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Analysis of interspecific competition in perennial plants using Life Table Response Experiments

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Abstract

The impact of interspecific competition is usually measured by its effect upon plant growth, neglecting impacts upon other stages of the life cycle such as fecundity which have a direct influence upon individual fitness and the asymptotic population growth rate of a population (λ). We used parameterized matrix models for three perennial plant species grown with and without interspecific competition to illustrate how the methodology of Life Table Response Experiments (LTRE) can be used to link any change in population dynamics to changes in any part of the life cycle. Plants were herbaceous grassland species grown for two years in a field experiment at Rothamsted Experimental Station, England. Interspecific competition reduced λ by over 90% in all species. Survival and growth were slightly affected by competition whereas plant fecundity was greatly reduced. Nearly all of the observed difference in λ between the competition treatments was explained by the fecundity terms, and more precisely by a large difference in the number of seeds, and a high sensitivity of λ to the germination rate. Whereas most competition studies focus on the measurement of change in individual fitness, our study illustrates how informative it is to take account not only of the effect of competition upon vital rates but also of how different vital rates affect population growth rate.

Introduction

Interspecific competition plays a dominant role in structuring plant communities and studies of its effects are certainly the most common kind of experiment conducted in plant ecology (Gibson et al. 1999; Freckleton and Watkinson 2000). Studies of annual plants have demonstrated that a mechanistic understanding of community dynamics can be obtained from competition models based upon demographic variables for individual species (Rees et al. 1996). Extending such studies to perennial plants is difficult because of their prolonged life cycles, and consequently most studies of competition among perennials are based upon measures of performance during only one growing season (Aarssen and Keogh 2002). Moreover, these studies mainly analyse competition effects in terms of growth reduction and therefore neglect potentially important components of individual fitness on population dynamics, such as survival or fecundity (Aarssen and Keogh 2002). If long-term experiments based on multiple fitness trait measurements through time are clearly needed in competition studies (Connolly et al. 1990), it is also crucial to understand how any change in individual fitness induced by the presence of competitors affects the dynamics of the species. In this paper we emphasize the usefulness of an existing method for this purpose, that is highly suited to the demographic analysis of competition experiments in plant species, but which appears not to have been used in this way before.

Life-Table Response Experiments (LTRE) are a powerful tool for investigating how populations respond to induced or natural environmental change (Caswell 1989, 1996, 2001). Observed changes in population growth rates are decomposed into contributions made by each of the vital rates which define the species life-cycle. The magnitude of the contribution made by a particular vital rate depends upon both its observed variation and the effect of this variation on population growth rate. LTRE analyses have been widely used for a variety of purposes in the last few years, both in fixed designs where one or more factors are manipulated, or in random designs where demographic parameters are analysed in natural unmanipulated conditions over time or space (Horvitz et al. 1997; Guàrdia et al. 2000; Miriti et al. 2001; Kiviniemi 2002). Fixed designs have been used in animal populations to investigate the demographic consequences of pollutant exposure (Levin et al. 1996; Hansen et al. 1999), food manipulation (Walls et al. 1991; Dobson and Oli 2001) or density manipulation (Oli et al. 2001). In plants, LTRE analyses have recently been used to assess the demographic consequences of pollinator availability or herbivory (Rydgren et al. 2001; Garcia and Ehrlen 2002), nitrogen deposition (Gotelli and Ellison 2002), fire management (Rydgren and Okland 2002), or allocation to sexual or clonal reproduction (Rydgren and Okland 2002). We are aware of only a single study (Miriti et al. 2001) that has applied the method to the demographic effects of plant competition, though this was not in the context of a manipulative experiment. Here, we demonstrate the relevance of LTRE analysis to the analysis of interspecific competition experiments by applying this method to three perennial species, *Achillea millefolium* L. (Asteraceae), *Anthoxanthum odoratum* L. (Poaceae) and *Trifolium pratense* L. (Fabaceae). More generally, we discuss the relevance of Life-Table Response Experiment analyses to the study of the impact of interspecific competition in plant species.

Methods

The context of the Park Grass Experiment

The Park Grass Experiment (PGE) was set up at Rothamsted Experimental Station in Hertfordshire (England) between 1856 and 1872 when an uniform hay-meadow was divided into 20 plots to investigate the effect of different fertilizer regimes on the production of a grassland community (Williams 1978). Following the application of fertilizers, a rapid change in species composition occurred in each plot. The community reached its equilibrium at the beginning of the XIXth century when the relative abundance of the three main components of grasses / legumes and other species stabilized (Silvertown 1980). Nevertheless, the constituent species changed over time within each component. A 60-year record based on the presence/absence of species in the different plots of the PGE showed that species could be classified according to four types of dynamics (Dodd et al. 1995), *i.e.,* (1) increasing species, (2) decreasing species, (3) species showing no secular trend, and (4) 'outbreak' species showing an outbreak in their distribution by increasing first and then decreasing over the plots. Dodd et al. (1995) suggested that differences in species dynamics were best explained by differences in mating system and differences in ruderalness between species. The role of these two life-history traits on the species dynamics was further investigated by Silvertown et al (2002), using standard methods (ANOVA). In this paper, we re-analysed a subset of the data from Silvertown et al (2002) using LTRE analysis.

Competition experiments

Two experiments with 23 grassland species were conducted at Rothamsted Experimental Station to simulate as closely as possible the conditions undergone by species growing in the PGE. Compared to Silvertown et al (2002), results for only three of the species are reported in this paper: the remaining 20 species did not flower in both treatments during the two-years of the experiment and there were therefore insufficient data for full LTRE analysis of the whole life cycle. The three species analysed were: *Achillea millefolium* (Asteraceae), *Anthoxanthum odoratum* (Poaceae) and *Trifolium pratense* (Fabaceae).

The first experiment was conducted at Long Hoos, a field on the Rothamsted Experimental station, to measure the germination rate g for each species in treatments with and without competition. The experiment was set up in four randomized complete blocks of two competition treatments with 23 species each, giving a total of 184 plots. The competition treatment was pre-sown with *Lolium multiflorum* at a rate of 32 g/m^{-2} to provide a grass canopy similar in height to that occuring at the time of seed germination in the

PGE. Competition-free plots were weeded regularly and therefore lacked any interspecific competition. For both experiments, seeds of each species were collected in the PGE in 1997 or 1998. Each target species was separately sown at a rate of 200 seeds/plot into the central 0.1 m × 0.1 m core of 0.5 m × 0.5 m field plots. Seed germination was recorded at regular intervals from February – May 1999. For each species, the germination rate *g* was calculated as the total number of seeds that had germinated in May 1999 over the 800 seeds that had been sown in each treatment.

The second experiment was located in Sawyer's field, adjacent to Long Hoos, on Rothamsted Experimental Station. In this experiment, post-germination demographic parameters for the emerged seed-to-flowering phase of the life cycle were measured over a two-year period from the winter 1997-1998 until August 1999. The experiment contained five randomized blocks and two competition treatments, with target species allocated separate plots. Half the plots in each block, chosen at random, were allocated to the competition treatment and were pre-sown with *Festuca rubra* in September 1997. In each block, one-competition free plot and one containing *F. rubra* were randomly allocated to each of the 23 species. Germinated seeds of each species were raised and then twenty-five of them were planted per block and per treatment during the winter 1997-1998 in 1 m × 1 m plots on a regular 5*5 grid. To remove edge effects, survival and fecundity data were analysed only for the nine plants located in the center of each plot. The number of seeds produced by each plant was counted in August 1998 and in August 1999.

In this study, the use of two different competitors was motivated by the attempt to simulate as closely as possible the conditions that prevail in the PGE. As *L. multiflorum* is a fast-growing species, a canopy similar in height and structure could be created at the time of seed germination. For later stages of the life-cycle, *F. rubra* was preferred to *L. multiflorum*, as this species is the most abundant species in most of the plots in the PGE, and therefore one of the main competitors encountered by the target species.

Matrix construction

Germination rates from the first experiment and individual data on plant size, survival and fecundity collected in the second experiment over a 24 month period were used to construct three-stage matrix models for *A. millefolium* and *T. pratense* (Figure 1a) and a two-stage matrix model for *A. odoratum* (Figure 1b). As our aim was to compare the response of each species to competition, the same life-cycle had to be defined for both competition treatments (i.e., with/without interspecific competition). The three-stage models included 1) a rosette stage (vegetative plants), 2) small flowering plants and 3) large flowering plants (Figure 1a). To ensure maximum sample sizes in the flowering classes, the limit between the two flowering stages was defined as the mean diameter of the first-year flowering plants in the competition treatment in *T. pratense*, and as the mean diameter of the first-year flowering plants over the two treatments for *A. millefolium*. In *A. odoratum*, there was no size overlap of the flowering plants between the two treatments. For this reason, only one class of reproductive plants could be defined (Figure 1b).

The projection model is given by: $n_{t+1} = An_t$ where n_t and n_{t+1} are the vectors whose elements n_i (t) correspond to the number of individuals in stage *i* at time *t* and time *t+1*, respectively, and A is a non-negative square matrix whose elements a_{ij} called hereafter the upper-level vital rates, are the numbers of stage *i* individuals produced per stage *j* individual over one time step (Caswell 1989). For each species, transition probabilities a_{ij} were calculated both in the competition and in the competition-free treatment over a one-year interval. Each transition probability from year *t* to year *t+1* was expressed as the product of the survival probability of stage *j*, s_j, the flowering probability of stage *j*, pf_j, and the probability of moving from stage *j* to stage i, g_{ij}. The fecundity of each flowering stage, *i.e.,* the mean number of new individuals (either rosettes, small or large flowering plants) produced by a given class of flowering plants was defined as the product of the mean number of seeds of each class n_s averaged over 1998 and 1999, times the germination rate *g*, calculated in the first experiment, times the survival probability of the emerged seeds s_0, estimated from the winter 1997-1998 until August 1998, times the probability of a surviving seed growing to stage *i*, p_{i0}. We assumed that the germination rate *g* and the fates of the surviving germinated seeds p_{i0} were independent of the stage of the flowering plants that had produced them. Some plants flowered in their first year. Thus, except for a_{i1}, each a_{ij} corresponds to the sum of a term describing the transition of plants being in stage *j* at time *t* to stage *i* at time *t+1*, and a fecundity term describing the

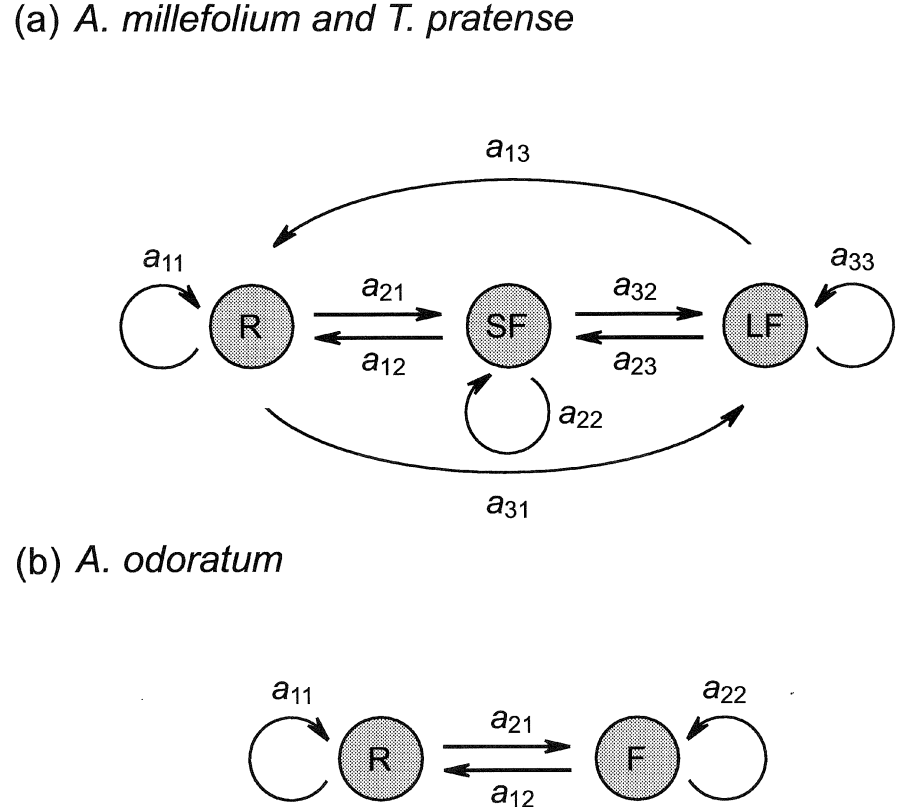

Figure 1. Life-cycle graph of a) *A. millefolium* and *T. pratense*, b) *A. odoratum*. Circles correspond to plant stages and arrows represent the possible transitions between stages. For the three-stage life-cycle (*A. millefolium* and *T. pratense*), transition probabilities between rosettes (R), small flowering plants (SF) and large flowering plants (LF) are defined as a function of the survival probability (s_0, s_1, s_2, s_3) of germinated seeds, rosettes, small flowers and large flowers, respectively, the flowering probability calculated conditional to the survival (pf_1, pf_2, pf_3) of rosettes, small flowers and large flowers, respectively, and the probability to grow from stage j to stage i, g_{ij}. The fecundity term is calculated as the product of the mean number of germinated seeds per flowering plant, ns_2 for small flowers and ns_3 for large flowers, by the germination rate g, by the survival of the emerged seeds s_0, by the probability of an emerged seed to enter the i-stage, p_{i0}. The same conventions are used for the 2-stage life-cycle of *A. odoratum* to calculate transition probabilities between rosettes (R) and flowering plants (F).

production by flowering plants in stage j at time t, of new individuals entering the stage i at time $t+1$. Hereafter, S_j, pf_j, g_{ij}, n_s, g, S_0 and P_{i0} will be referred to as lower-level vital rates.

According to these definitions, the a_{ij} in the three-stage life-cycle for *A. millefolium* and *T. pratense*, and the a_{ij} in the two-stage life-cycle for *A. odoratum* were expressed in terms of lower-level vital rates x_k as described in Table 1.

LTRE analysis

For each species, the asymptotic growth rate of the population λ was calculated as the dominant eigenvalue of the matrix A_{NC} in the treatment without competition and of the matrix A_C in the treatment with competition. The effect of competition was

Table 1. Expression of the vital rates a_{ij} in terms of the lower-level vital rates. Subscript numbers 1, 2 and 3 refer to rosettes, small flowering plants and large flowering plants, respectively. S_j represents the survival probability of stage j, pf_j the flowering probability of stage j, and g_{ij} the probability of moving from stage j to stage i over the one-year interval.

a_{ij}	*A. millefolium* and *T. pratense*	*A. odoratum*
a_{11}	$s_1*(1-pf_1)$	$s_1*(1-pf_1)$
a_{12}	$s_2*(1-pf_2) + ns_2*g*s_0*p_{10}$	$s_2*(1-pf_2) + ns_2*g*s_0*p_{10}$
a_{13}	$s_3*(1-pf_3) + ns_3*g*s_0*p_{10}$	–
a_{21}	$s_1*pf_1*g_{21}$	s_1*pf_1
a_{22}	$s_2*pf_2*(1-g_{32}) + ns_2*g*s_0*p_{20}$	$s_2*pf_2 + ns_2*g*s_0*p_{20}$
a_{23}	$s_3*pf_3*g_{23} + ns_3*g*s_0*p_{20}$	–
a_{31}	$s_1*pf_1*g_{31}$	–
a_{32}	$s_3*pf_3*g_{32} + ns_2*g*s_0*p_{20}$	–
a_{33}	$s_3*pf_3*(1-g_{23}) + ns_3*g*s_0*p_{30}$	–

analysed by LTRE analysis for a fixed design in terms of lower-level vital rates, x_k (Caswell 2001). For each species, the difference of asymptotic growth rate between the treatment without competition, λ_{NC}, and the treatment with competition, λ_C, was approximated by using a first-order Taylor series expansion:

$$\lambda_{NC} - \lambda_C \approx \sum_{i,j} \sum_{k} \left(x_k^{NC} - x_k^C\right) \frac{\partial \lambda}{\partial a_{ij}} \frac{\partial a_{ij}}{\partial x_k}$$

where the first derivative term in the equation is called the sensitivity of λ to a_{ij}. Each term in the summation is the product of two quantities: 1) the difference of lower-level vital rates between the two treatments, 2) the product of the derivative terms which translates any change in vital rates in terms of change in asymptotic growth rate. Both derivative terms were evaluated at the arithmetic mean matrix M defined as:

$$M = \left(A_{NC} + A_C\right)/2$$

The difference in λ can also be expressed in terms of the contributions of the upper-level vital rates a_{ij} to first order (Caswell 2001) as:

$$\lambda_{NC} - \lambda_C \approx \sum_{i,j} \left(a_{ij}^{NC} - a_{ij}^C\right) \frac{\partial \lambda}{\partial a_{ij}}$$

In our study, most a_{ij} are a combination of two different terms, *i.e.,* the fate of existing individuals present at time *t*, and the arrival at time *t+1* of newly individuals that were produced by flowering plants at time *t*. This complex structure arising from the life-cycle makes it difficult to interpret results of the LTRE analysis for upper-level vital rates, in terms of biological processes. In that respect, LTRE results for the lower-level vital rates were more informative and only these are reported. All matrix modelling was performed using MATLAB, Version 5.3 (The MathWorks, Inc., Natick, MA, USA).

Results

Effect of competition on the asymptotic growth rate

The competition treatment reduced the asymptotic growth rate λ in *T. pratense*, *A. odoratum* and *A. millefolium* by 91%, 95% and 99% respectively. Values of λ with and without competition were 3.95 and 46.13 for *T. pratense*; 17.2 and 320.3 for *A. odoratum*; 2.31 and 248 for *A. millefolium*.

Contribution of the lower-level vital rates

Accuracy of the first-order approximation – The contribution of the x_k to the observed difference of λ between the two treatments was assessed by using a first-order Taylor series expansion. The 1st order approximation was quite accurate for the three species as it predicted a difference within 2%, 6% and 10% of the observed difference of λ between the two treatments, for *A. odoratum*, *T. pratense* and *A. millefolium*, respectively.

Differences of lower-level vital rates between treatments – Values of lower-level vital rates for each species and each treatment are presented in Table 2. For each lower-level vital rates, the difference of values between the treatment with competition and the treatment without competition is shown in Table 3. The survival of plants (s_1, s_2, s_3) was very high in both treatments for all three species. For instance, whatever the treatment, none of the plants of *A. millefolium* and *A. odoratum* died during the 2-year experiment. The competition treatment affected only the survival of plants in *T. pratense*: the survival of rosettes (s_1) was reduced by 25% when plants were grown in competition. In contrast, the survival of small flowering plants in the competition-free treatment was slightly less than in the competition treatment, as one small flowering plant died during the 1998-1999 period in the competition-free treatment.

In both *A. millefolium* and *T. pratense*, rosettes that flowered the following year had a lower probability to become small flowering plants (g_{21}) than large flowering plants (g_1). Nevertheless, growth's response of plants to competition was slightly different between *A. millefolium* and *T. pratense*. In *T. pratense*, rosettes that flowered the following year had a larger probability becoming small flowering plants in the treatment with competition compared to the competition-free treatment ($g_{21} = 0.154$ and $g_{21} = 0.000$, respectively, Table 2), whereas small flowering plants were more likely to become large flowering plants the following year in the treatment with competition than in the competition-free treatment ($g_{32} = 1.000$ and $g_{32} = 0.875$, respectively, Table 2). The reverse was observed in *A. millefolium*. In none

Table 2. Values of the lower-level vital rates x_k in the competition-free treatment (NC) and the treatment with competition (C), for *A. millefolium*, *T. pratense* and *A. odoratum*. Subscript numbers 1, 2 and 3 refer to rosettes, small flowering plants and large flowering plants, respectively. S_j represents the survival probability of stage j, pf_j the flowering probability of stage j, and g_{ij} the probability of moving from stage j to stage i over the one-year interval. Sample sizes are indicated in brackets as subscripts.

		A. millefolium		*T. pratense*		*A. odoratum*	
	x_k	NC	C	NC	C	NC	C
Survival	s_1	$1.000_{(6)}$	$1.000_{(31)}$	$1.000_{(4)}$	$0.750_{(28)}$	$1.000_{(3)}$	$1.000_{(32)}$
	s_2	$1.000_{(23)}$	$1.000_{(12)}$	$0.889_{(9)}$	$1.000_{(5)}$	$1.000_{(42)}$	$1.000_{(13)}$
	s_3	$1.000_{(16)}$	$1.000_{(2)}$	$1.000_{(32)}$	$1.000_{(8)}$	–	–
Growth	g_{21}	$0.333_{(6)}$	$0.300_{(20)}$	$0.000_{(4)}$	$0.154_{(13)}$	–	–
	g_{31}	$0.667_{(6)}$	$0.700_{(20)}$	$1.000_{(4)}$	$0.846_{(13)}$	–	–
	g_{32}	$0.652_{(23)}$	$0.400_{(10)}$	$0.875_{(8)}$	$1.000_{(5)}$	–	–
	g_{23}	$0.000_{(16)}$	$0.000_{(2)}$	$0.000_{(32)}$	$0.000_{(8)}$	–	–
Flowering probability	pf_1	$1.000_{(6)}$	$0.645_{(31)}$	$1.000_{(4)}$	$0.619_{(21)}$	$1.000_{(3)}$	$0.844_{(32)}$
	pf_2	$1.000_{(23)}$	$0.833_{(12)}$	$1.000_{(8)}$	$1.000_{(5)}$	$1.000_{(42)}$	$1.000_{(13)}$
	pf_3	$1.000_{(16)}$	$1.000_{(2)}$	$1.000_{(32)}$	$1.000_{(8)}$	–	–
Fecundity	ns_2	$1799_{(33)}$	$583_{(24)}$	$123_{(10)}$	$84_{(7)}$	$918_{(87)}$	$165_{(53)}$
	ns_3	$3399_{(51)}$	$1338_{(22)}$	$820_{(75)}$	$423_{(32)}$	–	–
	g	$0.116_{(800)}$	$0.003_{(800)}$	$0.074_{(800)}$	$0.024_{(800)}$	$0.373_{(800)}$	$0.304_{(800)}$
	s_0	$1.000_{(45)}$	$1.000_{(45)}$	$1.000_{(45)}$	$0.911_{(45)}$	$1.000_{(45)}$	$1.000_{(45)}$
	p_{10}	$0.133_{(45)}$	$0.689_{(45)}$	$0.089_{(45)}$	$0.683_{(41)}$	$0.067_{(45)}$	$0.711_{(45)}$
	p_{20}	$0.511_{(45)}$	$0.267_{(45)}$	$0.200_{(45)}$	$0.122_{(41)}$	$0.933_{(45)}$	$0.289_{(45)}$
	p_{30}	$0.356_{(45)}$	$0.044_{(45)}$	$0.711_{(45)}$	$0.195_{(41)}$	–	–

Table 3. Effect of the competition treatment on the lower-level vital rates x_k. Subscript numbers 1, 2 and 3 refer to rosettes, small flowering plants and large flowering plants, respectively. S_j represents the survival probability of stage j, pf_j the flowering probability of stage j, and g_{ij} the probability of moving from stage j to stage i over the one-year interval. For each lower-level vital rate x_k, d is the difference between the value of x_k in the treatment without competition and the value of x_k in the treatment with competition. For each species, sensitivities s_k of λ to the x_k are calculated at the arithmetic mean matrix over the two treatments.

		A. millefolium		*T. pratense*		*A. odoratum*	
	x_k	d	s_k	d	s_k	d	s_k
Survival	s_1	0	0.154	0.250	0.179	0	0.160
	s_2	0	0.187	−0.111	0.003	0	0.999
	s_3	0	0.995	0	1.192	–	–
Growth	g_{21}	0.033	0.096	−0.154	0.031	–	–
	g_{31}	−0.033	0.180	0.154	0.166	–	–
	g_{32}	0.252	0.416	−0.125	0.218	–	–
	g_{23}	0	0.267	0	0.770	–	–
Flowering probability	pf_1	0.355	0.185	0.381	0.186	0.156	0.173
	pf_2	0.167	0.199	0	0.004	0	0.994
	pf_3	0	0.992	0	1.165	–	–
Fecundity	ns_2	1216	0.020	39	0.006	753	0.207
	ns_3	2061	0.014	397	0.022	–	–
	g	0.113	944	0.050	289	0.069	332
	s_0	0	56	0.089	15	0	112
	p_{10}	−0.556	0.767	−0.594	0.817	−0.644	1.004
	p_{20}	0.244	73	0.078	5	0.644	183
	p_{30}	0.312	137	0.516	29	–	–

of the species, large flowering plants became small flowering plants the year after ($g_{23} = 0.000$).

In all three species, the competition treatment induced a lower flowering probability in the vegetative plants (pf_1) compared to the competition-free treatment. This was also the case for the small flowering plants in *A. millefolium* (pf_2). Plant fecundity was greatly affected by competition. In all three species, the mean number of seeds per flowering plant was much less where plants were grown in competition

with *F. rubra* (Table 2, Table 3). Among all the remaining vital rates (with values bounded by 0 and 1), the probability of a seed becoming a rosette p_{10}, showed the largest difference between the two treatments. This difference was negative for the three species (Table 3). In contrast, the probability of a seed becoming a flowering plant was much larger in the competition-free treatment (p_{20}, p_{30}) than in the treatment with competition. For all three species, the germination rate g was only slightly larger in the competition-free treatment than in the treatment with competition, whereas the survival of germinated seeds s_0 was usually not affected at all by competition.

Contributions of the lower-level vital rates to the difference of λ – The difference in λ between the two treatments was almost entirely due to the contribution of the lower-level vital rates involved in the calculation of the fecundity term, ns_2, ns_3, g, p_{20} and p_{30} (Figure 2a, Figure 2b, Figure 2c). The high contribution of these vital rates was either explained by their high variation among the two treatments and a low sensitivity of λ, as is the case for the number of seeds (ns_2, ns_3), or a small variation among treatments and a large sensitivity of λ, as is the case for the germination rate g (Table 3). The probability of germinated seeds becoming flowering plants (p_{20} and p_{30}) had intermediate values of both variation and sensitivity to λ (Table 3). The contribution pattern of the vital rates was rather similar between species, except that the germination rate made a very low contribution in *A. odoratum* (Figure 2c), compared to what happens in *A. millefolium* and *T. pratense* (Figure 2a, Figure 2b, respectively).

Discussion

Effect of competition on the dynamics of A. millefolium, T. pratense and A. odoratum

Interspecific competition decreased asymptotic growth rates λ in all three species by more than 90%, although estimates remained much higher than the value of unity required for population viability in a deterministic model. Such high values of λ are unlikely to represent what happens in the field, as environmental stochasticity and density-dependence may further reduce asymptotic growth rates in natural conditions. The purpose of this experimental study was to compare species' responses to interspecific competition rather than to predict the demographic behaviour of each species under an unrealistic deterministic model.

As expected, for all species, the competition treatment induced an increase in generation time. When grown in competition, seeds had a higher probability of spending time at the rosette stage before flowering, as shown by the negative difference of p_{10} and the positive difference of p_{20} and p_{30} between the competition-free treatment and the treatment with competition. Moreover, in the competition treatment, rosettes had a lower probability of flowering during the second year of the experiment as shown by the positive difference of pf_1. Such an increase in generation time is a common outcome in competition studies. For all species, competition also greatly reduced the number of seeds produced per flowering plant. In contrast, the survival of plants (s_0, s_1, s_2 and s_3) was not strongly affected by competition in any of the three species.

In our study, nearly all of the observed differences in λ between competition treatments were explained by the high contributions of fecundity terms (ns_2, ns_3, g, p_{20} and p_{30}). The high contribution of the number of seeds was due to its large difference between competition treatments, as the sensitivity of λ to this parameter was small. In contrast, the large contribution of the germination rate g was explained by the high sensitivity of λ to this parameter, as the difference between treatments was relatively small for all three species. Overall, the contribution of the different lower-level vital rates was similar between species. Nevertheless, whereas the germination rate made the largest contribution in *A. millefolium* and *T. pratense*, this was not true for *A. odoratum* for which the number of seeds explained most of the difference in asymptotic growth rates. The high contribution of the number of seeds in *A. odoratum* was explained by the sensitivity of λ to this vital rate being about ten times greater in this species than in *A. millefolium* or *T. pratense*. This difference in contribution pattern among the three species was not an artefact of the difference of life-cycle between *A. odoratum* (life-cycle with two stages) and the two other species (life-cycle with 3 stages) because the same results were obtained when all three species were analysed using a two-stage life-cycle (data not shown).

At this stage, it is rather difficult to assess whether these differences between *A. odoratum* and the two other species can be explained in term of distinct adaptive strategies. Logistical problems make it diffi-

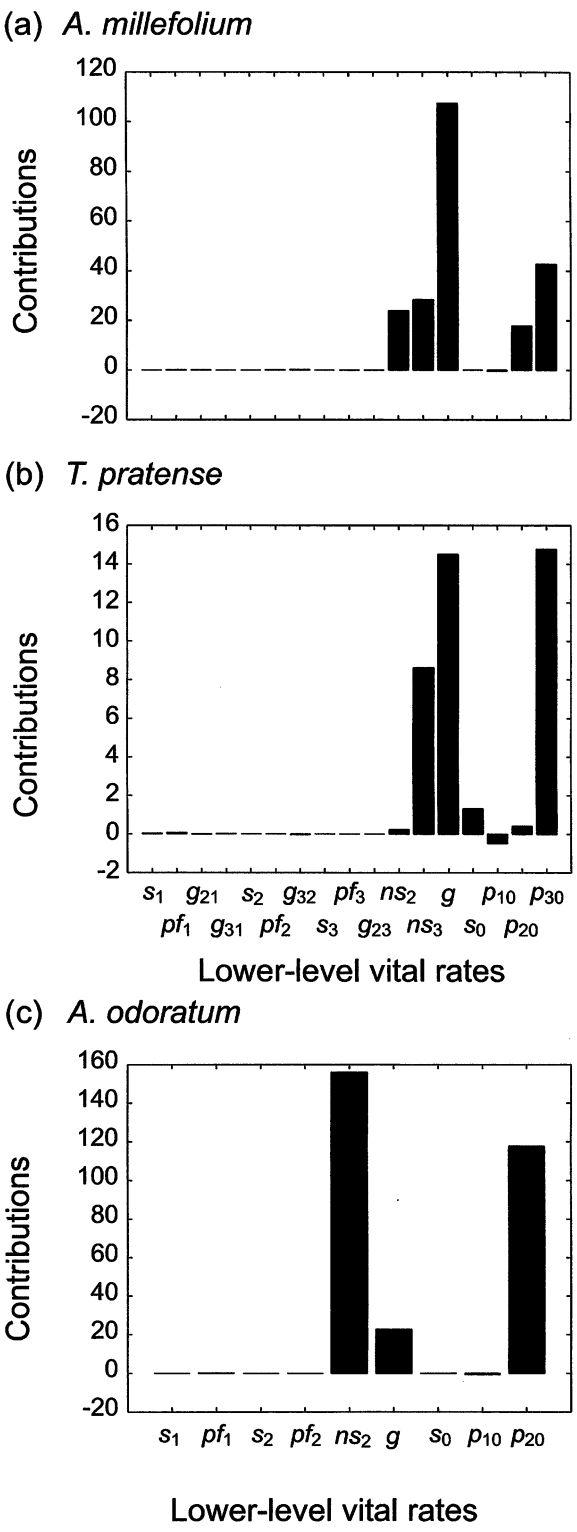

Figure 2. Contribution of the lower-level vital rates x_k to the observed difference of λ between the two competition treatments, for a) *A. millefolium*, b) *T. pratense*, c) *A. odoratum*. Note that there are fewer lower-level vital rates in Figure 2c compared to Figure 2a and b, as the life-cycle of *A. odoratum* includes only two stages.

cult to follow early stages in the life cycle. This creates three potential problems in the interpretation of our results. Firstly, we were unable to incorporate seed dormancy, although it has been described for *A. odoratum* and *T. pratense*. Secondly, seedling mortality occuring between the end of the first experiment and the start of the second experiment may be underestimated. Silvertown et al. (2002) measured the germination rate g in a separate experiment. Post-germiantion lower-vital rates were then estimated in a second experiment by planting seedlings that had reached a reasonable size. This means that the survival of emerged seeds s_0 may be overestimated in both treatments but probably more in the competition treatment if interspecific competition has a stronger effect on seedling survival than intraspecific competition. As λ has a high sensitivity to s_0, our analysis may underestimate the contribution of this lower-vital rate to the difference of λ between the two treatments. Thirdly, by using data from two different experiments, we also assume that there is no carry-over effect of early competition acting on the germination stage on later stages in the life-cycle. These are common problems in competition studies if ones want to work with a reasonable sample size and are not a feature of LTRE analysis.

As already described, out the 23 species described in Silvertown et al. (2002), the present analysis focused on only the three species for which matrix models could be built in both treatments from the 2-years of demographic data. Among the 20 remaining species, some were clearly more affected by competition than the three species investigated in this paper: for instance, plants of *Centaurea nigra* flowered the first year in the competition-free treatment whereas they had still not flowered the second year in the treatment with competition. A longer demographic survey would first allow us to test if a high contribution of the fecundity terms may also explain a change in asymptotic growth rates induced by the competition treatment in species that are highly affected by competition. Second, it would allow us to test wether there is any relationship between species' responses to the competition treatment assessed through LTRE and the different types of species dynamics observed in the PGE.

Usefulness of LTRE analysis in studies of competition

The usefulness of the LTRE approach is that it allows one to dissect how λ varies with changes in different vital rates caused by competition. Importantly, LTRE analysis takes account of the fact that the effect of any change in vital rates is not exclusively dependent upon the magnitude of the change, but also depends upon the sensitivity of λ to the vital rate in question. In our study, the LTRE analysis allowed us to identify the principle underlying causes of competitive effects upon λ which we found were mainly due to reductions in fecundity terms. These results are in agreement with those few other LTRE studies that have directly or indirectly investigated the demographic consequences of intra- or interspecific competition in long-lived species. For instance, Miriti et al. (2001) compared the dynamics of a desert shrub, defining four different types of individuals, depending on the presence-absence of adult neighbours (conspecific or not) at the beginning and at the end of the study period. The difference in population growth rate between the four subsets of the population was mainly due to differences in the fecundity of adults. A high contribution of fecundity was also found by Oli et al. (2001) when manipulating population density in uinta ground squirrels, and by Dobson and Oli (2001) when manipulating food supply in the columbian ground squirrel.

More generally, we suggest that other competition studies would gain additional insight by using LTRE analysis. Aarssen and Keogh (2002) recently argued that most studies of plant competition risk being flawed because they focus on the measurement of growth responses to competition and ignore fecundity and survival. Measuring only differences in growth could be misleading if one is interested in species dynamics, as change in population growth rate may arise from other parts of the life-cycle. Furthermore, demographic studies that have used LTRE analysis have shown that there is usually a lack of correspondence between the variation of the vital rates, that is the magnitude of the difference in vital rates induced by any treatment, and their contribution to the change in asymptotic growth rate. In fact, many demographic studies have shown either no relationship or a negative relationship between the variance of the a_{ij} and the sensitivity of λ to these a_{ij} (Canales et al. 1994; Horvitz et al. 1997; see Pfister 1998, for review). This suggests that it is very difficult to interpret any observed variation in population dynamics in terms of variation of the vital rates alone. The combination of classic competition experiments with LTRE analysis should make it possible to evaluate the effect of competition not only in terms of plant performance but also in terms of population growth rate.

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