found that elevated temperatures and higher proportions of bare ground after fires caused increased germination of *U. minor*. Other European heathland species, such as *Calluna vulgaris*, also show enhanced germination rates in response to high temperatures (Whittaker & Gimingham 1962).

Hoffmann's (1999) analysis of woody savanna plants suggested that frequent burning reduced the importance of sexual reproduction in maintaining population growth rate, whilst the importance of vegetative reproduction remained high. The relative importance of the two forms of reproduction was not tested systematically within this analysis but it is clear that *U. gallii* performed the better of the two species under high fire frequency due to a higher re-sprouting probability. Sprouting ability can have major impacts on plant populations: turnover of populations is reduced; the effects of disturbance are minimized, and the dependence on seeds for population maintenance might become negligible (Seligman & Henkin 2000; Bond & Midgley 2001). Some species only have the capacity to re-sprout when they are young (Kayll & Gimingham 1965; Hobbs & Mooney 1985), including many leguminous savanna trees. Others show a linear increase in the capacity to re-sprout as they grow larger and older (Stohlgren & Rundel 1986). The re-sprouting capacity of the *Ulex* species was measured within mature heath. It is clear therefore that older *Ulex* plants are capable of regeneration. Further experimentation is required to as-

certain what rate of re-sprouting can be maintained under different fire frequencies. It might be expected that the probability of re-sprouting would decline with more frequent burns as reserves are depleted; the likely impact an increase in the fire return interval at which populations can be maintained.

The relative success of dispersal strategies favoured by each species may vary with fire frequency and thus impact upon the population dynamics of species. Herbivores may also affect post-fire plant survival (Christensen & Muller 1975; Tyler 1996), both spatially and temporally. The effect of herbivory on the *Ulex* species remains little studied. However herbivory is likely to predominate in the first post-burn year when plants are young and tender, having a reduced impact on population growth rate as plants grow older.

It should be noted that the approach we used focuses upon a discrete environmental event (a fire either occurs or it does not). Investigation of the role of a quantitative variable, such as the intensity and seasonal periodicity of fires at different sites would provide further illumination on the population dynamic response. Studies of high intensity fires occurring in heathlands in Brittany (northern France) during July indicate that *U. minor* retains the ability to re-sprout when soil moisture conditions are lower (Gloaguen 1993). Successful recruitment and re-sprouting ability may be substantially influenced by the cumulative effects of repetitive fires. If the effects of a fire are not completely reversed between consecutive fires, fire effects may not only depend on the last fire but also on the interaction between successive fires (Bond & van Wigen 1996). High fire frequency leads to low fuel availability and low fire intensity with a low T_{max} (the maximum temperature attained during burning) at ground level (Auld & O'Connell 1991). This suggests that infrequent fires occurring in mature vegetation will develop higher temperatures than more frequent fires occurring in areas of lower plant biomass. Further field-based studies are necessary to incorporate any potential impacts of these processes into the periodic matrix population model.

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