

# Effects of intraspecific and interspecific density on the demography of a perennial herb, *Sanicula europaea*

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We examined the effects of intraspecific and interspecific competition on demographic processes in the perennial herb *Sanicula europaea* by manipulating the density of neighbouring plants. We followed the response in terms of survival, growth and reproduction and in terms of seedling recruitment. The demographic data from all phases of the life cycle enabled us to assess also the overall effects of treatments on population growth rate ( $\lambda$ ) by transition matrix models. We also decomposed the differences in  $\lambda$  between control and treatments, using life table response experiments (LTRE). To study the effects of competition on recruitment in more detail and to evaluate the role of seed availability, we sowed seeds at different densities with or without vegetation removal.

Vegetative growth and flowering frequency of established individuals was not significantly affected by removal treatments, which suggest no, or a delayed response to released competition. Neighbour removal had no effect on seedling emergence but enhanced recruitment through a higher seedling survival. Conspecific and simultaneous conspecific and heterospecific removal of plants led to an increase in population growth rate ( $\lambda$ ), whereas heterospecific removal alone led to a decrease. Emergence of seedlings and fate of vegetative established individuals contributed most to differences in  $\lambda$  between the control and the different treatments. Seed addition enhanced seedling emergence but, as seedling and juvenile survival were density dependent, densities of established individuals appear not to be seed limited.

In *S. europaea* removal treatments had different effects on established individuals and recruitment. This suggests that studies quantifying the effects of competition over the entire life cycle and performed in a natural environment are necessary to assess the importance of competition in perennial plant populations.

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The importance of competition for plant population dynamics is still largely unknown in spite of much research efforts. On the one hand, experiments such as cutting or killing competing plants, growing plants at various densities or decreasing the effect of competitors by increasing resources have frequently demonstrated effects on individual fitness or population size (Aarssen and Epp 1990, Goldberg and Barton 1992). On the other hand, demonstrating the significance of competitive interactions for plant abundances in nature has

often proved difficult since population densities within the range of densities typical for the community may be driven more strongly by forces external to the community than by density-dependence within the community (Connell 1990, Watkinson 1997). Intraspecific competition is assumed to be more intense than interspecific since individuals of the same species are more likely to share the same resource demands. Some studies (Berendse 1983, Gaston 1999) have demonstrated that competition within a species is more severe than compe-

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tition with other species whereas others have failed to detect such patterns (McCreary et al. 1983, Zammit and Westoby 1988).

If important, competitive interactions will influence population density through demographic rates (Goldberg and Barton 1992). Actually, differences in intensity of competition has been shown to influence a number of demographic parameters; seed set (Stöcklin 1997), flowering frequency (Watkinson and Harper 1978, Clay and Shaw 1981, Humphrey and Pyke 1998, Dyer and Rice 1999), vegetative growth (Bush and Van Auken 1990, Hartnett 1993, Stöcklin 1997, D'Antonio et al. 1998, Dyer and Rice 1999, Foster 1999) and clone expansion (Hartnett 1993). Several studies have also considered the effects of competition on seedling recruitment and establishment (Bush and Van Auken 1990, D'Antonio et al. 1998, Foster 1999, Silva Matos et al. 1999). Hence, the effects of lowered densities and released competition are often evaluated by studying responses of single demographic traits of established plants or by studying recruitment. However, the population level response to competitive release will depend both on the response of the established individuals and on the recruitment of new individuals and studies focusing on population dynamics therefore must take all life stages into account (Aarssen and Epp 1990, Goldberg and Barton 1992, Turnbull et al. 2000). For perennials, it is important to follow plants long enough to detect also delayed responses. Moreover, the extent to which recruitment rates can respond to a released competition will depend on if the sites made available can be saturated with seeds (Louda 1982, Primack and Miao 1992).

In this study, we examine how experimental decreases in intraspecific and interspecific plant density influence individual performance, recruitment and population growth rate in a population of the perennial forest herb *Sanicula europaea* L. Conspecific and heterospecific plant removal was done in a two-factorial design. Leaf removal treatments in established individuals of *S. europaea* result in some effects the same season whereas other effects are detectable only after two years (C. Gustafsson, pers. obs.). Hence, the response to treatments were recorded over a two-year period. In addition, we sowed seeds at various densities in intact plots and in plots in which all plants were removed. We asked the following specific questions: (1) Is the performance of established individuals affected by competition with neighbouring plants? (2) If so, does competitive effect differ between conspecific and heterospecific neighbours? (3) Is recruitment limited by competition? (4) How are recruitment rates influenced by seed availability in the presence or absence of established plants? Based on this information we tried to assess the overall effect of competition on the population dynamics of *S. europaea* in its natural environment.

## Material and methods

### Study species and study site

*Sanicula europaea* occurs throughout most of Europe and in parts of Africa and Asia. In Sweden the distribution of *S. europaea* is more or less restricted to the nemoral and boreonemoral forest. It is rare in most parts of its distribution range but frequent on Öland and Gotland where it is found in forests, shrub land, groves and meadows (Ingelög 1984). *S. europaea* has the ability to reproduce vegetatively by rhizome cleavages. It is evergreen and the leaves are thick, dark green and leathery. It starts flowering at the age of 8–16 years and the seeds have hooks that enable them to disperse by animal furs (Inghe and Tamm 1985). Annual mortality of established plants is low, 1% in some populations (Tamm 1956). However, Tamm (1948) suggested that seedling survival is low due to competition from established plants.

Our competition study was carried out in the vicinity of Jordtorpsåsen in the central part of the island of Öland in the south-east part of Sweden. The area has probably been forested for long and has from 1970 and backwards been used for grazing by cattle. The deciduous forest were the study population is situated is dominated by *Betula verrucosa* Ehrh., *Ulmus glabra* Huds., *Fraxinus excelsior* L., *Corylus avellana* L., *Crataegus* spp. and *Rosa* spp. The field layer is dominated by *S. europaea* with an average abundance of 142 individuals/m<sup>2</sup> (S.D. = 21, N = 16 plots) other frequent herbs are *Hepatica nobilis* Mill., *Fragaria viridis* Duch., *Anemone nemorosa* L., *Anemone ranunculoides* L., *Dentaria bulbifera* L. and *Orchis mascula* L. which one at a time all have lower densities than *S. europaea*. Seed sowings were done at four additional sites in Mittlandsskogen where *S. europaea* is naturally occurring and dominant in the herb layer.

### Methods

To examine the effects of inter- and intra-specific competition we set up a two-factorial experiment. We manipulated densities of *S. europaea* by removing 0 or 50–75% of individuals. The potential competition from other species was manipulated by removing all or no plants. Conspecific and heterospecific removals were crossed with four replicates per combination in 16 plots of sizes from 0.3 to 1.0 m<sup>2</sup>. Plot sizes were selected to include at least 30 randomly chosen *S. europaea* individuals in each experimental plot after the treatment. A margin of 10 cm around each plot was treated to avoid edge effects. Plants were removed in spring 1997. Before the removals the position and status (seedling, vegetative or flowering) of all *S. europaea* individuals was recorded and individuals remaining after the treat-

ment were numbered. Only above-ground parts were removed to avoid damaging remaining plants, only occasionally did removed plants regrow. Demographic data on status, survival, number of leaves and width of largest leaf were collected from each individual in the plots each spring and autumn from autumn 1997 to spring 1999.

In a second experiment, seeds were sown at different densities (0, 20, 50, 125 and 312 seeds per  $25 \times 25$  cm plot) in 1996, 1997 and 1998, at four different sites to examine the effects of seed and seedling densities. Two replicates of each sowing density were established in each year and in each site summing to 120 plots (96 with seeds added). In one of the two replicates all plants were removed before sowing. Emerging seedlings and their subsequent survival were recorded each spring and autumn until 1999. We refer to recruits from seeds as seedlings and established individuals refer to non-seedling individuals being present at the beginning of the experiment.

## Analyses

The effect of treatment on total leaf area (number of leaves  $\times$  (width of largest leaf)<sup>2</sup> (mm<sup>2</sup>)) autumn 1997, 1998 and 1999 and flowering probability of established individuals in 1998 and 1999 were examined with repeated measures ANCOVA. Conspecific removal and heterospecific removal were treated as fixed between subjects factors and time as within subject factor. Initial size (1997) and flowering (1997), respectively, were used as covariates.

The effects of treatment on recruitment in 1998 and 1999, estimated as number of seedlings per m<sup>2</sup> in plots was analysed with repeated measures ANOVA with conspecific removal and heterospecific removal as fixed between subjects factors and time as within subject factor. Survival of seedlings the first summer (1997, 1998 and 1999), the first winter (1997–1998 and 1998–1999) and the second summer (1998 and 1999) was analysed with repeated measures ANOVA, as above. Seedling survival the first summer for the three experimental years separately, was analysed for density dependence with ANCOVA with conspecific removal and heterospecific removal as independent factors and seedling density as covariate. Each plot mean value served as an observation in these analyses.

Demographic data representing all life-cycle stages were also analysed by transition matrices, to yield estimates of population growth rate ( $\lambda$ ) for each treatment (Caswell 2001). Transitions from the two time-intervals, 1997–1998 and 1998–1999, were pooled before analysis to achieve a larger number of individuals in each class. Individuals were classified according to their size or developmental stage as: seedlings (S); vegetative small (total leaf area  $< 5000$  mm<sup>2</sup>, Vs); vegetative

intermediate ( $5000 \text{ mm}^2 \leq \text{total leaf area} \leq 20000 \text{ mm}^2$ , Vi); vegetative large (total leaf area  $> 20000 \text{ mm}^2$ , V<sub>L</sub>) and flowering (F). We used life table response experiment (LTRE) analysis with a fixed design to analyse how differences in each of the transition rates contribute to the total difference in  $\lambda$  between respective treatment and the control.

The proportion of seeds that emerged as seedlings was examined by general linear models with site and sowing year as random factors and disturbance and seed density (20, 50, 125 and 312) as fixed factors. The proportion of seedlings that survived the first summer and the first winter was examined by similar models but with seed density replaced by the covariate seedling number. Numbers of seedlings and established individuals were log transformed and survival was arcsin square root transformed before the statistical analysis. The general linear models were performed with SAS 6.12 (SAS Institute 1990). Matrix analysis were made according to Caswell (2001) using Matlab 5.3.0 (The MathWorks, Inc. 1999). Other analyses were performed with SYSTAT 5.0 (Wilkinson 1992).

## Result

Of the established individuals, 6% disappeared, died or became dormant during the study. Average size of established individuals or change in total leaf area during the study, were not significantly influenced by treatments (Table 1, Fig. 1). Neither did the treatments have any effect on the flowering frequency of established individuals (Table 1).

There was a trend towards increased seedling emergence after conspecific removal (Table 1) and a significant increase in seedling survival the first summer (Table 2). Seedling survival the first summer was highest at low seedling densities in all three years (1997;  $b = -0.101$ ,  $F_{1,14} = 9.916$ ,  $p = 0.007$ , 1998;  $b = -0.133$ ,  $F_{1,14} = 6.975$ ,  $p = 0.019$ , 1999;  $b = -0.083$ ,  $F_{1,14} = 13.692$ ,  $p = 0.002$ ,  $b$  = partial regression coefficient). The survival of seedlings the first winter and the second summer was not affected by the treatments (Table 2). When testing each seedling cohort separately, there was however, a negatively density-dependent survival for one of the two cohorts the first winter (1997;  $F_{1,11} = 19.88$ ,  $p = 0.001$ , 1998;  $F_{1,11} = 0.51$ ,  $p = 0.49$ ), for one of the two cohorts the second summer (1997;  $F_{1,11} = 21.65$ ,  $p = 0.001$ , 1998;  $F_{1,11} = 2.838$ ,  $p = 0.126$ ), and for the second winter for the 1997 cohort ( $F_{1,11} = 24.94$ ,  $p = 0.001$ ).

Conspecific removal led to the highest population growth rate, 0.968, followed by 0.953 for the treatment group with both con- and heterospecific removal. The control group had a population growth rate of 0.893 and the lowest value, 0.769, was achieved for the treat-

Table 1. Effects of conspecific and heterospecific removal on size of established plants (autumn 1997, 1998 and 1999), flowering frequency in established plants (1998 and 1999) and seedling emergence (1998 and 1999) in *S. europaea* examined by repeated measures ANCOVA/ANOVA. Initial size (spring 1997) and flowering frequencies (1997), respectively, were used as covariates.

Factors		Size			Flowering frequency			Seedling emergence		
		df	F	P	df	F	P	df	F	P
Between subjects	Conspecific removal	1	0.06	0.80	1	0.29	0.60	1	3.54	0.06
	Heterospecific removal	1	0.56	0.82	1	0.09	0.77	1	0.69	0.42
	Con- × hetero-specific removal	1	0.24	0.63	1	0.02	0.88	1	0.23	0.64
	Initial size/flowering frequency	1	3.97	0.07	1	3.43	0.09			
	Error	11			11			12		
Within subjects	Time	2	0.33	0.72	1	0.06	0.78	1	1.76	0.21
	Time × conspecific removal	2	0.39	0.68	1	0.02	0.89	1	0.14	0.71
	Time × heterospecific removal	2	0.13	0.88	1	1.13	0.31	1	0.11	0.74
	Time × con- × hetero-specific removal	2	0.67	0.52	1	0.12	0.73	1	0.12	0.74
	Time × initial size/flowering frequency	2	0.36	0.70	1	0.81	0.39			
	Error	22			11			12		

ment group with heterospecific removal (for transition rates see the Appendix). LTRE analysis revealed that the higher  $\lambda$  for the conspecific removal treatment compared to the control, was mainly due to an increased survival and growth of vegetative individuals of all three vegetative size classes (Table 3). In flowering individuals increased seedling production contributed to the positive effect of the treatment whereas the probabilities to remain large and flowering decreased after conspecific removal. The increase in  $\lambda$  for the group with both con- and hetero specific removal compared to control was mainly due to an increased seedling production in flowering individuals, but also due to an increased probability of vegetative individuals to become flowering. The low  $\lambda$  for the heterospecific removal compared to control was due to a poorer performance of flowering individuals.

In the seed sowing experiment the proportion of seeds emerging as seedlings was influenced by sowing density, site and the interaction of site × year but not by the all plant removal treatment (Table 4). In sowing

plots with zero seeds added,  $2.042 \pm 0.57$  (mean  $\pm$  S.E.) seedlings emerged which serve as an estimate of the recruitment from the natural seed rain. Emergence rates decreased with increasing number of sown seeds (Fig. 2). The survival of seedlings the first summer was influenced by seedling density, sowing year and the interaction site × sowing year (Table 5). High seedling densities in the spring were associated with a lower survival the first summer. The all plant removal treatment did not have any significant effect on seedling emergence or first summer survival (Table 5). Seedling survival the first winter was not related to the seedling density in autumn but varied between sites (Table 5).

## Discussion

For *Sanicula europaea* the results suggest that competition is not important to the performance of established plants in this system. Vegetative growth and flowering frequency of established individuals was not affected by removal of conspecific or heterospecific neighbours. This is concurrent with results for the dwarf-shrub *Erica multiflora* (Vilà and Lloret 1996) and the rhizomatous *Phragmites australis* (Ekstam 1995) where released competition did not affect growth or survival. However, reduced competition have lead to increased reproductive allocation in other species (Vilà et al. 1994, Humphrey and Pyke 1998, Dyer and Rice 1999). LTRE analysis revealed that effects on established plants due to removal treatments, contributed to differences in  $\lambda$  compared to the control. Conspecific and simultaneous conspecific and heterospecific removal lead to changed life cycle transition rates for vegetative established plants that contributed to an increase in  $\lambda$ . While differences in the performance of flowering individuals contributed most to the lower  $\lambda$  for the heterospecific removal compared to control.

There was only a tendency of enhanced seedling emergence as intra-specific competition decreased

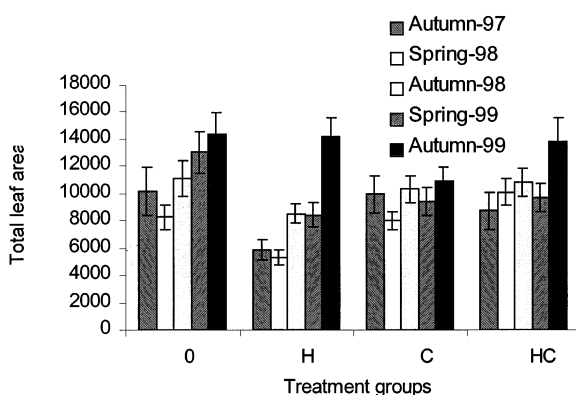


Fig. 1. Mean total leaf area ( $\pm$  SE) of established individuals of *S. europaea* at five occasions after four different neighbour removal treatments (0 = control, H = heterospecific removal, C = conspecific removal, HC = hetero- and con-specific removal) in spring 1997.

Table 2. The effects of conspecific and heterospecific removal on survival of *S. europaea* seedling cohorts during the first summer (1997, 1998 and 1999), during the first winter (1997–1998 and 1998–1999), and during the second summer (1998 and 1999), examined by repeated measures ANOVA.

Factors		First summer survival			First winter survival			Second summer survival		
		df	F	P	df	F	P	df	F	P
Between subjects	Conspecific removal	1	4.90	0.047	1	0.05	0.82	1	0.38	0.55
	Heterospecific removal	1	0.22	0.64	1	0.15	0.71	1	0.15	0.70
	Con- × hetero-specific removal	1	0.68	0.44	1	0.35	0.56	1	0.17	0.70
	Error	12			12			11		
Within subjects	Time	2	8.54	0.002	1	15.9	0.001	1	0.15	0.71
	Time × conspecific removal	2	1.45	0.26	1	0.24	0.63	1	0.17	0.70
	Time × heterospecific removal	2	3.04	0.067	1	0.46	0.51	1	2.00	0.19
	Time × con- × hetero-specific removal	2	0.53	0.59	1	1.33	0.27	1	0.37	0.55
	Error	24			12			11		

Table 3. Contributions by different transition rates to differences in  $\lambda$  between the control and the different removal treatments examined by LTRE analysis. Transitions are indexed as in the method section.

Transition	Conspecific removal	Heterospecific removal	Conspecific + heterospecific removal
S–S	0	0	0
S–Vs	0.004	–0.004	–0.002
S–Vi	–0.008	–0.005	–0.010
S–Vl	0	0	0
S–F	0	0	0
S–total	–0.004	–0.009	–0.012
Vs–S	0	0	0
Vs–Vs	–0.006	–0.015	–0.003
Vs–Vi	0.037	0.021	0.002
Vs–Vl	–0.010	–0.012	–0.010
Vs–F	0.005	0.004	0.033
Vs–total	0.026	0.002	0.022
Vi–S	0	0	0
Vi–Vs	–0.042	–0.007	–0.028
Vi–Vi	0.049	–0.004	–0.055
Vi–Vl	0.041	0.021	0.036
Vi–F	–0.023	–0.013	0.048
Vi–total	0.025	–0.003	0.001
Vl–S	0	0	0
Vl–Vs	–0.010	–0.013	–0.003
Vl–Vi	0.050	–0.016	0.015
Vl–Vl	0.012	0.034	–0.002
Vl–F	–0.032	0.023	0.008
Vl–total	0.020	0.028	0.018
F–S	0.036	–0.005	0.043
F–Vs	0.009	0.027	0.016
F–Vi	0.011	–0.078	0.022
F–Vl	–0.028	–0.057	–0.025
F–F	–0.020	–0.022	–0.025
F–total	0.008	–0.135	0.031
Total effect of treatment	0.075	–0.121	0.060

whereas inter-specific removal had no effect. Moreover, removal of all plants did not influence seedling emergence after sowing. This indicates that neighbouring established plants do not strongly suppress recruitment. However, competition may also influence recruitment through effects on seedling and juvenile survival. In this study, seedling survival was significantly enhanced by conspecific neighbour removal the first summer, but no effects of heterospecific removal or on subsequent seedling survival was observed. For

all time census periods in the removal experiment, seedling survival decreased with increased initial number of seedlings suggesting that seedling density is important for seedling establishment. Moreover, seedling emergence and early survival in the seed sowing experiment was negatively affected by seed and seedling densities. Our results thus indicate that seedlings of *S. europaea* are strongly affected by neighbouring seedlings whereas the effects of neighbouring established plants are weaker.

Table 4. Effects of site, experimental year, all plant removal treatment and number of sown seeds on the proportion of seeds emerging as seedlings in *S. europaea* examined by a general linear model. Fit of the model;  $F_{32,62} = 3.54$ ,  $p = 0.0001$ .

Source of variation	df	Type III mean square	F	P
Site	3	0.890	6.230	0.028
Number of seeds	3	0.174	8.058	0.016
All plant removal	1	0.014	1.437	0.353
Sowing year	2	0.352	3.801	0.189
Number of seeds $\times$ all plant removal	3	0.054	1.501	0.307
Number of seeds $\times$ sowing year	6	0.022	0.601	0.724
Site $\times$ sowing year	6	0.143	3.105	0.010
All plant removal $\times$ sowing year	2	0.010	0.277	0.767
All plant removal $\times$ sowing year $\times$ number of seeds	6	0.036	0.780	0.589
Error	62	0.046		

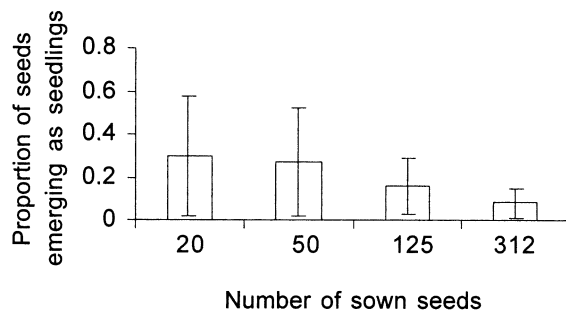


Fig. 2. The proportion of *S. europaea* seeds emerging as seedlings, calculated as Number of seedlings/Number of sown seeds  $\pm$  SD, the spring after sowing for four different seed densities. Pooled data from three experimental years 1997, 1998 and 1999.

The results from the seed sowing experiment where seedling number increased with seed number further indicate that recruitment is seed limited. This implies that if conditions for recruitment are improved by competitive release the population will be able to reproduce only to the extent that seeds are available. However, the fact that site and year influenced seedling emergence and first summer survival suggests also that site specific factors and climatic variation between years

are important and that the relative importance of seed availability vary. This is in agreement with earlier studies with this species (Inghe and Tamm 1985), as our experimental results are concurrent with their interpretation of long term data, that competition from other plants together with lack of seed producing individuals are causes of low seedling establishment in *S. europaea*. Although this study was not designed to assess the mechanisms of competition, it seems probable that competition for light should be important in the rich closed forests where the study populations occurred.

Taken together the results with *S. europaea* suggest that the effects of relaxed competition are mainly observed in terms of an enhanced recruitment whereas the response of established individuals is significant. This points at the importance of including all life-cycle stages when assessing the effects of manipulations in perennial plants. We also integrated information on the performance of established individuals and recruitment in demographic models to assess population growth rates. Although population growth rate was highest in plots with removal of *S. europaea* alone the results were inconclusive. Since all potential effects were included in this study and only very moderate effects of competition were demonstrated, we conclude that the overall importance of competition for *S. europaea* in the studied system is small.

Table 5. Effects of site, experimental year and all plant removal treatment on proportion of seedlings surviving the first summer and the first winter examined by a general linear model where initial number of seedlings was used as covariate. Fit of the model for first summer survival;  $F_{15,73} = 7.43$ ,  $p = 0.0001$ , and for first winter survival;  $F_{10,52} = 3.97$ ,  $p = 0.0005$ .

Source of variation	First summer survival				First winter survival			
	df	Type III mean square	F	P	df	Type III mean square	F	P
Site	3	0.383	1.852	0.236	3	1.150	9.719	0.038
All plant removal	1	0.919	8.224	0.098	1	0.078	0.174	0.749
Sowing year	2	2.602	11.57	0.017	1	1.051	2.871	0.333
Site $\times$ sowing year	6	0.212	2.430	0.034	3	0.117	0.835	0.481
Sowing year $\times$ all plant removal	2	0.112	1.290	0.281	1	0.450	3.206	0.079
Initial number of seedlings	1	0.733	8.416	0.005	1	0.019	0.132	0.717
Error	73	0.087			52	0.141		

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Appendix. Transition probabilities of five classes of *Sanicula europaea* individuals for four plant removal categories. Data are pooled for two time intervals, 1997–1998 and 1998–1999. Each matrix contains the probabilities that individuals in one class year  $t$  (columns in the matrix) will enter a class year  $t + 1$  (rows in the matrix). The first row gives the number of individuals from which probabilities are calculated.

Removals		Seedlings	Vegetative small	Vegetative intermediate	Vegetative large	Flowering
Control	Number	32	69	51	13	20
	Seedlings	0	0	0	0	0.762
	Veg. small	0.125	0.348	0.216	0.077	0
	Veg. Interm.	0.031	0.304	0.490	0.077	0.400
	Veg. large	0	0.101	0.078	0.231	0.350
	Flowering	0	0	0.118	0.462	0.200
Conspecific	Number	48	55	77	10	12
	Seedlings	0	0	0	0	2.750
	Veg. small	0.146	0.309	0.104	0	0.083
	Veg. Interm.	0	0.491	0.597	0.400	0.483
	Veg. large	0	0.054	0.156	0.300	0.167
	Flowering	0	0.018	0.078	0.300	0.083
Heterospecific	Number	32	100	77	5	13
	Seedlings	0	0	0	0	0.571
	Veg. small	0.094	0.270	0.195	0	0.154
	Veg. Interm.	0	0.390	0.481	0	0.039
	Veg. large	0	0.050	0.130	0.400	0.079
	Flowering	0	0.020	0.078	0.600	0.077
Conspecific + heterospecific	Number	111	67	60	18	29
	Seedlings	0	0	0	0	2.552
	Veg. small	0.117	0.328	0.117	0.055	0.103
	Veg. Interm.	0.001	0.313	0.328	0.167	0.517
	Veg. large	0	0.060	0.167	0.222	0.241
	Flowering	0	0.119	0.223	0.500	0.103