



Long-term influence of mowing on population dynamics in the rare orchid *Dactylorhiza lapponica*: The importance of recruitment and seed production

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ABSTRACT

Many orchids are currently red-listed due to changes in land use, and their future persistence will depend on management. Traditional land use like mowing is believed to favour orchids through increased survival and reproduction of established individuals, but the lack of data connecting their complex life cycle presently limits our ability to evaluate effects of management. Here we used data from 16 years of demographic monitoring to study how mowing affects population dynamics in two populations of the rare orchid *Dactylorhiza lapponica*. Both populations were characterized by long-lived individuals, low adult mortality and high seedling mortality. The traditional regime of mowing every second year strongly increased recruitment and reduced seed production in both populations, but had moderate effect on adult survival, growth rate and flowering probability. Population growth rate was positive for all population × treatment combinations. Traditional mowing significantly increased growth rate in both populations, and LTRE-analyses revealed that this primarily was a result of increased recruitment. The results indicate that demographic rates commonly associated with orchid persistence may be insensitive to traditional management, and underscores the importance of seed production and recruitment to maintain population growth in this long-lived species. The combination of low establishment success and no seed bank makes *D. lapponica* dependent on high seed input. Our results suggest that *D. lapponica* would benefit most from traditional mowing performed after seed dispersal in the study areas, but also suggest a high probability of future survival in the absence of mowing.

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1. Introduction

Changes in land-use practices during the last century are currently affecting species distribution patterns from the population to the landscape level, and are considered one of the most serious threats to the long-term survival of a number of plant and animal species. In Europe, a large number of declining species are associated with the traditional agricultural landscape, and their future persistence is expected to depend on some sort of management strategy. Accordingly, management actions in terms of grazing or mowing are increasingly undertaken, aimed at conserving specific nature types or species (Lennartsson and Oostermeijer, 2001; Moen and Øien, 2003; Brys et al., 2004; Wotavová et al., 2004; Johst et al., 2006; Endels et al., 2007). It has been increasingly realized that the efficiency of such actions will depend on knowledge of their detailed effects on demographic rates of target species, preferably connected through the whole life cycle (Ehrlén et al.,

2005), and in different environments (Lehtilä et al., 2006). However, the long-term data sets needed to address such effects are a limiting resource regarding many groups of species.

The need for studies that integrate effects across the whole life history is particularly challenging in species with complex life cycles and long life-spans. One such group is the orchids, where many European species currently are red-listed and believed to be diminishing due to changes in land-use practices (cf. Kull and Hutchings, 2006; Kålås et al., 2006). Orchids have an obscure, underground recruitment phase, and very little data exist on the early life stages in field populations. Duration of the underground seedling stage is unknown for most species, and it is also uncertain to what degree field germination rates generally correspond to the commonly used in vitro experiments (Rasmussen and Whigham, 1998). As a result, the recruitment of new individuals into a population is notoriously difficult to measure. Moreover, orchids may have a demanding long above-ground life-span coupled with some degree of vegetative dormancy (e.g. Nicole et al., 2005), and difficulties in separating dormancy from mortality can potentially be a problem in population models (Menges, 2000). In view of this complex life history it is not surprising that few studies have utilized population models comprising the whole life cycle in

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studies of orchids (but see Kéry and Gregg, 2004; Nicole et al., 2005; Coates et al., 2006; Pfeifer et al., 2006). At present, this strongly limits our understanding of orchid population dynamics in general, and of the effects of management in particular.

Long-term demographic monitoring combined with experimental manipulations of the environment provide excellent opportunities for achieving insight in the key life cycle phases affected by management actions, and for identifying robust management strategies. In the present study we examine the effects of mowing on demography and population dynamics in the rare orchid *Dactylorhiza lapponica*. This species is found in relatively large populations in a few localities in extremely rich (calcareous) fens in Fennoscandia, that traditionally have been utilized for haymaking (Moen, 1990; Øien and Moen, 2002). Mowing is likely to impact *D. lapponica* in numerous ways, both directly by damaging above-ground parts and indirectly by changing habitat characteristics (light intensity, litter accumulation, temperature etc.) or interactions with other individuals or species (intra- and inter-specific competition, pollination/herbivory). To assess total effects of mowing we combine data from 16 years of detailed monitoring in two field populations representing different climatic regions with data from a seed burial experiment (Øien et al., 2008) to construct and parameterize a population matrix model for *D. lapponica* in control and managed plots. We further use life-table response experiment (LTRE) analyses to reveal the demographic transitions that contribute to differences in growth rate between different management practices and populations. Our main aims are to evaluate how mowing affects population growth rate, and to examine which life-cycle transitions contribute most to population growth rate and potential growth rate differences between populations and treatments.

2. Material and methods

2.1. Study species

D. lapponica (Laest. ex Hartm.) Soó is a perennial tuberous orchid belonging to a genus that constitutes a large group of species occurring mainly in northern and central parts of Eurasia. The worldwide distribution of *D. lapponica* is limited to Fennoscandia, Scotland and alpine areas in Central Europe (Øien and Moen, 2002; Delforge and Harrap, 2006). In Fennoscandia *D. lapponica* is found in open lawn communities of extremely rich (calcareous) fens and springs in the boreal vegetation zones (zonation after Moen, 1999).

Individuals emerge above-ground approximately 2 weeks after snowmelt, usually in early June. Vegetative individuals form a leaf rosette that is fully grown by the end of June, while flowering individuals continue to grow during the flowering period in July. At maximum size, the relation between tuber mass and above-ground mass is 80/20 in vegetative individuals, and 55/45 in flowering individuals (Øien and Pedersen, 2005). In August, leaves wither and above-ground mass decays, and the new replacement tuber grows roots and a new shoot which emerges next spring. Flowering occurs in late June/early July, and 1–20 (mean \pm SD = 9 ± 3 , $n = 375$) flowers are produced. The minute seeds mature in August, and are spread by a passive ballistic mechanism in autumn. Germination experiments suggest that seeds are short-lived (<1 year), and that average germination probability in the field is about 11% (Øien et al., 2008). The underground seedling stage is believed to last for 1 year, as germination experiments suggest that the growing season in Scandinavia is too short to allow above-ground emergence as vegetative individuals during the first year after seed dispersal (Øien et al., 2008). There is no indication of any seedling/protocorm survival beyond the first year.

2.2. Field sites and treatments

The study was conducted in two nature reserves in Central Norway, Sølendet and Tågdalen, that both hold large populations of *D. lapponica*. The nature reserves are situated at the transition between the middle boreal and northern boreal vegetation zones (Moen, 1999) and experience a short growing season, usually lasting from late May until late August. The areas differ in conditions like temperature and precipitation (Table 1); Tågdalen has an oceanic climate, while Sølendet has a more continental climate. The distance between the study areas is 145 km. Both areas were used for haymaking until the 1950s, and the traditional regime was mowing every second year in August. In both areas the study species has been followed since the early 1980s as part of a long-term monitoring programme that includes more than 60 different plant species, among them 16 orchid taxa (see Øien and Moen, 2002 for a brief description of the programme at Sølendet).

In permanent plots of 5×2.5 m, individuals of *D. lapponica* have been monitored in detail. The plots are arranged in localities with two or more plots per locality, at least one of which has been mowed every second or fourth year since the mid 1970s and at least one left unmown since traditional haymaking ceased around 1950. Mowing is performed at the peak of plant production in early August, prior to seed maturation of *D. lapponica*. The studied plots cover about 700 m², and due to low detectability of vegetative rosettes it was decided that only flowering individuals were included when monitoring started in the early 1980s. All flowering individuals inside the study plots were marked and their position to the nearest cm was recorded. New individuals were included in the monitoring from the year they were first observed flowering, and subsequently followed irrespective of reproductive status. Plots were censused in early-mid July every year, and size, reproductive status and number of flowers were recorded. From 2004, the number of fruits has been recorded on reproductive individuals in early August. Since only flowering individuals were included from the start, new individuals noticed during the following years reflect both recruitment and previously reproductive individuals present as vegetative during the initial study years. The average span between two reproductive events is 2–3 years, and few individuals experience more than 7 years between flowerings (unpublished data). Accordingly, we discarded the first 8 years of collected data to avoid inflated estimates of population growth rate caused by erroneous estimates of recruitment. In the present study we include data from 1990 to 2006; collected in 28 plots in 6 localities at Sølendet (15 control and 13 mowed every second year) and in 30 plots in 12 localities at Tågdalen (15 control, 8 mowed every fourth year and 7 mowed every second year). Due to low sample sizes we were unable to include the four-year treatment from Sølendet.

2.3. Field sowing experiment

In 2003, seed packets containing 100–400 seeds were constructed according to the method of Rasmussen and Whigham (1993), and buried vertically at 2–4 cm peat depth in the field

Table 1
Characteristics of the two nature reserves used as study sites.

	Sølendet	Tågdalen
Latitude (N)	62°40'	63°03'
Longitude (E)	11°50'	9°05'
Annual precipitation (mm)	670	1507
Mean July temperature (°C)	10.5	11.2
Altitude (m a.s.l.)	700–800	380–490
Area (ha)	306	146

population. Twenty packets were retrieved for assessment of viability and germination in both 2004 and 2006 (details can be found in Øien et al., 2008). The seed germination experiment was only performed at Sølendet, and equal germination rates are assumed across populations and treatments.

2.4. Data analyses

To test differences in demographic rates between individuals subject to the control treatment vs. mowing every second year we used plot means as replicates in two-way ANOVAs including treatment and population as fixed effects. We examined differences in survival (from first observation to 2006), flowering/dormancy probability (number of years flowering/dormant divided by total number of years present), recruitment rate (averaged across years) and number of flowers, number of seeds and fruit set (averaged across years for each individual, fruit set (calculated as number of fruits divided by number of flowers) only in 2004–2006). We further used one-way ANOVAs to examine differences in plot means for the same demographic rates among the three treatments in the Tågöden population.

To estimate total treatment effects across demographic rates we used matrix population models of the form $n(t + 1) = An(t)$ (Caswell, 2001) to calculate population growth rate in the different populations and mowing regimes. We divided the life cycle of *D. lapponica* into four stages: seedlings, vegetative individuals, flowering individuals and dormant individuals (Fig. 1). The seedling stage includes all belowground phases (protocorm, mycorrhizome), and we assume that germinated seeds spend a year underground as seedlings and emerge the second year as vegetative individuals. There is no indication of a seed or protocorm bank in *D. lapponica* (Øien et al., 2008), and our baseline scenarios assume no seedling survival beyond the second year. However, we explicitly test the impact of this assumption by introducing a 10% survival rate.

Transition probabilities between the vegetative, flowering and dormant stages were calculated from data in field population plots for the 16 time intervals between 1990 and 2006. Based on long-term data, individuals were considered dead the third consecutive year after last appearance (additional data from 2007 to 2008 were used to determine individual fate in the two last study years included). In attempts to excavate missing individuals no tubers could be found ($n = 8$), and it is uncertain whether true dormancy exists in *D. lapponica*. Rather, the absence of a tagged individual in any year is likely to reflect herbivory by sheep, rodents or slugs prior to the yearly census, or failure to detect very small individuals. Fruit production was counted in tagged individuals for each population \times treatment \times year in 2004–2006, and was multiplied

with mean seed number per capsule (1043 ± 833 , $n = 6$) to estimate seed production per plant. Prior to 2004, seed production was estimated based on flower counts; seed number was calculated from regressions on number of flowers in the pooled data from 2004 to 2006 for each population \times treatment combination. The transition from flowering to seedling stage was calculated as seed number \times germination percentage, where the average germination rate of 11% obtained from the field sowing experiment at Sølendet was used for all population \times treatment combinations. We estimated recruitment by dividing the number of new vegetative individuals at time t (see below) by the number of seedlings at time $t - 1$. Since all individuals were flowering when first included in the monitoring we do not know the exact emergence year. All individuals spend at least 1 year as vegetative rosettes prior to the first flowering, and recruitment consequently has to be backdated. This was done by assigning new flowering individuals observed in year t to the vegetative stage in year $t - 1$. In order to explore the importance of variation in duration of the prereproductive phase we created three different scenarios: new flowering in year t emerged as vegetative rosettes in year $t - 1$ (baseline), $t - 3$ or $t - 7$ (assuming that all new flowering individuals observed in year t emerged in the same year). This backdating of recruitment corresponds to a lengthening of the prereproductive vegetative phase from 1 year (baseline) to 7 years (assuming 100% survival in the juvenile phase).

To increase sample sizes for matrix modelling, data were pooled across plots within each population \times treatment combination, and the 16-year average matrix for each combination was calculated (Table 1). Matrices were bootstrapped by resampling the fates of individuals and recalculating new matrices. We used 10,000 bootstrap estimates to calculate bias-corrected 95% CI for λ (Caswell, 2001). Randomization tests were used to assess the significance of λ differences between populations and treatments (Caswell, 2001), using the pooled dataset for each population \times treatment combination.

Total effects on population growth rate by treatment T and population P were decomposed into changes induced by each transition element by life-table response experiment (LTRE) analysis (Horvitz et al., 1997; Caswell, 2001). We initially included the control and 2 years treatment from both populations, and used a two-way factorial design in which a given λ of treatment T and population P is the sum of the dominant eigenvalue of the overall mean matrix ($\lambda^{(-)}$), the main effect of treatment T ($\alpha^{(T)}$), the main effect of population P ($\beta^{(P)}$), and the interaction term ($\alpha\beta^{(TP)}$):

$$\lambda^{(TP)} = \lambda^{(-)} + \alpha^{(T)} + \beta^{(P)} + (\alpha\beta)^{(TP)}$$

Both main effects were estimated first, ignoring the interaction term (Caswell, 2001):

$$\alpha^{(T)} = \sum_{ij} (\alpha_{ij}^{(T)} - \alpha_{ij}^{(-)}) (\delta\lambda / \delta\alpha_{ij})$$

$$\beta^{(P)} = \sum_{ij} (\alpha_{ij}^{(P)} - \alpha_{ij}^{(-)}) (\delta\lambda / \delta\alpha_{ij})$$

in which the differences between each matrix element and the corresponding element of the overall mean matrix $A^{(-)}$ are multiplied by the sensitivity of that element at a midway matrix between the two matrices being compared (Caswell, 2001). The interaction effect quantifies how much the growth rate of a single matrix differs from that expected by considering main effects alone, and is calculated similarly, but subtracting the contributions from the associated main effects:

$$\alpha\beta^{(TP)} = \sum_{ij} (\alpha_{ij}^{(TP)} - \alpha_{ij}^{(-)}) (\delta\lambda / \delta\alpha_{ij}) - \alpha^{(T)} - \beta^{(P)}$$

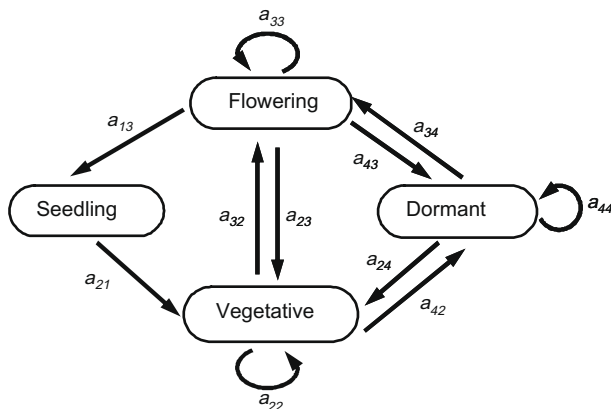


Fig. 1. Life cycle diagram for *Dactylorhiza lapponica*, where a_{ij} are transitions from stage j to stage i in 1-year time intervals.

Small interaction terms indicate that main effects impact λ independently. We further used a one-way fixed design to compare the three different treatments at Tågdalen (control, 4 years, 2 years). The contribution of a specific transition to the treatment effect on population growth is given by:

$$\delta\lambda = \sum_{ij} (\alpha_{ij}^{(T)} - \alpha_{ij}^{(c)}) (\delta\lambda / \delta\alpha_{ij})$$

where c is the control treatment and T the experimental treatment.

Finally, we calculated elasticities for all five matrices. Elasticities sum to one and reflect the relative importance of life-cycle transitions with respect to population growth rate (Caswell, 2001). The relative influence of different processes in the life cycle may be compared by adding up all elasticities involved, e.g., fecundity (seed production and recruitment), survival (stasis and retrogression) and growth (Silvertown et al., 1993). All models were run in Matlab 7.0 (The MathWorks, Inc., 1984–2004).

3. Results

3.1. Demographic rates and life history

The total numbers of individuals recorded during the study were 795 at Sølendet and 988 at Tågdalen. Both populations were dominated by vegetative individuals, and the observed population structure was nearly identical to the stable population structure predicted from the matrix models (Fig. 2). Control matrices from the two populations were characterized by a high degree of stasis in the vegetative stage, a high probability of remaining vegetative in the year following flowering, as well as high mortality rates

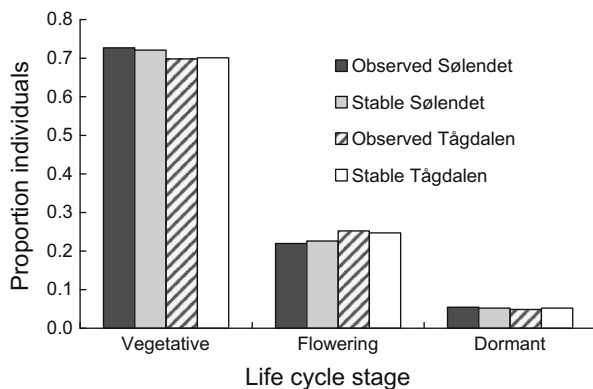


Fig. 2. The observed and stable population structure of *Dactylorhiza lapponica* in unmanaged plots in both study populations (excluding seedlings).

Table 3

P-values from ANOVAs examining population and treatment effects on survival, probability of flowering, probability of dormancy, recruitment rate, fruit set (number of fruits/number of flowers) and number of flowers and seeds ($P < 0.05$ in bold). Response variables are averages of all individuals within a plot. Recruitment rate was ln transformed, and fruit set was arcsine square-root transformed prior to analyses. The treatment factor has two levels (control/mowed every second year) in the two-way ANOVA including both populations, and three levels (control/mowed every second year/mowed every fourth year) in the one-way ANOVA including the Tågdalen population. Comparisons of treatments in the one-way ANOVA are Bonferroni-adjusted pairwise tests of mean differences for factors with a significant main effect.

Factor	Survival	Probability of flowering	Probability of dormancy	Recruitment rate	Number of flowers	Fruit set	Number of seeds
<i>Two-way ANOVA</i>							
Population	0.019	0.0093	0.32	0.036	0.22	0.00088	<0.0001
Treatment	0.90	0.77	0.0041	<0.0001	0.10	0.11	<0.0001
Population × treatment	0.087	0.66	0.49	0.33	0.41	0.35	0.0027
<i>One-way ANOVA</i>							
Treatment	0.50	0.12	0.017	<0.0001	0.29	0.73	<0.0001
Control-4 years			0.041	0.017			0.17
Control-2 years			0.051	<0.0001			<0.0001
4 years-2 years			0.99	0.056			0.00088

Table 2

Average transition matrices for the period 1990–2006 for the two *Dactylorhiza lapponica* populations. SØL = Sølendet, TÅG = Tågdalen, Control = unmowed, 2 years/4 years = mowed every second/fourth year. S = seedling, V = vegetative, F = flowering, D = dormant, † = dead.

Population/treatment	S	V	F	D
<i>SØL control n = 634</i>				
S	0	0	170	0
V	0.0046	0.637	0.571	0.892
F	0	0.273	0.221	0.049
D	0	0.042	0.115	0.059
†	0.995	0.049	0.093	0
<i>SØL 2 years n = 161</i>				
S	0	0	101	0
V	0.017	0.575	0.561	0.955
F	0	0.296	0.242	0.015
D	0	0.029	0.047	0.030
†	0.983	0.100	0.150	0
<i>TÅG Control n = 613</i>				
S	0	0	284	0
V	0.0020	0.594	0.707	0.836
F	0	0.319	0.184	0.066
D	0	0.047	0.066	0.099
†	0.998	0.040	0.043	0
<i>TÅG 2 years n = 107</i>				
S	0	0	118	0
V	0.0074	0.576	0.764	1.00
F	0	0.381	0.146	0
D	0	0.011	0.024	0
†	0.993	0.032	0.065	0
<i>TÅG 4 years n = 268</i>				
S	0	0	268	0
V	0.0042	0.487	0.759	0.905
F	0	0.426	0.117	0.048
D	0	0.018	0.028	0.048
†	0.996	0.069	0.096	0

during the seedling stage coupled with low adult mortality (Table 2). Average survival probability during the study period was higher at Tågdalen, while flowering probability was higher at Sølendet (Tables 2 and 3). Dormancy rates were low and did not differ between the populations (Tables 2 and 3). Neither was there any difference in flower production (Table 3), but fruit set was higher at Tågdalen (30% vs. 20% at Sølendet, estimated marginal means from two-way ANOVA), resulting in significantly higher seed production (Tables 2 and 3). In contrast, the recruitment rate was more than twice as high at Sølendet (Tables 2 and 3).

Effects of management were qualitatively similar in the two populations; mowing every second year markedly reduced seed production and increased recruitment rates (Table 2). The reduction in seed production was stronger in the Tågdalen population (as demonstrated by a significant population × treatment interaction,

Table 3); average fertility in managed plots was only 42% of that in control plots, compared to 59% at Sølendet. Recruitment was 3.7 times higher in both populations. Mowing also significantly decreased dormancy rates in both populations (Tables 2 and 3). Effects of mowing on transitions between the vegetative and flowering stage were minor (Table 2), and there were no significant treatment effects on average survival or flowering probability (Table 3). Mowing did not significantly affect flower production or fruit set (Table 3). Mowing had only minor effects on the observed and stable population structure in both populations (not shown).

At Tågdalen, mowing every fourth year significantly increased recruitment rate compared to the control treatment, and there was also a marginally significant reduction in recruitment compared to mowing every second year (Tables 2 and 3). In contrast, mowing every fourth year did not strongly affect seed production compared to control plots (Tables 2 and 3). There were no significant differences between mowing every second or fourth year in terms of average survival, probability of flowering, probability of dormancy, flower production or fruit set (Table 3).

3.2. Population growth rate

All population × treatment combinations yielded positive growth rates (Fig. 3), in accordance with observed population development (Fig. 4). The deterministic growth rate for control plots was nearly identical in the two populations (population contrast $P = 0.86$, randomization test), and there was a significant

positive effect of management in both populations (treatment contrast $P < 0.001$ at Sølendet, $P = 0.003$ at Tågdalen), also confirmed in the observed data (Fig. 4). Mowing every second year tended to increase projected population growth more at Sølendet than at Tågdalen (population contrast $P = 0.06$, Fig. 3), while no clear difference was seen in the observed data (Fig. 4). Predicted population growth was higher than observed population growth for all population × treatment combinations, and the discrepancy was mainly due to a strong decline in population size from 1993 to 1994 (Fig. 4). This ‘outlier’ year had little effect on average matrices, and projections based on population sizes in 1990 overestimated population growth during the study period by a factor of 2–10. Projections based on population sizes in the ‘bottom’ year 1994

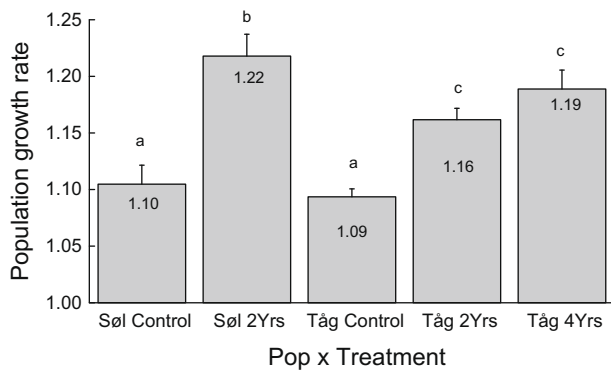


Fig. 3. Population growth rate (λ) with 95% CI in relation to management regime in the two populations. Søl = Sølendet, Tåg = Tågdalen, Control = unmowed, 2 years/4 years = mowed every second/fourth year. Different letters indicate significant differences (randomization test).

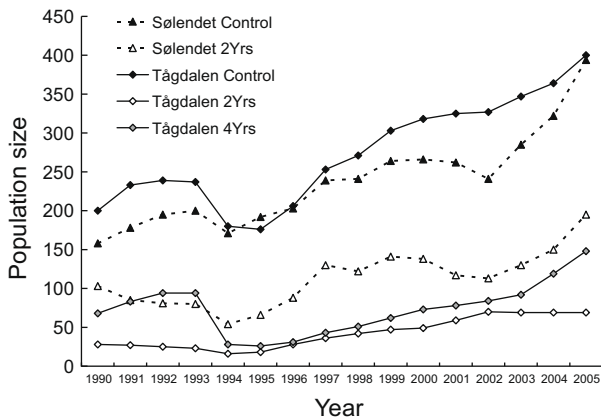


Fig. 4. Observed population size of *Dactylorhiza lapponica* during the study period (excluding seedlings).

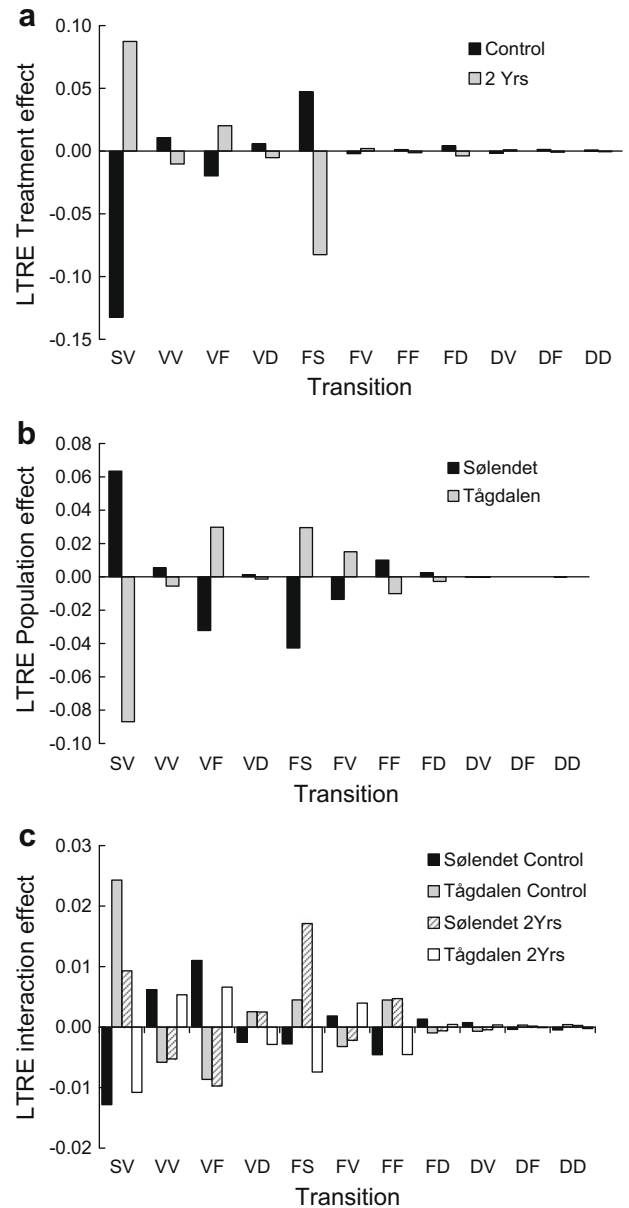


Fig. 5. Contributions to differences in population growth rate calculated by two-way LTR E analysis for 11 different life-cycle transitions in *Dactylorhiza lapponica*. Transitions are denoted by two-letter codes where the first letter corresponds to the stage in year t and the second letter to the stage in year $t + 1$. The stages are: S = seedling, V = vegetative, F = flowering, D = dormant. (a) Control treatment vs. mowing every second year, (b) Population at Sølendet vs. Tågdalen, (c) LTR E interaction effects of treatment × population. Note the different scales on the y-axes.

corresponded much better with observed trends during the rest of the study, but still overestimated population growth (by a factor of 2.4 in mowed plots at Sølendet, 1.2 for all other combinations).

The two-way LTRE-analysis demonstrated that mowing mainly affected growth rate through counteracting influences on recruitment and seed production; the positive contribution from increased recruitment was partly offset by a negative contribution from reduced seed input (Fig. 5a). At Sølendet, the overall higher recruitment rate compensated the lower fertility compared to the Tågdalen population (Fig. 5b), explaining the small difference in growth rate between the two populations. The predicted higher increase in λ following mowing in the Sølendet population was due to a weaker reduction in fertility combined with a stronger increase in recruitment rate compared to the Tågdalen population (Fig. 5c, Table 2).

Mowing every fourth year at Tågdalen increased both estimated and observed λ compared with mowing every second year (Figs. 3 and 4), but the difference was not significant (treatment contrast $P=0.17$). The one-way LTRE-analysis confirmed the positive recruitment contribution following mowing, but with 4-year intervals a high seed input was maintained, avoiding the negative effects of the reduced flowering to seedling transition seen with 2-year intervals (Fig. 6).

3.3. Elasticity patterns

Both control treatments had similar elasticity structure. Elasticities were highest for stasis in the vegetative stage followed by the

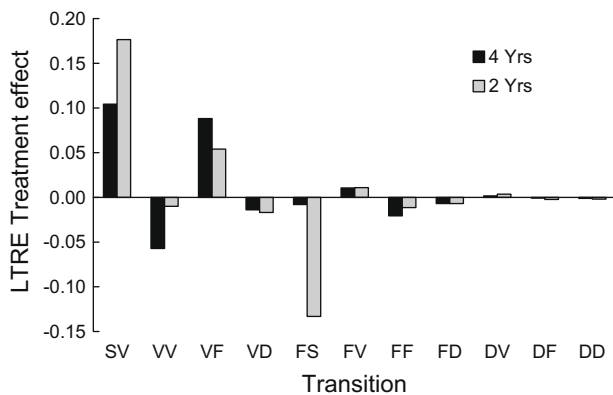
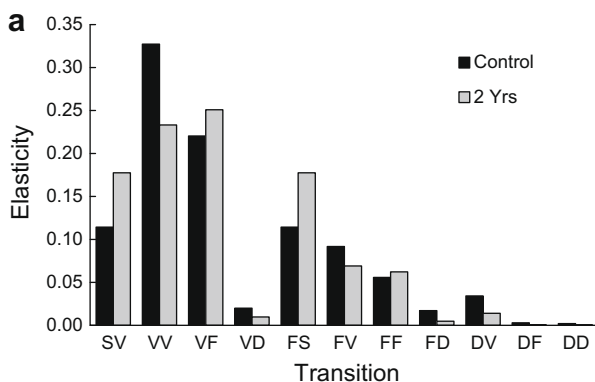


Fig. 6. Contributions to differences in population growth rate for 11 life-cycle transitions in control treatment vs. mowing every fourth (4 years) or second year (2 years) at Tågdalen, calculated by one-way LTRE analysis.



transition from vegetative to flowering (Fig. 7). In total, the vegetative stage contributed 57% to population growth rate in both unmanaged populations. Fertility and recruitment also had quite high elasticity values (Fig. 7), and the flowering stage contributed 28% vs. 29% to population growth at Sølendet vs. Tågdalen. Mowing every second year increased elasticities of recruitment and fertility in both populations, and also reduced the elasticity of stasis in the vegetative stage relative to entering the flowering stage (Fig. 7). This pattern was augmented with 4-year intervals (Fig. 7b).

3.4. Scenarios

An extension of the prereproductive phase logically increased the elasticity of survival ($e_{V_{t-1}} = 0.33$, $e_{V_{t-7}} = 0.44$) relative to growth ($e_{V_{t-1}} = 0.22$, $e_{V_{t-7}} = 0.17$) in the vegetative stage, but had only minor effects on population growth rate ($\lambda_{t-1} = 1.10$, $\lambda_{t-7} = 1.05$, all values from the control treatment at Sølendet). Results were consistent for all population \times treatment combinations (not shown). The effects of introducing 10% seedling survival (by including $\alpha_{t-1} = 0.10$, cf. Fig. 1, Table 1) were negligible regarding both population growth rate and elasticity patterns (increased λ by 0.011 – 0.019, elasticity of seedling survival was always less than 0.02, results not shown).

4. Discussion

Suggested conservation programmes for declining orchids in outlying hayfields and grasslands commonly include mowing as a factor that should benefit orchid populations, but have rarely been based on experimental studies that explicitly test the effects of mowing through the whole life cycle of the concerned species (e.g. Moen and Øien, 2003; Jacquemyn et al., 2007). In the present study we demonstrate that traditional mowing increases population growth rate in *D. lapponica*, despite unexpectedly small effects on life-cycle transitions between established stages. The higher growth rate in mowed plots was caused by an increase in recruitment rate, and suggests that population viability is tightly linked to seed production and successful establishment in *D. lapponica*.

4.1. Population dynamics in *D. lapponica*

Population dynamics in unmanaged sites in the two studied populations were surprisingly similar despite differences in environmental factors like precipitation and temperature. Both populations were characterized by high survival of vegetative and flowering individuals, and a lower recruitment rate at Tågdalen was compensated by a higher fertility rate, resulting in almost

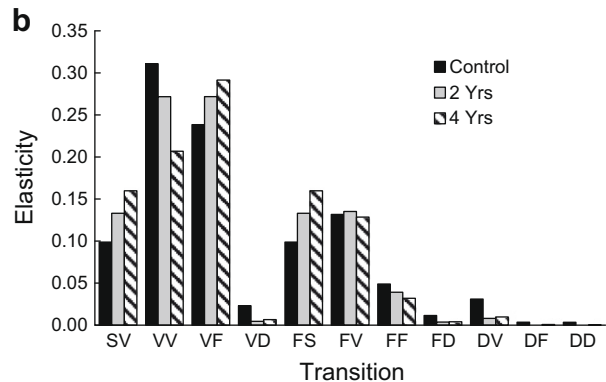


Fig. 7. Elasticity values for 11 life-cycle transitions in *Dactylorhiza lapponica* in relation to management (Control = unmowed, 2 years/4 years = mowed every second/fourth year) in the populations at Sølendet (a) and Tågdalen (b).

identical population growth rate estimates ($\lambda = 1.1$). Observed population sizes confirm a similar growth rate in both populations, but also demonstrate that the matrix model overestimated total population growth during the 16-year period. Following an extremely cold summer in 1993, population sizes in 1994 mostly dropped below initial 1990 size (Fig. 4), and this event substantially reduced actual population growth. The use of deterministic models based on long-term averages reduces the impact of such rare, extreme years, and stochastic models are likely to yield more accurate predictions of long-term dynamics.

The driving force behind the observed population increase despite the lack of mowing is at present uncertain. Orchid populations are often at their maximum for a period after management has ceased (Tamm, 1991; Moen and Øien, 2003), and we may still observe a response to the abandoning of traditional mowing in the 1950s. A majority of the permanent plots containing *D. lapponica* are open lawn communities of mire expanse, with a deep peat layer and a rather high groundwater level in summer (Moen, 1990). Changes in abundance and diversity after abandoning of traditional haymaking are quite slow in these communities, mainly because the high groundwater prevents establishment and growth of tall herbs and shrubs (Moen, 1990). In dry lawn communities overgrowing processes are faster, and a decline in the population size of the rare orchid *Nigritella nigra* has been observed in such communities in our study area during a comparable time interval (Moen and Øien, 2003). Additionally, the observed population growth may be associated with climatic factors. Long-term studies on the orchid *Himantoglossum hircinum* found an association between population growth and the occurrence of warm, wet winters and hot summers in Western Europe (cf. Carey et al., 2002; Pfeifer et al., 2006). At both our study sites, measurements of above-ground biomass during the last decades show that fen productivity has increased (unpublished data), and at present this is thought to be linked to increasing summer temperatures. Studies that relate temporal variability in transition values to environmental factors are underway, and may help to reveal the factors underlying the positive growth rate.

4.2. Effects of mowing

Mowing every second year increased growth rate in both populations, and LTRE-analyses revealed that the response mainly resulted from the contradicting effects of decreased seed input and increased establishment, where the positive contribution through higher recruitment rates had strongest impact (Fig. 5a). A positive effect on recruitment is expected, since mowing may reduce the density of the field and litter layers, thereby reducing competitive interactions and increasing the number of available microsites for establishment (cf. Stammel et al., 2006; Janečková et al., 2006). Mowing also influences physical factors, and a higher ground water level and larger diurnal variation in surface temperature have been observed in recently mowed plots (unpublished data). Seeds of *D. lapponica* are in a state of physiological or physical dormancy when shed (Rasmussen, 1995), and larger variation in soil temperature may enhance processes involved in breaking seed dormancy. A higher water level may prevent seeds from drying out during germination, potentially contributing to a higher germination percentage. However, the increment following mowing was surprisingly large, with nearly four times as high rates in plots mowed every second year in both populations. Since *D. lapponica* lacks a seed bank, seed input is likely to become limiting for population growth as the recruitment rate increases, and continuous replenishment of the seed pool will be necessary to be able to exploit the increased opportunities for establishment following mowing. The difference between the 2- and 4-year treatments at Tågdaalen further illustrates the interaction of seed production

and recruitment: Mowing every fourth year only doubles the recruitment rate, but estimated population growth rate is higher than in plots mowed every second year due to the higher seed production (Fig. 6). Although this difference was nonsignificant in the randomization test, observed population sizes since 1994 confirm that growth rate in Tågdaalen is highest in plots mowed every fourth year, suggesting that *D. lapponica* would benefit if mowing was performed later in the season, securing both high seed input (seeds mature and spread before the treatment) and recruitment.

In contrast to findings in several other orchids (e.g. Hutchings et al., 1998; Willems and Melser, 1998; Wotavová et al., 2004), management had small effects on established individuals of *D. lapponica*. Reduced light availability as a result of overgrowing processes is considered to be a main cause of rapid decline in many orchid species (e.g., Dorland and Willems, 2002), and the absence of shading and strong competition may explain the positive growth rate of *D. lapponica* in plots left unmanaged for decades. Still, the lack of significant treatment effects on survival and flowering probability in *D. lapponica* is surprising in view of the considerable direct effects on flowering individuals, that carry a large proportion of their biomass in the flowering stem and stem leaves that are cut off during mowing. We know that reproduction involves a cost in terms of reduced tuber size and stored biomass in *D. lapponica* (Øien and Pedersen, 2005), and mowing before seed maturation should lower the cost of flowering in managed plots, and allow higher reproductive effort in years between treatments. However, there were no significant differences in total flowering probability or flower production in unmanaged and mowed plots. This could suggest that plants have allocated their resources to seed production before mowing occurs, and that only seed maturation remains at this point. Alternatively, the direct negative effects of reduced assimilation capacity caused by mowing may have annulled positive effects of reduced reproductive effort. In areas that are mown annually, both survival and flowering probability of *D. lapponica* are reduced (Øien and Moen, 2002). The significant reduction in dormancy rate associated with mowing could in part be due to an increased probability of detecting small vegetative individuals in open, mowed plots.

4.3. Elasticity patterns

In long-lived plants, survival and growth usually have the largest impact on population growth (Silvertown et al., 1993, 1996). Elasticity analyses in stable (i.e. $\lambda = 1$) *Cypripedium calceolus* populations have confirmed this pattern, with stasis and dormancy contributing 98.8% to population growth rate (Nicole et al., 2005). Indeed, in the present study elasticity analyses in unmanaged plots identified survival and growth of established individuals as the main key to persistence at both sites (ca 70%), but seed production and recruitment also made interestingly large contributions (10–11%). Dormancy, in contrast, made very minor contributions (4%). This is similar to the pattern found in a growing *H. hircinum* population ($\lambda = 1.23$), where fertility and recruitment also made large contributions to population growth rate (22% and 13% respectively, Pfeifer et al., 2006). Our assumption of 100% survival in the juvenile phase may have contributed to the high importance of vegetative survival in our *D. lapponica* populations. More realistically, a survival probability of less than one should increase the importance of recruitment and transition into the flowering stage, relative to survival in the vegetative stage.

Mowing every second year altered the relative ranking of transitions. Mowing reduced the contribution from vegetative stasis and increased the contribution from fertility, recruitment and the transition from vegetative to flowering (Fig. 7). Mowing every fourth year had similar, but stronger effects. This indicates a reinforcing effect of mowing; it both alters the seed input and

recruitment rate, as well as increases the impact of these alterations. Taken together, our data illustrates the different insights that may be gained by prospective versus retrospective analyses (Horvitz et al., 1997; Ehrlén and van Groenendael, 1998; Lehtilä et al., 2006). Whereas elasticity values identified survival of vegetative individuals as the most important transition regarding population growth in *D. lapponica*, LTRE-analyses showed that mowing has little effect on this transition, but instead influences population growth rate through increasing recruitment. The importance of recruitment for population and treatment differences is in accordance with other studies on long-lived plants, where survival and growth have been found to be relatively insensitive to experimental treatments (Ehrlén et al., 2005).

5. Conclusions

Many orchids share a life cycle characterized by a long-lived adult phase, and survival is commonly believed to be the key to persistence (Shefferson et al., 2003; Øien and Pedersen, 2005). In the present study, we were able to integrate management effects across the whole life history in a long-lived orchid, and our results show that management effects on single fitness components like survival and flowering probability may be weakly correlated with total effects (cf. Ehrlén, 2003). Though managing for high survival seems intuitive in a long-lived species, the overall significance of recruitment for population and treatment differences underscores the value of including this part of the life cycle. Many temperate orchids seem to have low seed survival and a limited seed bank (Whigham et al., 2006), and our data suggest that this may limit population growth more than commonly expected. This may be of particular significance in deceptive species like *D. lapponica*, that typically have low fruit set (reviewed in Neiland and Wilcock, 1998). In contrast to most earlier orchid studies we benefited from field-derived estimates of seed survival and germination rate. Still, these estimates are based on a single-year experiment in one of the populations, and recruitment is clearly the transition requiring most assumptions. To be able to identify promising candidate traits for targeted management in long-lived species in general, and in orchids in particular, future studies should strive to close the 'recruitment-gap' in the life history.

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