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Population Ecology of *Eriophorum latifolium*, a Clonal Species in Rich Fen Vegetation

Thesis for the degree of Philosophiae Doctor

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PREFACE

It was the spring of 2005, and it was the right time to move onwards. A position as a research fellow working with long-term time series at the Museum of Natural History and Archaeology at the Norwegian University of Science and Technology (NTNU) was announced, and a PhD-project was developed with the studies of former haymaking lands at Sølendet and Tågdalen nature reserves as a starting point. Work began in earnest in January 2006, and continued at an ever increasing pace until July 2010, when all the parts of the thesis were finally completed and assembled.

The study was financed by NTNU, and was carried out at the Museum of Natural History and Archaeology and the Institute of Biology, both NTNU.

I am deeply grateful to my main supervisor Professor Asbjørn Moen at the Museum of Natural History and Archaeology, and my co-supervisor Associate Professor Bård Pedersen at the Institute of Biology. This project rests on the long-term studies of rich hayfens that were initiated by Asbjørn 40 years ago, and that are still ongoing, much due to his continuous effort. Without Asbjørn, there simply would be no thesis. Bård has been an equally important factor (to put it statistically) to the end result, especially in the long process of turning vague ideas into scientific questions. The quality of this thesis has been hugely improved by his lucid, analytical and clear thinking. I thank you both, for the opportunity, the guidance and the support.

The collaboration with Radboud University Nijmegen, Institute for Water and Wetland Research, Department of Experimental Plant Ecology in The Netherlands has been particularly fruitful. I'm grateful for the kind reception during my visits there, and I want to thank Professor Hans de Kroon and, of course, Post. Doc. Eelke Jongejans. Eelke introduced me to, and guided me patiently through, the bewildering world of matrix models.

Many others have been involved at different stages or in different parts of the project. Lester Rocha at the Institute of Biology has been invaluable in teaching me statistical methods, and also in how to successfully fight R. My long-term colleague Dag-Inge Øien has been, and still is, vital to the long-term studies, and his contribution is manifest throughout the thesis. I also want to thank Nina Sletvold, Line Johansen, Sverre Lundemo and Sølvi Wehn for help and good advice. The field work could not have been completed without the conscientious and patient help of Eva Ulvan, Ane Fremstedal, Sigrid Hansen and Christine Halseth. You managed to make measuring ”grass” quite fun! Credit is also due to James Speed and Richard Binns for proofreading manuscripts and correcting my English.

I want to thank my family for helping out, Jan Eirik and Beate for their friendship, and Tonje for taking care of me (and feeding me), especially during the last months of writing. Finally, thank you Arvid and Sondre for reminding me there are things in life more important than a thesis.

Synopsis

CONTENTS

Synopsis

LIST OF PAPERS

This thesis is based on four papers.

I) Lyngstad, A., Moen, A. & Øien, D.-I. 2010. Rich fen vegetation and hay crop on traditionally used outlying land in central Norway. (manuscript)

II) Lyngstad, A. 2010. Opposite effects of mowing on size of *Eriophorum latifolium* ramets in rich fen carpet and lawn communities. (manuscript)

III) Lyngstad, A., Rocha, L. & Jongejans, E. 2010. Population dynamics of *Eriophorum latifolium* in boreal rich fens vary with mowing regime and plant community. (manuscript)

IV) Lyngstad, A., Moen, A. & Pedersen, B. 2010. Effects of mowing and climate on flowering in *Eriophorum latifolium* in boreal rich fens, results from long-term monitoring. (manuscript)

Declaration of contributions

The ideas for the papers were conceived and developed jointly by Lyngstad and the supervisors Moen and Pedersen. Papers I and IV are based on long-term data (1967-2008) collected, assembled and maintained by Moen with the help of numerous co-workers. Øien and Lyngstad has participated in this task since 1992 and 1999 respectively. Papers II and III are based on a field experiment planned by Lyngstad, Moen and Pedersen, and Lyngstad carried out the field work. The analyses of classification and ordination in paper I were chiefly done by Moen and Øien, whereas the analyses of hay crop were carried out by Lyngstad. Moen and Lyngstad have written the major parts of paper I. The modelling approach in Paper III was envisioned and worked out by Jongejans and Lyngstad, and data analyses was done by Lyngstad in collaboration with Rocha. Model development in Paper IV was done by Pedersen, and statistical analyses performed by Lyngstad. Lyngstad wrote papers III and IV with contributions from the co-authors.

GENERAL INTRODUCTION

Boreal rich fens

Fens are mires that are influenced by both precipitation and water from the mineral soil. There are three local vegetation gradients used to differentiate fen vegetation in the Fennoscandian tradition of mire studies. The poor – rich gradient reflecting the pH and mineral concentration, the mire expanse – mire margin gradient (often) reflecting the peat depth, and the hummock – mud bottom gradient reflecting the groundwater level (e.g. Tuomikoski 1942, Sjörs 1948, Ruuhijärvi 1960, Persson 1961, Eurola 1962, Malmer 1962a, b). The poor – rich gradient in fens separates poor fen, intermediate fen, moderately rich fen and extremely rich fen (Du Rietz 1949, Sjörs 1983), poor fen has pH between 4 and 5.5, intermediate and moderately rich fen between 5 and 7, while extremely rich fen has pH from 6.8 to 8 (Rydin & Jeglum 2006). Moderately and extremely rich fen lawns in boreal areas in Norway often have *Campylium stellatum* as the dominant species in the bottom layer and *Trichophorum cespitosum* ssp. *cespitosum* as the dominant species in the field layer. Other abundant species are e.g. *Thalictrum alpinum*, *Eriophorum latifolium*, *Molinia caerulea* and *Scorpidium cossonii* (Moen 1990). Some exclusive extremely rich fen species in boreal Norway are *Dactylorhiza lapponica*, *Listera ovata*, *Carex atrofusca*, *C. capillaris*, *C. capitata*, *C. hostiana*, *Kobresia simpliciuscula*, *Schoenus ferrugineus*, *Barbilophozia rutheana*, *Fissidens adianthoides* and *Palustriella commutata* (Moen 1990: 197, Fremstad 1997).

Mowing in outlying lands

Traditional mowing of outlying lands to make hay for winter fodder has ceased in Scandinavia (Emanuelsson 2009), leading to successional changes in the plant cover. The upper boreal rich fens were traditionally mowed every second year using a scythe, and the typical hay crop (see Material and methods, Paper I) was 100-150 g/m^2. Studies in boreal hay fens in central Norway (Moen 1990, Aune et al. 1994, 1996, Moen et al. 1999) have shown a reduction in the hay crop as well as the above- and below-ground biomass of the field layer with increasing mowing frequency. An increase in the ratio of the above-ground/below-ground biomass shows that mowing forces the plants to mobilise resources from their below-ground organs (Fitter 1986, Aune et al. 1996). The succession in formerly mown boreal grasslands and fens is slow, and recommenced mowing has largely resulted in changes in species' abundance, whereas turnover of species has been minor. However, the changes have been more pronounced in the relatively more productive grassland and fen margin vegetation than in open fen areas (Moen 1990). This is in accordance with the model of secondary succession in unproductive environments (Grime 2001), where productivity is vital to explain the rate of successional change.

Mowing affects individual plants through disturbance (Crawley 1997a), and the level of disturbance is determined by the intensity and frequency of mowing. Intensity can be assessed by how much stubble is left after mowing (Moen 1990). Mowing favours plants that either avoid or are resilient to the mowing treatment. Low-growing plants (often with rosettes) and plants reproducing early in the season can avoid being mowed, and plants with low positioning of meristems and clonal growth are often resilient to mowing (Klimešová et al. 2008). Outlying lands, and fens in particular, often have low nutrient availability (Øien & Moen 2001), and stress tolerant species (Grime 2001) are at an advantage, at least if the disturbance (mowing intensity and frequency) is moderate.

Clonal growth

Clonal growth in vascular plants is a common trait in wet, nutrient-poor or cold habitats, reflecting benefits of clonality when nutrients are scarce and climate is harsh (Callaghan et al. 1997, Jónsdóttir & Watson 1997, Klimeš et al. 1997). These ecological conditions all apply to boreal mires (including rich fens), and the majority of vascular plants found in boreal mires are clonal (Sjörs 1948: 253). One definition of clonal growth in plants is ”the capacity of individual plants in nature to form ramets by vegetative means that are potentially independent” (de Kroon & van Groenendael 1997). Thus, ramets are the smallest viable, autonomous units in clonal plants. A genet is the collection of all the ramets that descend from one zygote, and these ramets may or may not be interconnected. Clonal fragments are made up of ramets physically connected via rhizomes or stolons, and clonal species with fragments that maintain physiological connections between ramets are termed “integrators” as opposed to “splitters” (Oborny et al. 2000, Oborny et al. 2001). Integration enables distribution and recycling of nutrients, water and assimilates throughout clonal fragments. Higher survival probability of daughter ramets and buffering of environmental heterogeneity are implications of integration that are particularly beneficial in heterogeneous and nutrient-poor habitats (Oborny & Cain 1997, Oborny et al. 2000, Fischer & van Kleunen 2001, Oborny et al. 2001, Herben 2004). Physiological integration causes dependence between ramets in clonal fragments, and studies of the dynamics in populations of physiologically integrated clonal plants should therefore account for demographic processes at the level of clonal fragments.

Flowering

Fecundity, including flowering, is a fundamental aspect of the life history in vascular plants, contributing to the long-term survival of plant populations through genetic recombination and recruitment of genets (Grace 1997). Evidence as to whether plants generally have to grow larger than a certain size to be able to flower (as shown by e.g. Werner (1975) and Worley & Harder (1996)) or if no such size threshold exists (e.g. Ohlson 1988) has been conflicting. A recent review concludes that both strategies are present in clonal plants, they usually exhibit a linear relationship between plant size and investment in sexual reproduction, and some have size thresholds below which they will not flower (Weiner et al. 2009). A size threshold implies that plants invest all available resources in growth and survival up to a certain point, and this can be viewed as a sign of cost of reproduction (Crawley 1997b). The negative impact of flowering in year t - 1 on flowering in year t in *Sanicula europaea* (Inghe & Tamm 1985, 1988) and *Dactylorhiza lapponica* (Øien & Moen 2002) can be interpreted as a result of cost of reproduction through a trade-off between flowering and resource storage.

Disturbance (Crawley 1997a) caused by mowing may affect flowering density (number of flowering ramets per unit of area) adversely in the short run through damage or removal of biomass, and hence, reduction in the resource storage. The long-term effects of mowing may, however, be positive for stress-tolerant species when competition is reduced (Grime 2001). Many low-growing grassland and fen species are well adapted to the disturbance caused by traditional mowing, and show a decrease in flowering when mowing ceases, and an increase when mowing is reintroduced (Moen & Øien 2003, Brys et al. 2004, Endels et al. 2007b). Conversely, flowering density in species that are less adapted to disturbance (e.g. woody plants and tall-growing herbs) declines when they are subject to mowing (Moen et al. 1999). Higher productivity requires shorter mowing intervals to achieve the same effects from mowing because plants compensate lost biomass faster in more productive habitats (Buttler 1992, Wilson & Clark 2001, Oostermeijer et al. 2002, Øien & Moen 2002, Jantunen et al. 2007). Thus, the outcome of mowing on flowering depends on the species, the productivity of the vegetation, and the intensity of the mowing regime.

Climatic conditions like precipitation, temperature and the length of the growing season can affect flowering either directly through its impact on flower development, or indirectly through the effect on resource storage. Evidence of effects on flowering have been found for drought (Inghe & Tamm 1985, 1988), waterlogging (Ejankowski 2008), snow cover and depth (Bullard et al. 1987, Inouye et al. 2002, Saavedra et al. 2003, Blinova 2008) and temperature (Bullard et al. 1987, Øien & Moen 2002, Blinova 2008), and effects on biomass have been found for temperature (Moen 1990) and the length of the growing season (Hudson & Henry 2009). Ultimately, flowering density is a result of the consorted effects of vegetation, mowing, cost of reproduction and climatic factors.

AIMS

The main purpose of this study has been to understand how vegetation, climate and management affects the long-term population dynamics of *Eriophorum latifolium* Hoppe in boreal rich fens. This has been addressed through the comparison of size parameters in ramets, demography of clonal fragments, and assessment of flowering on a long-term scale in different plant communities in two populations, one from an oceanic study area, the other from a continental study area.

The specific objectives of the papers were:

I) To interpret vegetational gradients, classify and compare boreal rich fen vegetation in one oceanic and one continental area in central Norway formerly used for haymaking, and to assess how hay crop varies between plant communities mowed at different intervals.

II) To establish how mowing affects the size of ramets in *E. latifolium* under field conditions, and to see if the outcome varies along a wet – dry gradient in rich fen vegetation.

III) To determine which vital rates contribute the most to population growth rate in clonal fragments in *E. latifolium*, and to evaluate how different mowing regimes affect demographic processes in rich fen communities separated along a wet – dry gradient in one oceanic and one continental study area.

IV) To quantify the short- and long-term effects of different mowing regimes on flowering in *E. latifolium*, and whether these effects vary along a wet – dry gradient in boreal rich fen. Further, to evaluate the relative importance of cost of reproduction, identify the climatic variables affecting flowering density directly and indirectly, quantify the contribution of the most important climatic variables, and assess how short- and long-term effects of mowing, climate and cost of reproduction combined explains the variation in flowering density among years.

STUDY SPECIES

Eriophorum latifolium (Cyperaceae) is a rich fen and spring species growing in areas with base-rich peat with pH most often in the range 5.5-7.5, and with electrical conductivity in surface water mostly above 100 µS (Kutschera et al. 1982, Moen 1990, Petraglia & Tomaselli 2003). It is widely distributed throughout Europe (Hultén & Fries 1986, Elven 2005), reaching 2100 m a.s.l. in the Alps (Jäger et al. 1965) and 1120 m a.s.l. in Norway (Elven 2005), where it is rather common in boreal areas up to the climatic forest limit. It may be locally abundant or dominant in open rich fen lawn communities, particularly on sloping fens formerly utilised for hay-cutting (Moen 1990).

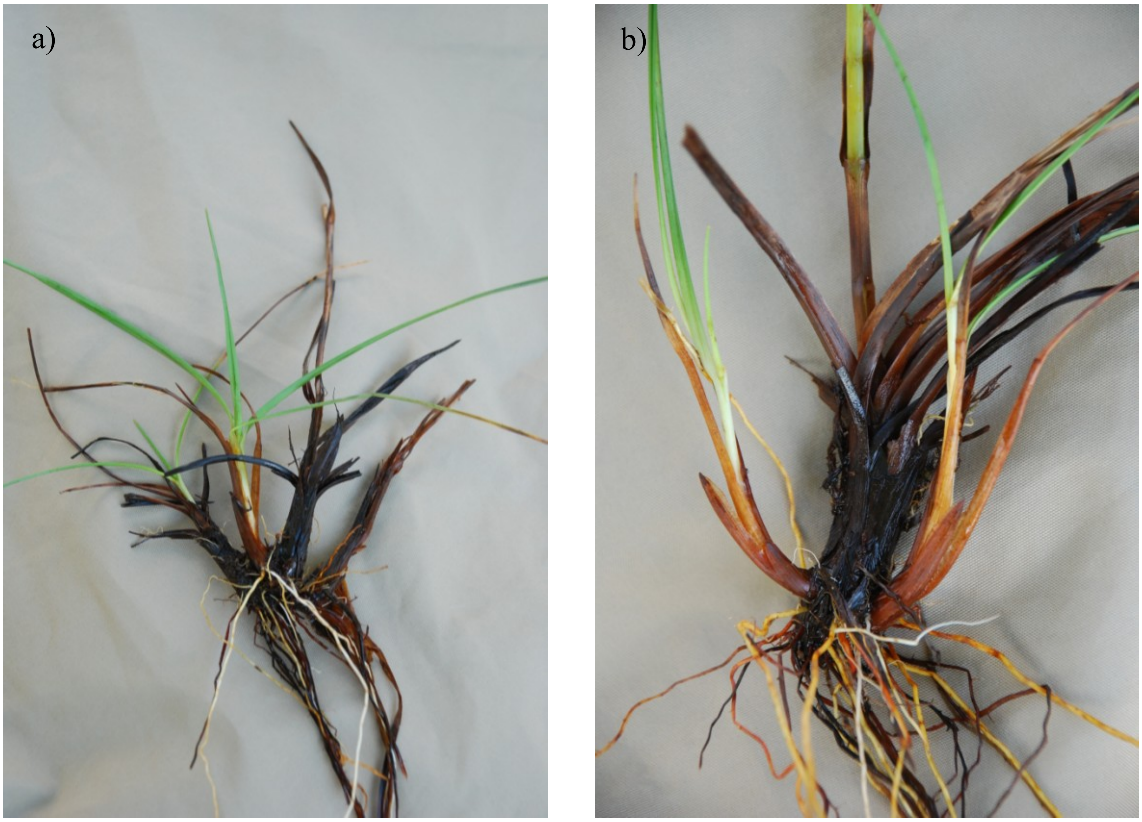

Fig. 1. a) A clonal fragment in *E. latifolium* with two live ramets and two still attached, dead ramets. The remains of a flowering stalk can be seen on the largest of the dead ramets, and it was probably flowering in the previous year. b) Clonal reproduction in *E. latifolium*. Two new ramets emerge from the base of a flowering ramet, in this case about 3 cm below the surface. Rich fen lawn vegetation in Sølendet. Photos: A. Lyngstad, August 2008.

Fig. 2. Numbered plastic sticks used to mark ramets in the demographic census of *E. latifolium* (Papers II and III). Two characteristic, rosette forming vegetative ramets are seen in the middle of the picture. Rich fen carpet vegetation in Sølendet. Photo: A. Lyngstad, July 2008.

The density of *E. latifolium* ramets is higher in mowed than unmowed fen areas (92 m^{-2} and 35 m^{-2} respectively), and this pattern is also seen for above-ground biomass (21 and 14 g/m^2) and below-ground biomass (29 and 24 g/m^2) (Aune et al. 1996). Thus, total biomass and root/shoot (biomass) ratio is higher in mowed than unmowed areas, but the weight of individual ramets is lower in mowed areas.

Clonal fragments in *E. latifolium* typically consist of one to three (occasionally up to ten) perennial ramets (Fig. 1a) connected with rhizomes (Paper III). Each mother ramet can produce 1-4 daughter ramets (Fig. 1b), and the short rhizomes emerge from below-ground leaf axils (Raunkiær 1895). New ramets typically remain within 5 cm of their mother ramet, and the species forms loose tufts (pers. obs.). The roots are mostly 10-20 cm long, and in rich fen in Fennoscandia they extend 10-20 cm down (Metsävainio 1931).

Fig. 3. Flowering stalks of *E. latifolium*, the largest with six spikelets in the inflorescence. Rich fen lawn vegetation in Sølendet. Photo: A. Lyngstad, July 2008.

Vegetative ramets form rosettes with normally three to five slender leaves (Fig. 2), while flowering ramets produce an on average 40 cm tall, elongated flowering stalk (Fig. 3) lacking a basal rosette (Paper II). In general, apical meristems are transformed and consumed when ramets in monocarpic (sensu de Kroon & van Groenendael 1997) species flower (Jónsdóttir & Watson 1997), and ramets of *E. latifolium* also die after flowering. Induction of flower primordia has been shown to depend on either low temperatures or short day length in four boreal or alpine species of *Carex* (Heide 2002). Similar requirements can be assumed in *E. latifolium*, i.e. that apical meristems transform into floral meristems some time during late autumn or winter. The seeds are about 1.5 mm long with a 100-seed weight of 0.04 g (Kutschera et al. 1982), and have attached numerous, up to 25 mm long cotton-like bristles that facilitate wind dispersal (Tutin et al. 1980, Elven 2005, Vrijdaghs et al. 2005). This trait is shared with the closely related *E. angustifolium*, in which seeds can travel several kilometres (Grime 2001, Soons 2006). The species flowers in early to mid summer (June or early July in central Norway), and seeds ripen and spread in late summer (late July and August). *E. latifolium* has a transient seed bank (Mika 1978, Thompson et al. 1997), and germination of seeds is affected positively by chilling (Maas 1989).

STUDY AREAS

Sølendet Nature Reserve

Sølendet Nature Reserve is situated close to the Swedish border in Røros municipality, Central Norway (Fig. 4, Table 1). Sølendet has large areas of species rich fens and grasslands formerly utilised for hay production, but the traditional use of the area ceased around 1950, and a 25 year long hiatus followed. The nature reserve was established in 1974, and management began in 1976 with reclamation of overgrown areas and mowing to prevent further encroachment (Moen 1990). The traditional way of using the outlying lands at Sølendet was mowing with a scythe every 2nd year, drying the herbage on the ground and gathering the dried hay in hay barns or hay stacks. The hay was transported by sledge down to the farms during the winter. About 160 haa of Sølendet Nature Reserve is currently managed by mowing, 18 haa is mowed intensively (every 2nd to 3rd year), and 140 haa is mowed extensively (every 4th to 10th year). A motorised mower is used, and the herbage is either transported out of the area or burned (Øien & Moen 2006).

Fig. 4. The location of Sølendet and Tågdalen nature reserves.

Extremely rich fen vegetation (sensu Sjörs 1948, 1952) covers 44 % of the nature reserve, grassland and heathland vegetation (mostly wooded) covers about 20 % and 35 % respectively, and the remainder is made up of reed swamp and poorer mire vegetation types. A base-rich grey-green phyllite dominates the solid geology in the area around Sølendet (Solli & Nordgulen 2008), and the drift deposits in the fen and wooded grassland areas are of a fine-grained, almost clayey, phyllitic type of moraine. The hydrology of Sølendet is characterised by more than 50 springs (mostly eustatic (sensu Dahl 1957)) discharging calcareous water (mean pH > 7.7 in spring water), and these occur mainly between 750 and 780 m a.s.l., in a transition zone between coarse and poor moraine deposits on higher ground, and fine-grained moraine below (Moen 1990). Constant waterflow from these springs facilitates paludification in areas with phyllitic moraine, resulting in the open, sloping fens (mostly 3-5^g) typical for Sølendet (Fig. 5).

Fig. 5. Characteristic landscape with open, sloping fens in an area mowed every 3rd year in Sølendet Nature Reserve. Photo: A. Lyngstad, July 2008.

Tågdalen Nature Reserve

Tågdalen Nature Reserve is situated in Surnadal municipality in Central Norway (Fig. 4, Table 1), and is part of the larger Nordmarka landscape. The traditional use of the outlying lands at Tågdalen is parallel to that at Sølendet, both in terms of mowing practises and duration of the usage. The nature reserve was established in 1996, and management commenced in 2002 (Moen 2000).

Fig. 6. Flowering of *E. latifolium* in steep, sloping fen in Tågdalen Nature Reserve. Photo: A. Lyngstad, August 2006.

Table 1. Characteristics of Sølendet and Tågdalen nature reserves. *ETS* = effective temperature sum (see section concerning climate below).

	Sølendet	Tågdalen
Latitude (N)	62°40’	63°03’
Longitude (E)	11°50’	9°05’
Mean annual precipitation (mm)	637	1583
Mean annual *ETS* (day degrees)	578	639
Mean July temperature (°C)	10.5	11.2
Mean January temperature (°C)	-9.5	-2.7
Altitude (m a.s.l.)	700-800	380-490
Area (ha)	306	146

The geology of Tågdalen is dominated by base-rich rocks like phyllite and greenstone (Solli & Nordgulen 2008), but with harder rock types occurring in low ridges traversing the area in the east-west direction (Moen 2000). The terrestrial vegetation at Tågdalen is a mosaic of open mire (56 %), open grassland (1 %), open heath (3 %) and several forest types (40 %). The quaternary deposits are mostly shallow moraines. Rich springs are common in Tågdalen, discharging calcareous water ($pH > 7$) to the moderately and extremely rich fens that cover 20 % of the nature reserve. The south-facing, sloping rich fens typically seen in this area (Fig. 6) arise through a combination of topographical, geological, hydrological and climatic (see below) features. The steepest fens at Tågdalen have an inclination of about 20^g (Moen 2000).

Vegetation regions and climate of Sølendet and Tågdalen nature reserves

Vegetation zones and sections

Both study areas are in the transition between the middle boreal and northern boreal vegetation zones (Fig. 7) (Moen 1999). However, the vegetation at Tågdalen has more features associated with the middle boreal zone than the vegetation at Sølendet. This is reflected in the flora of the areas, some species like *Epipactis helleborine* and *Schoenus ferrugineus* with a lowland affinity occur only at Tågdalen, while others like *Carex atrofusca* and *Kobresia simpliciuscula* with an alpine affinity occur only at Sølendet.

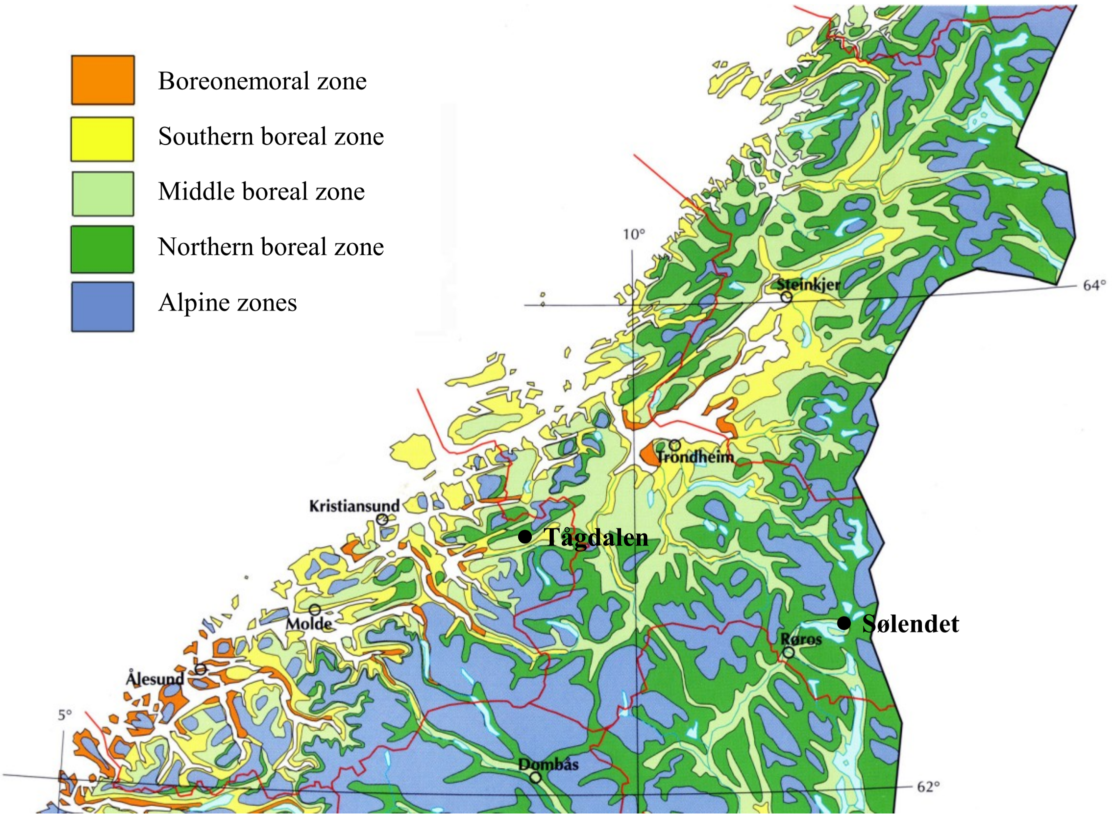

Fig. 7. Vegetation zones in central Norway with the location of Sølendet and Tågdalen nature reserves. Map after Moen (1999).

The oceanity – continentality gradient separates the study areas (Fig. 8), with Tågdalen in the markedly oceanic vegetation section and Sølendet bordering between the slightly oceanic and the indifferent vegetation section (Moen 1999). The prevailing westerly winds and the steep mountains along the coast makes this gradient steep in Norway, and the transect Tågdalen – Sølendet covers a distance along the oceanity – continentality gradient corresponding roughly to the differences in oceanity between parts of Britain (e.g. northern England) and central Europe (e.g. southern Germany and northern Switzerland) (Grünig 1994, Moen 1999, Crawford 2000). The oceanic climate of Tågdalen is characterised by high precipitation and humidity, mild, snow-rich winters and temperate summers. The more continental Sølendet has lower precipitation and humidity, colder winters with less snow, but summer temperatures are quite similar to those at Tågdalen (Table 1). Western species like *Erica tetralix* and *Narthecium ossifragum* are only found at Tågdalen, while eastern species like *Carex heleonastes* and *Pedicularis sceptrum-carolinum* appear at Sølendet alone.

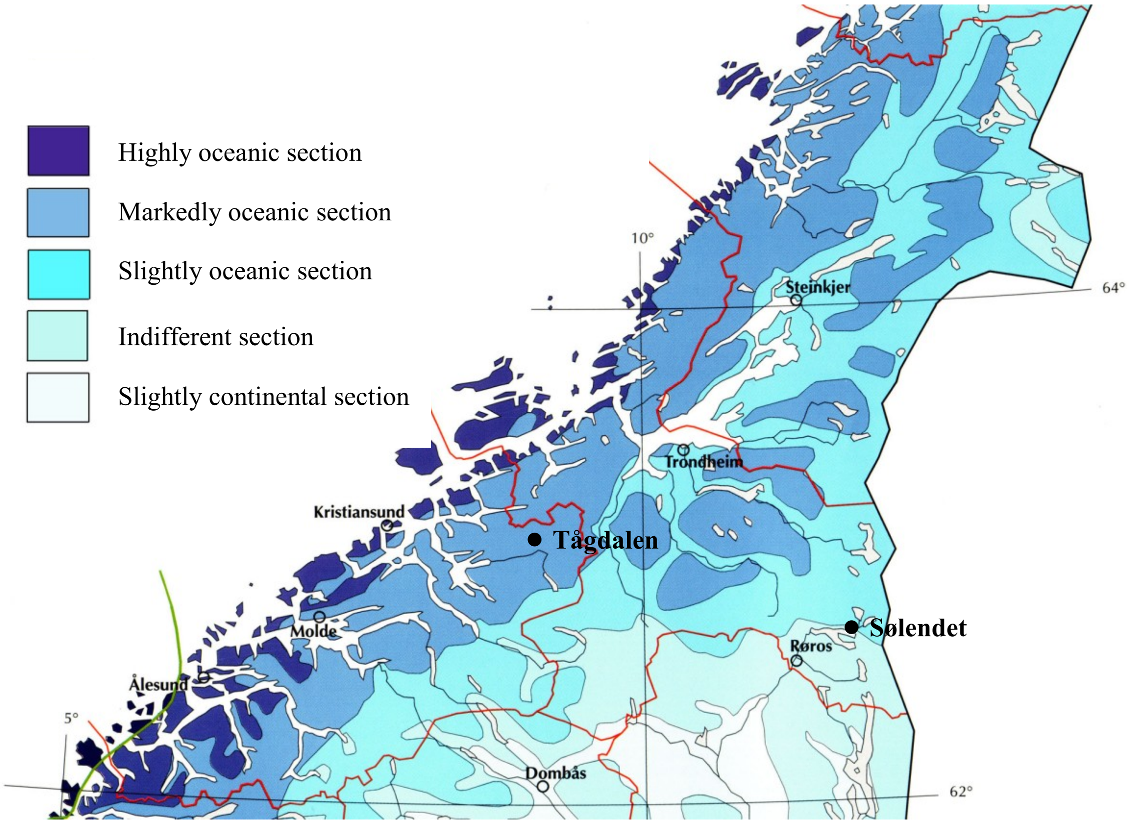

Fig. 8. Vegetation sections in central Norway with the location of Sølendet and Tågdalen nature reserves. Map after Moen (1999).

Climatic data

Spatially interpolated estimates of temperature and precipitation was provided by the Norwegian Meteorological Institute for both study areas. The method applied to estimate temperature was residual kriging, and for precipitation it was triangulation with terrain adjustment (Tveito et al. 2005). The target elevations used in these estimations were 460 m a.s.l. for Tågdalen and 725 m a.s.l. for Sølendet, i.e. the estimates were based on typical elevations at the study areas (Øien & Moen 2003). Rindal weather station (231 m a.s.l.) some 5 km east of Tågdalen provided precipitation and temperature data (Moen 2000), while the duration of snow cover was estimated using data from Søvatnet weather station (306 m a.s.l.) 22 km northeast of the nature reserve.

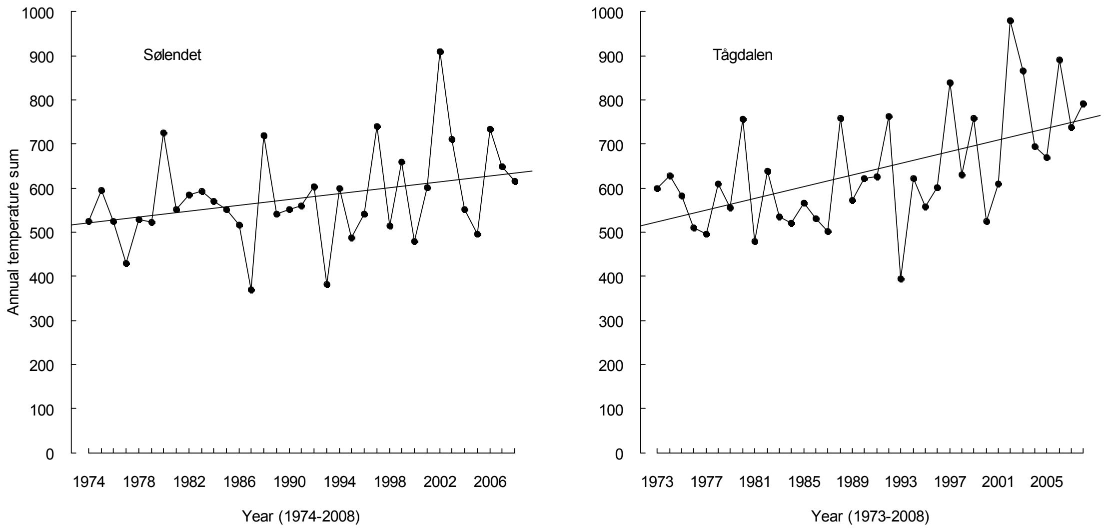

Fig. 9. Annual effective temperature sum (*ETS*) in the period 1973/74-2008 with trendlines added for Sølendet (left) and Tågdalen (right).

Brekken weather station (712 m a.s.l.) 3-4 km southeast of Sølendet was the closest with precipitation measurements, and Røros (628 m a.s.l.) 25 km southwest of Sølendet was the closest with temperature measurements (Moen 1990). Time series with temperature and precipitation data were defined from 1973 to 2008 at Tågdalen, and from 1974 to 2008 at Sølendet (Figs 9 and 10). Precipitation was aggregated to mean monthly precipitation, whereas the temperature data was used to calculate monthly effective temperature sum (*ETS*). A model for *ETS* developed by Laaksonen (1979) for the boreal vegetation zone was used:

$$ETS = \sum_{n=a}^{b} T_m - 5^\circ , \qquad \text{eqn 1}$$

where T_m is the mean daily temperature, *a* is the third day in the first five-day period in spring with mean $T_m > 5$ °C and no snow cover, and *b* is the third day in the last five-day period in autumn with mean $T_m > 5$ °C and no snow cover. Thus, *ETS* incorporates both the duration and warmth of the growing season. The length of the growing season was defined as the period between *a* and *b* in eqn 1, and was calculated for both study areas from 1980 to 2008 (Fig. 11).

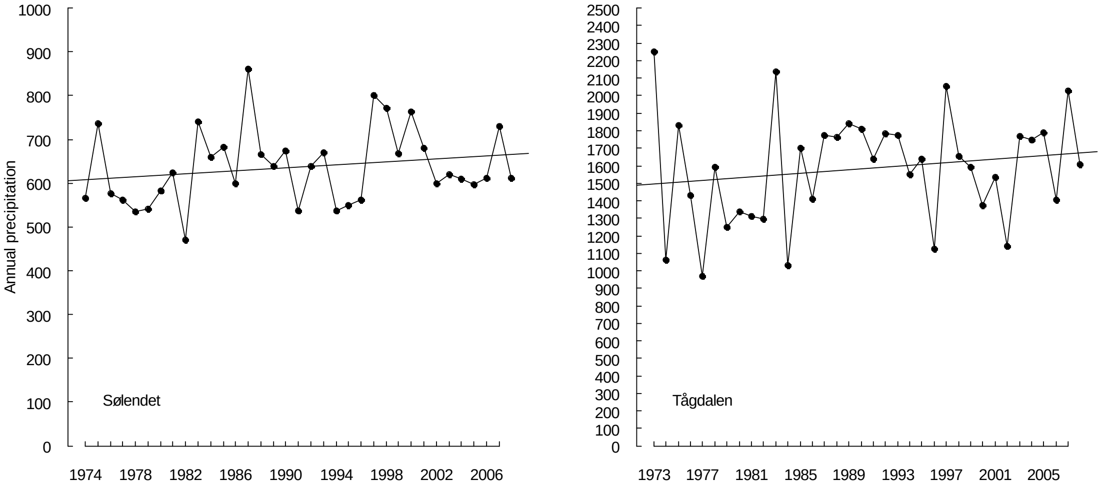

Fig. 10. Annual precipitation in the period 1973/74-2008 with trendlines added for Sølendet (left) and Tågdalen (right). Note the differences in scale.

Effective temperature sum

Mean monthly *ETS* at Sølendet (1974-2008) and Tågdalen (1973-2008) is shown in Fig. 12. The months May through September were the only ones with *ETS* > 0, restricting the growing season to these months at both study areas. The *ETS* at the study areas was similar in May-July, but August and September were warmer at Tågdalen than at Sølendet. There was a significant increase in annual *ETS* at Tågdalen from an estimated

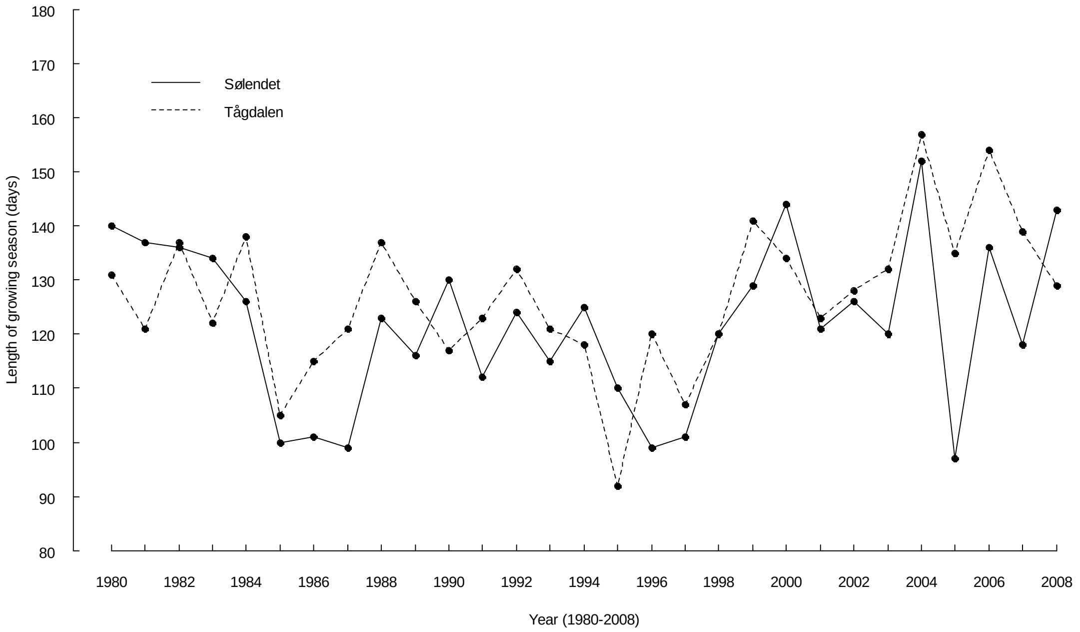

Fig. 11. The length of the growing season at Sølendet and Tågdalen (1980-2008).

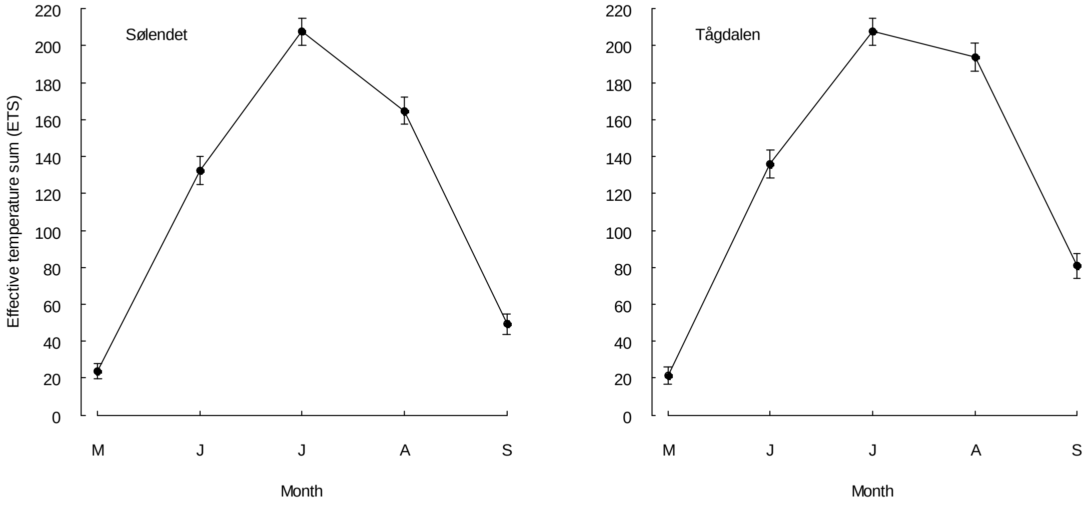

Fig. 12. Mean monthly effective temperature sum (*ETS*) (+/- se) at Sølendet (1974-2008) to the left, and at Tågdalen (1973-2008) to the right.

ETS = 516.12 in 1973 to *ETS* = 755.63 in 2008, or 6.65 day degrees per year over the period (Table 2, Fig. 9). There was likely an increase at Sølendet as well (albeit significant on a 10 %-level only), from an estimated *ETS* = 518.28 in 1974 to *ETS* = 634.58 in 2008, or 3.32 day degrees per year (Fig. 9).

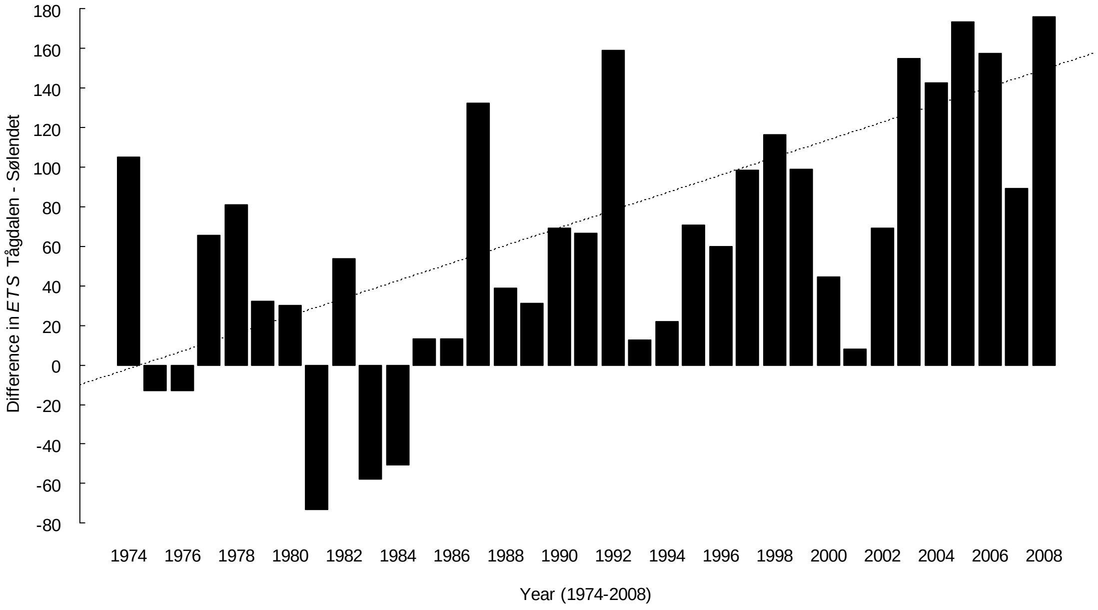

Fig. 13. The difference in annual *ETS* calculated as $ETS_{\text{Tågdalen}}$ - $ETS_{\text{Sølendet}}$ over the period 1974-2008. The difference between the study areas increases with time (linear regression, $r^2 = 0.34$, $p<0.001$, dotted line).

The difference in annual *ETS* between the study areas increased significantly from 1974 to 2008 ($p < 0.001$, $r^2 = 0.34$, linear regression), and Tågdalen now has higher annual *ETS* than Sølendet (Fig. 13). Analogous tests of possible trends in monthly *ETS* revealed a significant increase in July, August and September at Tågdalen, and in July alone at Sølendet (Table 2). Thus, the increase in *ETS* at Tågdalen was caused entirely by elevated temperatures in mid- to late summer and autumn. The annual trend at Sølendet, weak as it was, was similar to that at Tågdalen. There was no evidence of changes in *ETS* in neither spring nor autumn at Sølendet.

Table 2. Trend in monthly *ETS* (May-September), annual *ETS*, monthly precipitation (January-December), and annual precipitation at Sølendet (1974-2008) and Tågdalen (1973-2008). All tests are linear regressions with r^2, estimated yearly change in day degrees or mm precipitation +/- se, and p-values ($p < 0.05$ in bold, $0.05 \leq p < 0.10$ in italics).

	Sølendet				Tågdalen			
	r^2	estimate	se	p-value	r^2	estimate	se	p-value
Trend in *ETS*								
May	0.01	-0.28	0.40	0.491	0.07	0.71	0.45	0.122
June	0.01	0.35	0.77	0.652	0.03	0.73	0.74	0.329
July	0.12	1.50	0.70	**0.039**	0.22	1.90	0.62	**0.004**
August	0.05	1.01	0.74	0.180	0.16	1.74	0.69	**0.017**
September	0.05	0.74	0.54	0.183	0.18	1.58	0.58	**0.010**
Annual	0.10	3.32	1.72	*0.062*	0.29	6.65	1.78	**0.001**
Trend in precipitation								
January	0.00	0.02	0.42	0.957	0.01	0.95	1.71	0.584
February	0.11	0.66	0.32	**0.049**	0.14	2.45	1.04	**0.024**
March	0.00	0.09	0.23	0.694	0.02	0.85	1.04	0.422
April	0.01	-0.16	0.26	0.558	0.01	-0.68	0.99	0.495
May	0.04	0.39	0.35	0.267	0.04	0.67	0.60	0.273
June	0.00	0.03	0.45	0.944	0.06	1.06	0.71	0.142
July	0.00	0.16	0.53	0.767	0.03	-1.21	1.21	0.325
August	0.10	0.90	0.46	*0.059*	0.09	1.97	1.09	*0.079*
September	0.01	-0.33	0.49	0.505	0.00	-0.51	1.34	0.705
October	0.00	-0.07	0.38	0.853	0.03	-1.56	1.55	0.319
November	0.08	0.56	0.34	0.104	0.02	1.45	1.58	0.367
December	0.04	-0.55	0.46	0.244	0.00	-0.28	1.61	0.862
Annual	0.04	1.72	1.44	0.241	0.03	5.13	5.04	0.316

Precipitation

Mean monthly precipitation (+/- se) at Sølendet (1974-2008) and Tågdalen (1973-2008) is shown in Fig. 14. Precipitation was lowest in spring and peaks in mid- and late summer at both study areas, but remained at a higher relative level throughout autumn and early winter in Tågdalen than at Sølendet. Precipitation was markedly higher at Tågdalen with a mean of 1583 mm year^{-1} compared to a mean of 637 mm year^{-1} received at Sølendet, highlighting the main climatic difference between oceanic Tågdalen and continental Sølendet (Table 1, Fig. 10). The absolute variation between years was also much higher at Tågdalen (968-2254 mm year^{-1}) than at Sølendet (471-862 mm year^{-1}). There were no significant changes in annual precipitation at either study area in this time period, but monthly precipitation showed a coinciding increase in February at both study areas (Table 2).

The length of the growing season

The length of the growing season was similar between the study areas in the period 1980-2008 (Fig. 11). The mean length at Sølendet was 122 days, with a maximum and minimum length of 152 and 97 days respectively. There was no trend in the length of the growing season at Sølendet ($p = 0.728$, $r^2 = 0.005$, linear regression). The equivalent observations at Tågdalen were 127, 157 and 92 days, and there was no clear trend ($p = 0.080$, $r^2 = 0.110$, linear regression).

Increasing effective temperature sum

There was an increase in effective temperature sum (*ETS*) at Tågdalen in the period 1973-2008, and while the same trend seemed to be present at Sølendet, it was not significant. The study areas were comparable in terms of received *ETS* at the beginning of the period of observations, but have become increasingly divergent over the last 35 years. A mean increase in spring *ETS* (January-April) of 3.6 day degrees per year has been documented in the period 1992-2007 for 12 sites throughout Britain (Morecroft et al. 2009). The results from central Norway were in accordance with this as far as the trend of *ETS* was concerned, but Morecroft *et al.* (2009) reports a uniform increase at all sites, whereas the increase documented here was more pronounced at Tågdalen than at Sølendet. This may be due to a larger overall climatic difference between the study areas, because the total *ETS* of the growing season was incorporated, or because the *ETS* time series were longer. An evaluation of trends in *ETS* in the Nordic Arctic (1901-2002) shows an almost uniform increase in *ETS* in this area from 1970 to the present. The weather stations diverging from this pattern are located in Greenland or in northeastern Fennoscandia, chiefly Finnish Lapland (Førland et al. 2004). Matthes et al. (2009) documents a significant increase in *ETS* in the period 1958-2008 for all Arctic regions except parts of Western Russia (including the Kola peninsula). While bearing in mind that Sølendet is situated in the boreal vegetation zone, and is more oceanic than (most) northeastern parts of Fennoscandia and Kola, it is possible that the lower increase in *ETS* at Sølendet than at Tågdalen reflects a regional climatic pattern governing temperatures in continental parts of Fennoscandia and Western Russia.

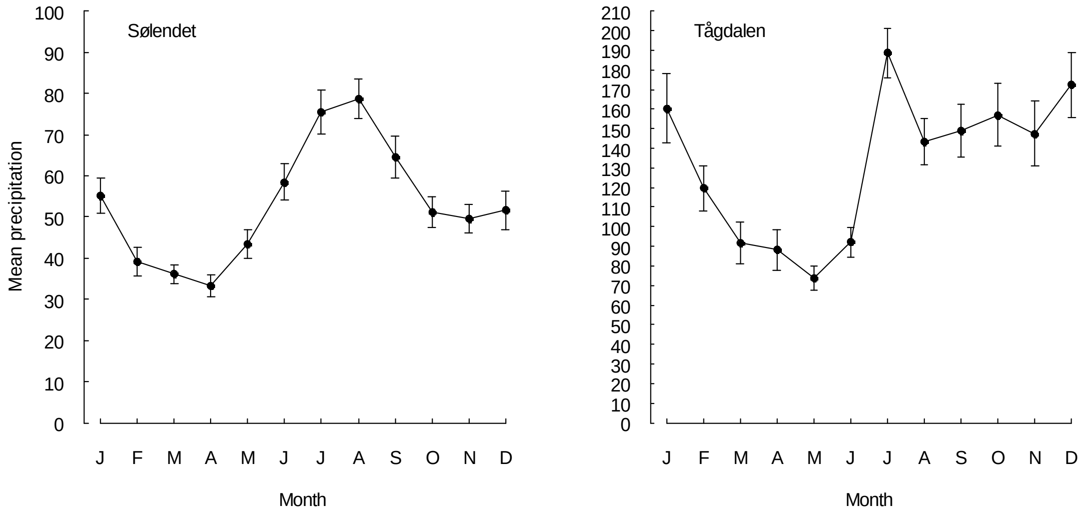

Fig. 14. Mean monthly precipitation (+/- se) at Sølendet (1974-2008) to the left and Tågdalen (1973-2008) to the right. Note the differences in scale.

Stable precipitation and length of growing season

Significant increases in precipitation has been documented for most areas in Northern Europe generally (The BACC Author Team 2008), and in Britain specifically (Morecroft et al. 2009). Annual precipitation levels did not change significantly during the period of observation at either of the study areas, and remained about twice as high at Tågdalen as at Sølendet. There may, however, be a slight positive trend in precipitation (Fig. 10), but a definite conclusion depends on future observations.

The length of the growing season showed no trend between 1980 and 2008, and it remained similar between the study areas. This is contrasted by the results for Northern Europe (The BACC Author Team 2008) and most of the Arctic region (Matthes et al. 2009) where an increase in the duration of the growing season is documented. These studies employ longer time series on the length of the growing season (1871-1990 and 1958-2008 respectively) than were used for Sølendet and Tågdalen, and the short period of observations (in this context) may explain why an increase was not detected.

MATERIALS AND METHODS

Paper I. Rich fen vegetation and hay crop

The rich fen vegetation of Sølendet and Tågdalen was described and classified based on 134 samples from permanent plots (mostly 25 or 12.5 m^2) taken between 1967 and 2008. The permanent plots were either mowed every year, every 2nd year, every 3rd year, every 4th year or left unmowed (Fig. 15). The samples were all from rich fen vegetation formerly used for haymaking, they represented homogeneous areas, had full species lists of vascular plants, bryophytes and macrolichens, and the cover scale could be rescaled into a six degree scale (close to the Hult-Sernander-Du Rietz scale (Malmer 1962a)). The vegetation was separated into a shrub layer (woody plants 0.3-2 m), a field layer (herbs, graminoids and woody plants < 0.3 m) and a bottom layer (bryophytes and macrolichens). A tree layer did not occur. Altogether, 200 entries of taxa were used in the multivariate analyses, 195 species and five shrubs occurring in two vegetation layers. Classification was performed in TWINSPAN (Hill & Šmilauer 2005) with six cut levels, no weighting of samples, species or pseudospecies levels, and seven as the maximum number of indicator species per division. Characteristic species were more or less restricted to one community, and differential species were more or less confined to one or some communities compared to others. Indicator species were used as defined in Hill & Šmilauer (2005); they are highly preferential species in each TWINSPAN division. DCA – ordination (using CANOCO for Windows 4.5 (ter Braak & Šmilauer 2002)) with detrending by segments and no exclusion of species was carried out on the same data set as for the TWINSPAN classification.

The same permanent plots that were used in the classification of the rich fen vegetation were used to measure hay crop (g/m^2). Hay crop includes the above-ground biomass and the litter attached to living plants, but excludes the stubble left after mowing (Moen 1976, 1990, Aune et al. 1996). Three plant community groups were defined based on the classification; fen carpet, fen lawn and fen margin. The mowing regimes were: every year, every 2nd and every 4th year since 1974 at Sølendet, and every 2nd and every 4th year since 1973 at Tågdalen, and mowing was performed with a scythe in early August. Plant community group and mowing regime were used as fixed factors in the statistical analyses of hay crop. Hay crop was measured (n = 902) between 1982 and 2009, and differences between the study areas was analysed using data from permanent plots mowed every 2nd and 4th year, while differences between plots mowed every year, every 2nd and every 4th was assessed using data from Sølendet alone. The experimental design was nested, and generalised linear mixed models (GLMM) (McCulloch & Searle 2001, Zuur et al. 2009) that take spatial nesting into account was used in both modelling approaches. The statistical analyses of hay crop were conducted in the R statistical environment (R Development Core Team 2008), and this statistical software was also used in Papers II – IV.

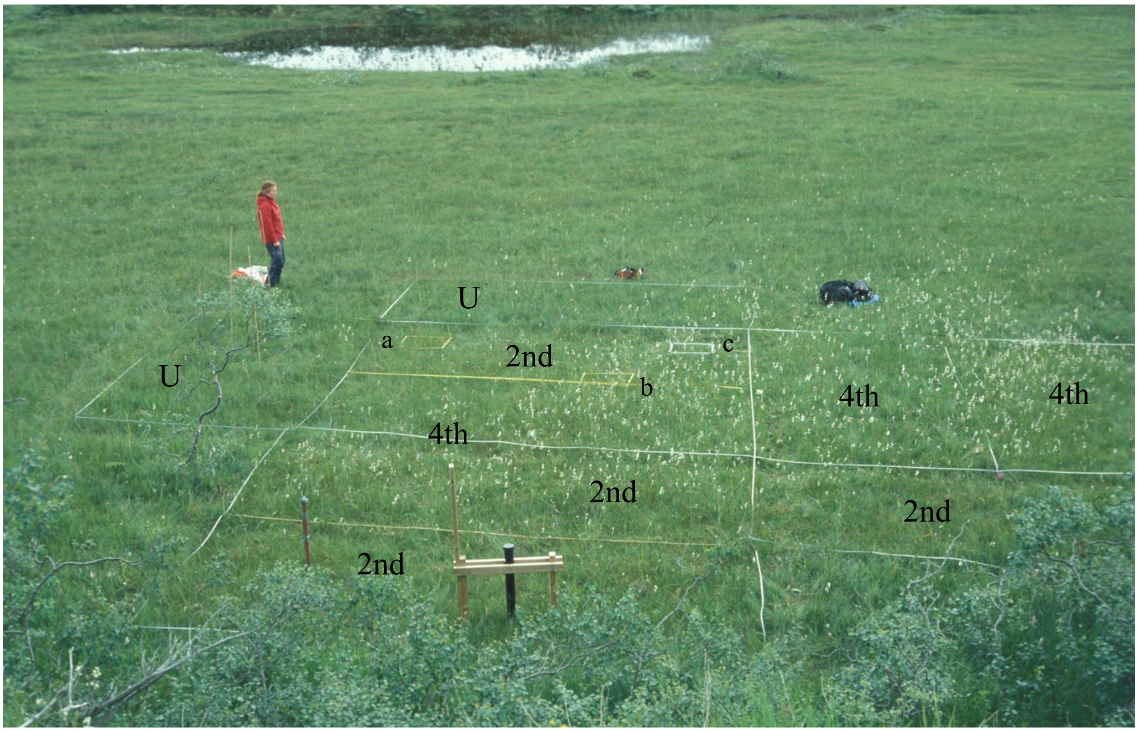

Fig. 15. *Eriophorum latifolium-Campylium* lawn community in locality IA25 at Tågdalen with permanent plots (2.5 x 5 m) mowed every 4th year, every 2nd year or unmowed (U). Hay crop and flowering density was measured on the permanent plot level (Papers I and IV). Three sample plots (a – c, 0.5 x 0.5 m) are indicated within permanent plot IA25A, vegetation samples used in the classification were based on analyses in 3-5 sample plots in each permanent plot (Paper I), and demographic censuses of *E. latifolium* were also conducted in sample plots (Papers II and III). Flowering ramets of *E. latifolium* are conspicuous in several of the mowed permanent plots. Photo: A. Lyngstad, July 2007.

Paper II. Size of *E. latifolium* ramets

Ramets of *E. latifolium* (n = 683-895) were identified and marked with numbered plastic sticks (Fig. 2) in 32 plots (small quadrats, 0.5 x 0.5 m), 15 at Sølendet and 17 at Tågdalen. The length of the longest leaf (n = 2954), the width of the widest leaf (n = 2953), number of mature leaves (> 2 cm long, n = 2973) and number of emerging leaves (< 2 cm long, n = 2658) was recorded in vegetative ramets, and the height of the stalk (n = 161), number of stalk leaves (n = 161) and number of spikelets (n = 75) in flowering ramets. Censuses were carried out in middle or late summer during 2006-09. The plots at Sølendet were either mowed every 3rd year (five plots), extensively mowed (every 8th year on average, six plots) or unmowed (four plots), and a motorised mower was used. The mowing at Tågdalen was carried out using a scythe, and the mowing regimes were every 2nd year (eight plots) and unmowed (nine plots). Mowing commenced between 1973 and 1985 in the various plots. The Sølendet data was analysed with generalised linear models (GLM) (Crawley 2007), while the Tågdalen data was analysed with generalised linear mixed models (GLMM) (McCulloch & Searle 2001, Zuur et al. 2009) due to a nested experimental design. The fixed factors considered for both study areas were mowing regime, vegetation (as vegetation cluster) and year.

Paper III. Population dynamics of *E. latifolium*

The demography in clonal fragments of *E. latifolium* was surveyed between 2006 and 2009 using the same experimental layout as that described for Paper II. Physical connection between ramets (n = 683-895) was recorded and used to define clonal fragments (n = 470-483). The clonal fragments were assigned to size classes based on how many ramets were contained in each clonal fragment, and whether they held flowering ramets or not. A total of 21 classes were defined, ten each for vegetative and flowering clonal fragments, and one for seedlings. Fundamental aspects of the life-history of a clonal plant like *E. latifolium* are survival, fragmentation, growth, retrogression, flowering, and seedling establishment (de Kroon & van Groenendael 1997). A model was developed to clarify the demographic processes affecting the transition of clonal fragments from year *t* to *t* + 1, with separate pathways for seedlings, fragmented, and intact clonal fragments (Fig. 16). The vital rates defined either the probabilities or the outcomes of demographic processes between *t* and *t* + 1 (see Table 3 for details), and were modelled separately for the study areas.

Table 3. Definitions of vital rates affecting the transition of clonal fragments in *E. latifolium* from year *t* to *t* + 1.

Vital rate	**Demographic process**
σ_j	Survival probability from year *t* to year *t* + 1 of clonal fragments with one or two ramets
κ_j	Fragmentation probability between year *t* and year *t* + 1 of surviving clonal fragments
π_j	Number of new clonal fragments at year *t*+1 emerging from each fragmenting clonal fragment
γ_j	Growth probability in surviving and intact clonal fragments
γ_{dj}	Growth probability in surviving and fragmented clonal fragments
ρ_j	Retrogression probability in surviving, intact and non-growing clonal fragments
ρ_{dj}	Retrogression probability in surviving, fragmented and non-growing clonal fragments
ω_j	How much a surviving, intact and growing clonal fragment grows
ω_{dj}	How much a surviving, fragmented and growing clonal fragment grows
ν_j	How much a surviving, intact and non-growing clonal fragment shrinks
ν_{dj}	How much a surviving, fragmented and non-growing clonal fragment shrinks
φ_j	Flowering probability at year *t* + 1 of surviving and intact clonal fragments
φ_{dj}	Flowering probability at year *t* + 1 of surviving and fragmented clonal fragments
τ_j	Mean number of flowering ramets at year *t* in flowering clonal fragments
ε	Seedling establishment probability as seedlings m^{-2} at year *t*+1 / flowering ramets m^{-2} at year *t*
σ_s	Survival probability from year *t* to year *t* + 1 of seedlings
γ_s	Probability of surviving seedlings to grow to size 2 at year *t* + 1

The modelling approaches were GLM, GLMM, negative binomial GLM or zero-truncated GLM (McCulloch & Searle 2001, Crawley 2007, Zuur et al. 2009), depending on the distribution of the data and whether the experimental design was nested or not. The fixed factors considered in the vital rates models were mowing regime, vegetation (cluster), year (transition), if the clonal fragment was flowering in year *t* or not, and how large the clonal fragment was in year *t* in terms of number of ramets.

The population dynamics of *E. latifolium* was modelled with a stage-based matrix model of the form $n_{t+1} = \mathbf{A}_{ij} n_t$ (Caswell 2001), where the stage classes corresponded to the 21 clonal fragment size classes. At Tågdalen, the population growth rate (λ = largest eigenvalue of $\mathbf{A}_{ij}$ (van Groenendael et al. 1988)) was calculated for 12 combinations of year (three transitions), two vegetation clusters and two mowing regimes, and at Sølendet for 18 combinations of year (three transitions), two vegetation clusters and three mowing regimes.

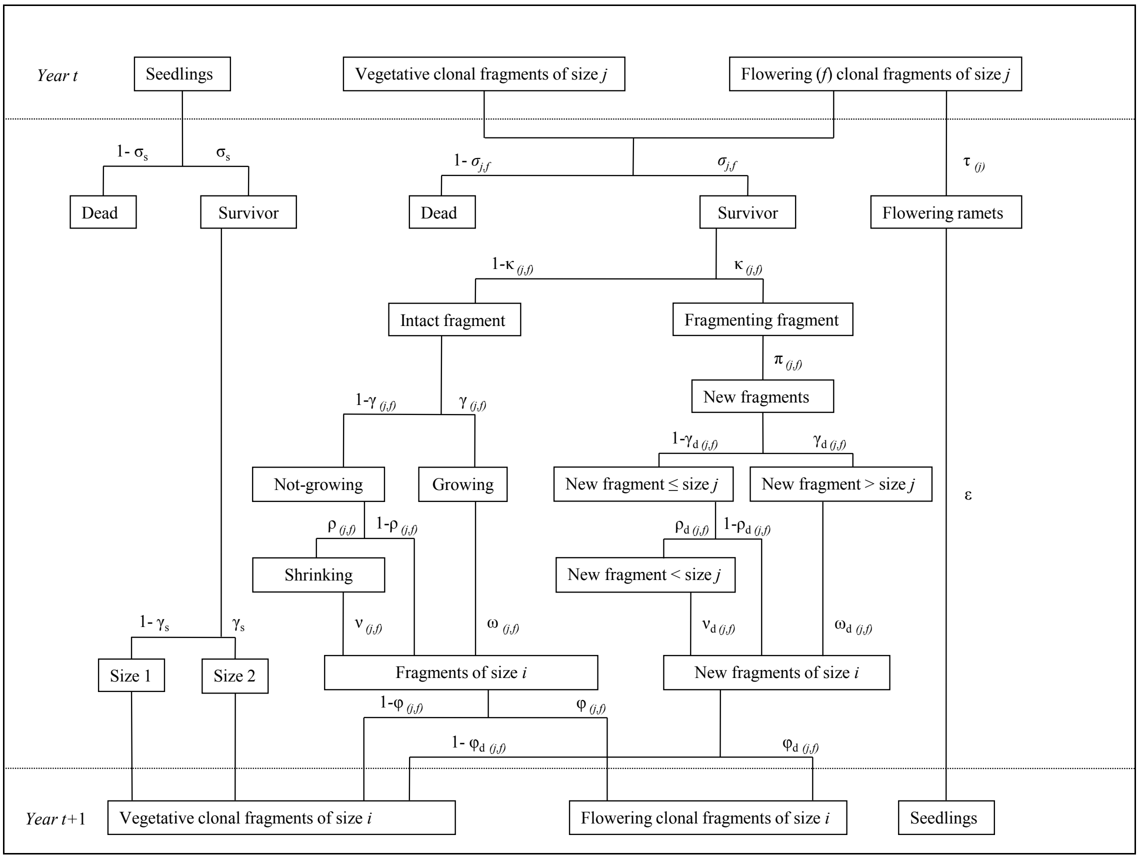

Fig. 16. A model of demographic processes and vital rates in *E. latifolium*. The lines show the relationships between vital rates, with the ones positioned relatively lower conditional on those above. The subscript $_{(j,f)}$ denotes the assumed dependence of probabilities of vital rates on the clonal fragment size *j* at year *t* and on whether the fragment is vegetative or flowering *(f)*.

Elasticities were calculated for mean matrices (unmowed situations) of vital rates for each vegetation cluster within study area, showing how and how much a change in a vital rate would impact λ on a relative scale (de Kroon et al. 1986, Franco & Silvertown 2004). Nested LTRE's (Elderd & Doak 2006, Endels et al. 2007a, Jacquemyn et al. 2010, Jongejans et al. 2010) were used to pinpoint which vital rates contributed to the differences in λ between years, study areas, vegetation clusters and mowing regimes, and how large their positive or negative contributions were. The nested decomposition model was defined as follows:

$$\lambda^{kmnq} \cong \lambda^{\cdot\cdot\cdot\cdot} + \alpha^{k\cdot\cdot\cdot} + \theta(\alpha)^{km\cdot\cdot} + \mu(\alpha\theta)^{kmn\cdot} + \beta^{\cdot\cdot\cdot q} + \alpha\theta\mu\beta^{kmnq} \qquad \text{eqn III}$$

in which the indices refer to the k^{th} study area, the m^{th} vegetation cluster within study area k, and the n^{th} mowing regime within vegetation cluster θ and to the q^{th} year. Vital rates were used as model components in the LTRE's, and the contribution from a given vital rate x_j was quantified in two steps. The difference between x_j in the matrix of interest (e.g. the matrix for the unmowed situation at Tågdalen) and x_j in the appropriate reference matrix (the overall unmowed matrix) was calculated, and the difference multiplied by the sensitivity of x_j computed from the midway matrix between the matrix of interest and the reference matrix (Caswell 2001).

Paper IV. Flowering time series in *E. latifolium*

Time series with annual counts of flowering ramets of *E. latifolium* in permanent plots stretch back to 1982 at Sølendet (67 time series) and 1983 at Tågdalen (59 time series) (Fig. 17), with a total of 2879 observations of flowering density (number of flowering ramets m^{-2}). All included time series had 15 years or more of uninterrupted observations with the same mowing regime. The mowing regimes of the permanent plots were mowed every year, every 2nd year, every 4th year or unmowed, and mowing was performed with a scythe after the count of flowering in early August. The rich fen vegetation of the plots was separated along a wet – dry gradient, and the three plant community groups fen carpet, fen lawn and fen margin were recognised.

A conceptual model exploring the relationship between flowering density, mowing, the amount of stored resources, and climatic factors affecting flowering directly and indirectly (through the amount of stored resources) was developed (Fig. 18). The model

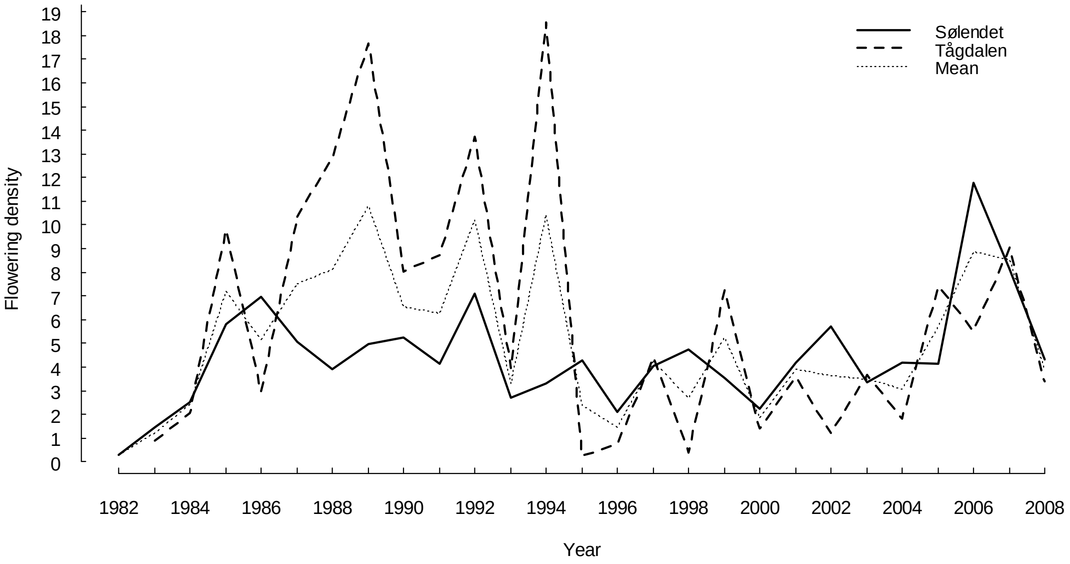

Fig. 17. Annual flowering density in *E. latifolium* (1982-2008) at Sølendet and Tågdalen.

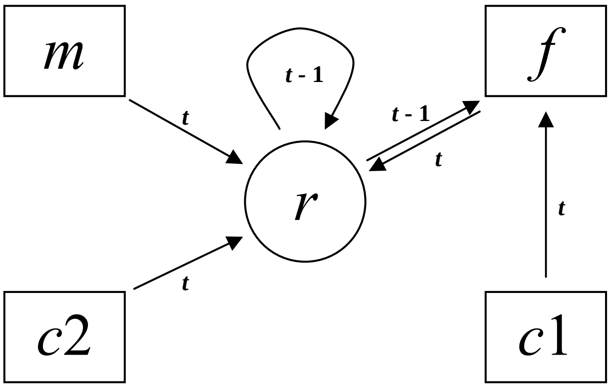

Fig. 18. A conceptual model describing the relationship between stored resources (*r*), flowering (*f*), climate (*c*1 and *c*2) and whether a plot is mowed or not (*m*). Arrows marked with t indicate effects operating within the same growing season, while effects operating between years are marked with *t* - 1. Measured variables are enclosed in squares, while the unmeasured variable *r* is in a circle.

explains the development in stored resources and flowering density over years by identifying the factors affecting them and the pathways through which they work. Flowering density possibly consumes resources through a cost of reproduction, consequently reducing the amount of stored resources. The disturbance caused by mowing potentially reduces flowering the following year through a reduction of the amount of stored resources. Direct climatic factors impact flower development, while indirect climatic factors relate to the effect climate has on production of biomass, and thus the amount of resources that may be allocated to flowering in the next growing season. The amount of stored resources was the sole unknown factor, and an autoregressive model was derived where flowering density could be assessed without information about the resource storage.

Using this approach, flowering density in year t is explained by what the flowering density was in year t - 1, whether the plot was mowed in year t - 1, and the impact of seven climatic variables. The climatic variables were monthly precipitation or effective temperature sum (*ETS*) data (Laaksonen 1979), and they were chosen based on which variables correlated the most with flowering density (linear regression). The direct climatic variables included were *ETS* May - June$_t$ and precipitation December - January$_t$, and the indirect climatic variables were the length of the growing season t - 1, precipitation May - June$_{t\text{-}1}$, *ETS* July - September$_{t\text{-}1}$, precipitation in July$_{t\text{-}1}$ and precipitation in October$_{t\text{-}1}$. The correlation between mowing, climatic variables and flowering was analysed by fitting the autoregressive model to each of the 126 time series. Mean flowering density and trend in flowering density (linear regression) was also obtained for each time series. The parameters estimated in these analyses were used as response variables in GLM's and GLMM's to ascertain whether there were differences in the impact on flowering density of mowing, climatic variables and previous flowering density due to study area, community group or mowing regime.

RESULTS AND DISCUSSION

The vegetation and hay crop in boreal rich fen

Sloping fens with rich (including extremely rich) fen vegetation of lawns and open margins were the main study objects. They represented the alliances Caricion atrofuscae at Sølendet, which included several alpine and continental species lacking in Tågdalen, and Schoenion ferruginei in Tågdalen, which included a number of oceanic species missing from the flora at Sølendet. Both alliances were originally described by Nordhagen (1936). Two lawn communities were distinguished, *Equisetum variegatum-Thalictrum-Campylium* at Sølendet, and *Eriophorum latifolium-Campylium* at Tågdalen. The open fen margin community *Gymnadenia-Succisa-Campylium* occurred in both study areas, but was represented mostly by samples from Sølendet. *Campylium stellatum* was the constant, dominant species in both lawn and margin vegetation. The shrub-dominated fen margin community *Galium boreale-Molinia-Hylocomiastrum pyrenaicum* included a number of grassland species, and was classified in the alliance Sphagno-Tomentypnion (Dahl 1957). It was found in both study areas. Samples in flat fens with carpet vegetation had *Scorpidium cossonii* and *S. scorpioides* as the most common species, and were classified in the alliances Stygio-Caricion limosae and Caricion lasiocarpae, with the communities *Drosera anglica-Scorpidium scorpioides* and *Eleocharis quinqueflora-Cinclidium*. The two fen margin communities had the highest species diversity with 50 and 56 species per plot (12.5 m^2) respectively. The numbers in carpet and lawn communities of fen expanse were in comparison 30-39. Species that invaded the areas after traditional mowing finished about 50 years ago contribute, but the potential species pool is also larger because some species predominantly found in grassland vegetation can enter the fen margins. These findings fit well with both the intermediate disturbance hypothesis (Connell 1978), and the humped-back model of species richness (Grime 2001).

In both study areas, mowing every 2nd year gave a hay crop of 109 g/m^2, while mowing every 4th year yielded about 140 g/m^2. Mowing every year (Sølendet only) yielded about 65 g/m^2, and it is apparent that the traditional practise of mowing every 2nd year was cost-effective, as mowing every year returns 60 % of the hay crop compared to mowing every 2nd year. Fen carpet had lower hay crop than both lawn and margin, while the latter two were similar. This did not vary between the study areas, indicating strongly that production is similar in ecologically similar rich fen plant communities, despite their classification into different alliances. A standing crop above 200 g/m^2 under mowed conditions (most common every year) is the norm in central Europe (Diemer et al. 2001, Hájková & Hájek 2003, Peintinger & Bergamini 2006, Rozbrojová & Hájek 2008), reflecting the warmer climate and, at least in some cases, the higher macronutrient availability compared to the upper boreal in central Norway.

It has been shown that production in rich fen vegetation is limited by both nitrogen and phosphorus, and also that the availability of these macronutrients in the soil is not reduced by mowing. Thus, the reduction in production caused by mowing is interpreted as mainly a result of disturbance (Øien & Moen 2001, Øien 2004). The hay yields documented here match those found by Moen (1990) twenty years ago, showing that the vegetation is adapted to the disturbance caused by mowing. We conclude that long-term mowing represents a major disturbance of the plant cover that tends to equalise biomass production in rich fens.

The impact of long-term mowing on ramets of *E. latifolium*

The average vegetative rosette had three mature leaves and one small (emerging) leaf, and the longest and widest leaves were on average 10 cm long and 3 mm wide. The average flowering ramet was 40 cm tall with three stalk leaves and four spikelets in the inflorescence. Mowing reduced the length, width and number of leaves in rosettes of *E. latifolium* in fen lawn at Tågdalen and fen carpet at Sølendet, but increased the same size parameters in fen lawn at Sølendet. This demonstrated, firstly, that the response to mowing in *E. latifolium* ramets was different in similar types of vegetation in two study areas, and, secondly, that the same mowing regime had opposite effects in carpet and lawn vegetation at Sølendet. The different impact of similar mowing intervals in similar vegetation in the two study areas may be explained by the use of a scythe and a two-year mowing interval at Tågdalen, and a motorised mower and a three-year mowing interval at Sølendet. The scythe is known to leave shorter stubble, and the intensity of disturbance is therefore higher when a scythe is used. Light may become a limiting resource (Tilman 1997) for rosette plants like *E. latifolium* in the absence of mowing as litter accumulates and plants grow taller. Elongation of leaves is a possible way for plants to avoid shading (Janečková et al. 2006), and the particularly long (and relatively narrow) leaves registered in *E. latifolium* in unmowed fen carpet may be a result of elongation. Thus, it may be that a larger proportion of the resources available to ramets in fen carpet were invested in above-ground structures, resulting in a larger relative impact of mowing. The opposite effects of mowing in carpet and lawn vegetation underscores the need for a thorough assessment of the vegetation when management plans are adopted because the same treatment is likely to yield different effects in different types of vegetation.

Most size parameters were affected by any mowing regime, but the width of leaves responded only to mowing every 3rd year. Thus, the leaves in *E. latifolium* ramets affected by disturbance through mowing decrease in length before they decrease in width. This reduces the amount of biomass likely to be removed during mowing, contributing to the long-term competitiveness of the species under mowed conditions. Flowering ramets had more stalk leaves in unmowed plots at Sølendet and more spikelets in unmowed plots at Tågdalen, whereas the effect of mowing on the height of flowering stalks was not clear. Flowering stalks at Sølendet were taller in carpet than lawn vegetation, while the number of spikelets was lower in carpet than lawn, suggesting a possible trade-off between vegetative and generative structures in flowering ramets.

Population dynamics of *E. latifolium*

The estimated population growth rates in Tågdalen were in the range 0.80-1.04, and at Sølendet in the range 0.77-1.00. Estimated and observed growth rates matched well at Tågdalen, whereas estimated growth rates was systematically lower at Sølendet. The seedling establishment ratio was the vital rate causing much of the differences in population growth rate between the study areas. This was calculated per plot as the ratio seedlings $t + 1$ / flowering ramets t, assuming a relationship between flowering and seedling emergence on a plot level. Seeds in *E. latifolium* can travel large distances (Soons 2006) and a spatial scale larger than plots could have yielded more realistic estimates, also, seedlings were rare, but tended to be temporally and spatially aggregated. The resulting seedling establishment ratio had a distribution that made it difficult to develop a model yielding accurate probabilities of this process. The recruitment phase is the least known part of the life history in *E. latifolium*, and deserves future attention.

Population growth rate in perennial vascular plants is often sensitive to changes in survival probability (Silvertown et al. 1993, Franco & Silvertown 2004, Jacquemyn et al. 2010, Sletvold et al. 2010), and this was also the case in *E. latifolium*. Survival probability had high elasticity in all the studied rich fen communities. The elasticity patterns were similar in both fen carpet and lawn at Sølendet and fen lawn cluster 4 at Tågdalen. Here, survival probability was paramount, but fecundity related vital rates were also of some importance. Lawn cluster 5 at Tågdalen represented a different pattern where fecundity had no impact, but where fragmentation and growth were important in addition to survival. This diverging elasticity pattern was likely a result of incipient succession in the relatively dry vegetation of this cluster towards a shrub-dominated fen margin/wet grassland community. Accumulated litter may impede seedling establishment (cf. Facelli & Pickett 1991), leaving fecundity without influence. Further, the clonal fragments in unmowed lawn in cluster 5 were large, and large clonal fragments had a much higher probability of fragmenting ($\kappa_{\geq 4}$ = 45.7 %, $\kappa_{<4}$ = 6.4 %), as reflected in the high elasticities involving fragmentation. Fragmentation as a demographic process may be of importance to maintain populations of clonal plants in unfavourable habitats. However, a model study emphasises that in a habitat where fragmentation is advantageous (in terms of fitness), then only "Splitters" (= clonal fragments disintegrate completely) can benefit from fragmentation (Oborny & Kun 2001). Fragmentation as we see it in *E. latifolium* may therefore be a result of stochastic factors (internal or external) rather than an adaptive trait.

Mowing affects plant populations in boreal rich fens for the most part through disturbance (Øien & Moen 2001), and mowing with a scythe every 2nd year (Tågdalen) was a severe enough disturbance to cause a decrease in population growth rate through lower growth and survival probabilities. Mowing with a motorised mower every 3rd year (Sølendet) yielded an increase in population growth rate through a higher seedling establishment ratio, indicating that *E. latifolium* thrived with this level of disturbance. We defined growth as an increase in the number of ramets in a clonal fragment from year *t* to *t* +1. Hence, the lower growth at Tågdalen could have been caused by either higher mortality of ramets within clonal fragments or decreased clonal reproduction. The mortality among ramets was higher in mowed than unmowed plots at Tågdalen, while the production of clonal offspring was similar between the mowing regimes. This indicated that mowing increased ramet turnover, but that clonal reproduction was unable to make up for the increased ramet mortality. Increased turnover of ramets within clonal fragments has also been found in *Carex membranacea* and *C. stans* (Tolvanen et al. 2001) and *Agrostis stolonifera* and *Lolium perenne* (Bullock et al. 1994) in disturbed (grazed) areas.

While long-lived species rarely exhibit high elasticities for fecundity (Silvertown et al. 1993, Franco & Silvertown 2004), elasticities involving flowering can occasionally be substantial (Ehrlén et al. 2005, Sletvold et al. 2010). Flowering probability had low elasticity but explained much of the year-to-year variation in population growth rate in *E. latifolium*, emphasising that vital rates with low elasticity can be of importance when they have high variability (Paper IV).

The impact of climate, mowing and cost of reproduction in *E. latifolium*

The annual flowering density (number of flowering ramets m^{-2}) in *E. latifolium* varied considerably between years (1982-2008) in the study areas. At Tågdalen, the peak density in 1994 (18.5 ramets m^{-2}) was about 70 times higher compared to the minimum in 1995 (0.26 ramets m^{-2}) (Fig. 17). The short-term effect of mowing was a reduction in flowering density, likely as a result of a reduction in the resource storage. This negative short-term disturbance effect (Crawley 1997a) was balanced by the positive long-term effect of mowing on both the mean and the trend in the flowering density, highlighting the need for long-term monitoring to assess long-term phenomena. Boreal rich fens often have low nutrient availability (e.g. Øien & Moen 2001), and stress-tolerant species (Grime 2001) are at an advantage if the disturbance is moderate. The mean flowering density was lower with mowing every year compared to mowing every 2nd or 4th year.

The trend in flowering (1982-2008) was, however, positive for all mowing regimes. So, even if mowing every year resulted in a lower flowering density than longer mowing intervals, there was no reduction with time. This suggests that mowing every 2nd or 4th year is optimal for *E. latifolium* in boreal rich fen, and also that the disturbance caused by mowing every year is tolerable, but that sexual reproduction is limited because of the constant removal of stored resources.

The autoregressive modelling approach allowed a simultaneous assessment of the relative impact of mowing and flowering at year *t* - 1 and direct and indirect climatic effects on flowering density. A cost of reproduction (Calvo & Horvitz 1990, Ehrlén & Eriksson 1995) in *E. latifolium* was demonstrated in all the flowering time series, irrespective of study area, mowing regime or plant community. The cost of reproduction was the factor with the highest impact on flowering density, and this is a reflection of the overall pattern of alternate “good” and “bad” years for flowering (Fig. 17).

In boreal areas, plant growth is generally hampered by low temperatures (Crawley 1997a). Warm conditions in spring can therefore be assumed to be beneficial for plant development in our study areas, and we found a positive correlation between *ETS* in spring and flowering density the same year. Warm conditions in summer year *t* - 1 affected flowering density in south-facing, steeply sloping fens at Tågdalen negatively, while wet conditions affected flowering density positively. This suggests drought as an important, negative factor in dry fen communities at Tågdalen. A wet spring in year *t* - 1 had an adverse effect on flowering density at Sølendet, possibly as a result of inundation that hinders resource storage. The fens at Sølendet are less sloping than those at Tågdalen, and they are fed spring water at constant rates throughout the year. They may therefore become waterlogged more easily when exposed to high levels of precipitation. A long growing season in year *t* - 1 caused an increase in flowering density at Tågdalen, presumably through an increase in resource acquisition and storage.

The population at oceanic Tågdalen was more sensitive to the impact of climatic variables than the population in continental Sølendet. This seems to be caused partly by larger year-on-year variations in precipitation at Tågdalen, and partly by local topographical and hydrological differences that rendered the population at Tågdalen more susceptible to climatic variation. The collapse in flowering density in 1995 at Tågdalen was likely caused by a combination of cost of reproduction and several climatic factors accentuating their reciprocal effects on flowering density in the period 1993-95.

CONCLUSIONS AND FURTHER STUDIES

This study has focused on *E. latifolium* on the level of the ramet, the clonal fragment, and the population, and the boreal rich fen as a system has been the backdrop throughout. The comparison of two populations of the species has revealed both similarities and discrepancies in the response to mowing, and this could in part be explained by the regional differences between the study areas. The oceanic climate at Tågdalen contributed to larger fluctuations in flowering density in *E. latifolium* in this study area, while the dynamics of flowering to a large extent was governed by cost of reproduction at Sølendet with a more continental climate. This further suggests that the more stable course of flowering density through time at Sølendet is a consequence of stronger internal control through cost of reproduction, whereas the more fluctuating progress in flowering density at Tågdalen is caused by climate temporarily overriding this controlling mechanism. Whether larger fluctuations in flowering density is a general consequence of a varying oceanic climate is a topic suitable for further studies. Flowering density has been followed in a number of species at Tågdalen and Sølendet, and similar analyses of the effects of climate on flowering makes an interesting prospect. This allows for the comparison of species with different growth habit or distribution in the light of the oceanic –continental gradient represented by the study areas, and could further our understanding of the effects of climate on plant populations.

Large areas of formerly mowed hay fens are currently undergoing a succession, and at least fen margins can be expected to change towards shrub-dominated fens resembling wet grassland communities. In an unmowed situation, *E. latifolium* will likely persist in carpet and lawn expanse, but may disappear from fen margins. This was indicated by the changes in demographic patterns in a moderately overgrown dry lawn community, where flowering and seedling establishment had a very low impact on population growth rate, and fragmentation and growth of adult clonal fragments was more important than in unmowed carpet and wetter lawn communities.

At Tågdalen, mowing every 2nd year in lawn communities had a negative impact on the size of individual ramets, and also lowered the population growth rate compared to unmowed areas. This was the opposite at Sølendet, where mowing increased both the size of ramets and the population growth rate. This difference may be attributed to a mowing regime with somewhat higher frequency and intensity at Tågdalen. In the study of flowering there was no difference in mowing regimes, and flowering density responded similarly to mowing in both study areas. The short-term effect was negative because of damage and loss of biomass (disturbance), but the long-term effect was positive, with higher flowering density in mown plots. Mowing every year lowers the flowering density, and represents a severe disturbance to *E. latifolium*. Mowing every 2nd year with a scythe is positive for flowering density, but may still affect the species negatively, as suggested by the smaller ramets and reduced growth rate. Mowing every 3rd and 4th year has positive effects on ramet size, growth rate and flowering, and these mowing regimes are optimal for this species in boreal rich fen. A population transition matrix model based on biomass or total leaf area of clonal fragments rather than number of ramets may be biologically more realistic, but the data needed is also more difficult to obtain. A study comparing these approaches would be of interest to determine whether the gain in terms of realism outweighs the incurred costs. There is a need for more information about the seedling establishment phase of *E. latifolium*. This is without doubt the least known part of the life history of this species, and a better understanding will likely improve estimates of population growth rate considerably, and further the possibility of accurately analysing its population dynamics.

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Paper I

Rich Fen Vegetation and Hay Crop on Traditionally Used Outlying Land in Central Norway

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Abstract

The vegetation and hay crop in upper boreal (sub-alpine) rich hay fens was investigated in permanent plots in a long-term study in the nature reserves Sølendet (continental climate) and Tågdalen (oceanic climate). The main aims were to classify the rich fen vegetation and assess the hay crop in different plant communities mowed every year, every 2nd year and every 4th year. The description of the vegetation was based on 134 sample plots and 200 taxa, using TWINSPAN classification and DCA ordination, and the relationship between hay crop, study areas, vegetation and mowing regimes were analysed using generalised linear mixed models. The vegetation was classified into six plant communities and ten vegetation clusters. Sloping fens with rich (including extremely rich) fen vegetation of lawns and open margins were most common, representing the alliances Caricion atrofuscae at Sølendet (including alpine/continental species lacking in Tågdalen) and Schoenion ferruginei in Tågdalen (including oceanic species). *Campylium stellatum* was the constant dominant species in both lawn and margin vegetation. Samples in flat fens with carpet vegetation in both study areas (with *Scorpidium cossonii* and *S. scorpioides* as the most common species) were classified in the alliances Stygio-Caricion limosae and Caricion lasiocarpae. Shrub-dominated fen margin communities were classified in Sphagno-Tomentypnion. Two fen margin communities had the highest species diversity, with 50 and 56 species per plot (12.5 m^2) respectively. The numbers in carpet and lawn communities of fen expanse were in comparison 30-39. This fits well with both the intermediate disturbance hypothesis and the humped-back model of species richness. In both study areas, the traditional mowing frequency of mowing every 2nd year gave an average hay crop of 109 g/m^2, while mowing every 4th year yielded about 140 g/m^2. Mowing every year (Sølendet only) yielded about 65 g/m^2, showing that the traditional practise of mowing every 2nd year was effective. Fen carpet had lower hay crop than both lawn and margin, while the latter two were similar. This did not vary between the study areas, indicating that biomass production is similar in ecologically similar rich fen plant communities. We conclude that long-term mowing represents a major disturbance of the plant cover that tends to equalise biomass production in rich fens.

Keywords

Biomass · Boreal region · Caricion atrofuscae · Schoenion ferruginei · DCA · Long-term studies · Permanent plot · TWINSPAN · Vegetation ecology

Introduction

Vegetation ecology (Mueller-Dombois & Ellenberg 1974: 7) is plant ecology at the community level, and two major ways of relating the plant communities to one another and to the environment are distinguished:

- Classification groups communities into classes (community types, syntaxonomy) that may be characterised and treated as discontinuous with another. Phytosociology is the approach that emphasises the classificatory perspective (van der Maarel 1979: 163).
- Gradient analysis deals with variations in vegetation and ecological factors along gradients. The arrangement of samples in relation to environmental gradients as a basis for gradient analyses is termed ordination (Whittaker 1973).

The basis of vegetation ecology is plot samples (relevées) which are brought together in tables. A vegetation table can be seen as an information matrix with a two-way structure, generally with species in rows and samples in columns. There are two main types of samples-by-species matrices (Gauch 1982). The species space has species as axes with the samples as points in the multidimensional space, while in the sample space the samples are axes with the species as points. In the central European phytosociological tradition (Braun-Blanquet 1964, Dierssen 1982, Ellenberg 1988), the sample space is emphasised, and a species restricted to a limited volume of sample space is a character species. This approach is concerned with the character species, and it is necessary to have at least one character species to identify an association. The central European tradition for classifying mire vegetation follows this system (e.g. Dierssen 1982, Rybniček et al. 1984). Scandinavian phytosociologists (e.g. Nordhagen 1928, 1943, Dahl 1957) have generally compared points in species space, and used degree of dominance and differential species to separate units; a species only occurring in one unit is considered a characteristic species (Dahl 1987). In classification of vegetation (including mires), the syntaxonomic system is rather close to the central European system.

The Fennoscandian tradition in the study of mire vegetation has a more ecologically based conception, distinguishing principally between ombrotrophic and minerotrophic vegetation (e.g. Tuomikoski 1942, Sjörs 1948, Du Rietz 1949, Ruuhijärvi 1960, Persson 1961, Eurola 1962, Malmer 1962a, b). Further differentiation is based on the three local vegetation gradients, poor – rich, reflecting the pH and the mineral concentration, mire expanse – mire margin, (often) reflecting the peat depth, and hummock – mud bottom, reflecting the groundwater level. However, these gradients are complex, and several environmental factors change more or less in the same direction. This system has commonly been used in Scandinavia of late (e.g. Moen 1990, Økland 1990, Moen 1995, Rydin & Jeglum 2006). In this paper, we deal with rich fen vegetation (mainly extremely rich vegetation) in both mire expanse and mire margin, and lawn and carpet vegetation along the third gradient. In recent decades, vegetation ecology has benefited from the development of efficient multivariate methods for summarising relationships in vegetation and relating variation to ecological factors. This paper uses both classification (TWINSPAN) and gradient analysis (DCA ordination).

The upper boreal rich fens were traditionally used to make hay for winter fodder. Mowing was done every 2nd year using a scythe, and the typical hay crop was 100-150 g/m^2. Studies in boreal hay fens in central Norway (Moen 1990, Aune et al. 1996, Moen et al. 1999) have shown a reduction in the hay crop as well as the above- and below-ground biomass of the field layer, and an increase in the ratio of the above-ground/below-ground biomass with increasing mowing frequency. Thus, mowing forces the plants to mobilise resources from their below-ground organs (Fitter 1986, Aune et al. 1996). Øien & Moen (2001) found no depletion of soil nitrogen or phosphorus as a result of mowing, and the much lower biomass in the regularly mowed plots was regarded as being mainly a result of disturbance caused by the mowing rather than stress induced by nutrient limitation. There is reason to believe that long-term mowing will affect vegetation differently in different plant communities. Estimates of hay crops given by Moen (1990: 134) suggest an overall lower field layer production in fen carpet than lawn or margin vegetation.

The aims of this study are to classify and compare the rich fen vegetation in two upper boreal areas in central Norway formerly used for haymaking, interpret gradients in the vegetation, and assess how hay crops vary between plant communities mowed at different intervals. The study areas are floristically and ecologically rather similar, but vary along the oceanic – continental climatic gradient. We utilised 134 vegetation samples (1967-2008) to describe the plant communities of rich fens and relate the communities in our study areas to descriptions in existing European mire literature. Hay crop measurements (n = 902, 1982-2009) were applied to evaluate the long-term effects of three mowing frequencies on hay crops in fen carpet, lawn and margin, respectively. We hypothesise a decrease in the hay crop with increasing mowing frequency, and a larger hay crop in lawn and margin than in carpet. Hay crop yields and responses to mowing are expected to be similar in the two study areas.

Material and Methods

Study Areas

The study was conducted in two areas in central Norway, Sølendet Nature Reserve in Røros and Tågdalen Nature Reserve (with its immediate surroundings) in Surnadal and Rindal (Fig. 1). For detailed descriptions of the study areas, see Moen (1970, 1990, 2000). Both study areas are situated in the transition between the middle boreal and northern boreal vegetation zones (zonation after Moen 1999) and experience a short growing season, usually lasting from late May to late August. The distance between the study areas is 145 km, and they differ in conditions like temperature and precipitation (Table 1). Tågdalen has an oceanic climate with a mean annual precipitation of 1583 mm and a thick, long-lasting snow cover, while Sølendet has a more continental climate with a mean annual precipitation of 637 mm and less snow. The study areas are both dominated by base-rich rocks like grey-green phyllite, mica schist and greenstone (Solli & Nordgulen 2008). The bedrocks and the moraine yield a base-rich, fine-grained soil which tends to become readily waterlogged, leading to paludification (peat formation).

Both Sølendet and Tågdalen have large areas of rich fen vegetation dominated by lawn communities. The rich fens are influenced by base-rich water from the mineral soil or spring areas. Sloping fens (slope > 3^{g}) cover large areas in both nature reserves. At Tågdalen, the slope of fens reaches 20^{g}, and in areas with a slope of $3\text{-}7^{g}$, the peat layer mostly exceeds 50 cm. In general, the steeper the slope the shallower the peat, and the steepest sloping fens have only a few cm of peat. At Sølendet, the steepest sloping mires are up to about 8^{g}, and the peat layer in sloping fens is mostly shallow (< 50 cm). In fens with a slope of less than 3^{g} and on flat fens and springs, the peat layer reaches 80 cm at Sølendet and often exceeds 2 m at Tågdalen. The rich fens in both study areas were used for haymaking for centuries, but traditional mowing ceased around 1950. The traditional regime was mowing every 2nd year, drying the herbage on the ground and gathering the dried hay in hay barns or hay stacks.

Sample Plots, Cover Scale and Vegetation Layers

Altogether 134 samples from permanent plots (mostly 25 or 12.5 m^2) were included in the multivariate analyses, 61 from Sølendet and 73 from Tågdalen. The permanent plots were nested in 29 localities at Sølendet and 28 localities at Tågdalen, some localities contained more than one plot, and in some plots samples were taken several times between 1967 and 2008. A locality is, in this context, a spatially congregated group of permanent plots. The permanent plots were either mowed every year, every 2nd year, every 3rd year, every 4th year or left unmowed, and the time since the last mowing of a plot has ranged from one to about 50 years. At Tågdalen, 36 of the samples were from 1967-68 (included in Moen (1970)); the remainder were new analyses or re-analyses in the same plots from the period 1975-2008. At Sølendet, 47 of the samples were from

1974-1986 (included in Moen (1990)); the remainder were more recent analyses in the same localities made during 1992-1999. The sample plots satisfied the following criteria:

- They represented rich fen vegetation previously used for haymaking, i.e. open lawn and carpet vegetation, and mire margin vegetation invaded by shrubs in recent decades.
- They represented areas with homogeneous vegetation (stands). The sample plot was restricted to the homogeneously mowed area in localities with plots mowed at different frequencies.
- The samples had full species lists of vascular plants, bryophytes and macrolichens.
- The cover scale of the sample plots could be rescaled into a six degree scale (close to the Hult-Sernander-Du Rietz scale (Malmer 1962a) with the classes 1: < 6.25 %, 2: 6.3 - 12.5 %, 3: 12.6 - 25 %, 4: 26 - 50 %, 5: 51 - 75 % and 6: 76 - 100 %.

The vegetation was separated into a shrub layer (B, woody plants 0.3-2 m), a field layer (C – E, herbs, graminoids and woody plants < 0.3 m) and a bottom layer (F – H, bryophytes and macrolichens). A tree layer did not occur. A majority of the samples was made as a synthesis of three to five small quadrats (0.25 m^2) analysed inside the larger plot. The “plot cover” was calculated as the mean of the cover degree of the small quadrats, based on the mean value of the cover classes (Malmer 1962a, Moen 1990). Species occurring in the plot, but not in the small quadrats, were given a cover value in the sample. 200 entries of taxa were used in the multivariate analyses, 195 taxa (hereafter generally called species) and the five shrubs (*Alnus incana, Betula nana, B. pubescens, Salix glauca* and *S. myrsinifolia)* occurring in two vegetation layers. Consult Appendix 1 for a list of the names and abbreviations of the 200 species.

Taxonomic Notes and Taxa Used

The nomenclature follows Elven (2005) for vascular plants, Frisvoll et al. (1995) for mosses and liverworts, and Krog et al. (1994) for lichens. A number of separate taxa were either merged or included in other taxa in the multivariate analyses. Species of the genera *Alchemilla* and *Cephaloziella* were considered as one taxon, *Anthoxanthum odoratum* may include *A. nipponicum*, *Carex vaginata* included the hybrid *C. panicea* x *vaginata*, *Dactylorhiza lapponica* included *D. lapponica* hybrids, *Pyrola rotundifolia* included *P. norvegica*, *Salix myrsinifolia* coll. included *S. borealis* and *S. myrsinifolia* hybrids and *Viola palustris/epipsila* included the two species and perhaps the hybrid between them. *Bryum pseudotriquetrum* may include close taxa like *B. creberrimum* and *B. pallescens*, *Palustriella commutata* included *P. falcata* (the latter was the more common species) and *Philonotis fontana* included *P. tomentella*. *Rhytidiadelphus squarrosus* may include *R. subpinnatus*, *Sphagnum auriculatum* coll. may include *S. inundatum*, *Cephalozia lunulifolia* coll. may include close taxa like *C. loitlesbergeri* and *Chiloscyphus pallescens* may include *C. polyanthus*. *Dactylorhiza cruenta* and *D. incarnata* were regarded as species (subspecies in Elven (2005)).

Classification

TWINSPAN for Windows 2.3 (Hill & Šmilauer 2005) was used for classification. The number of cut levels was set to six, reflecting the six degree scale of cover, and neither samples, species nor pseudospecies levels were weighted. The maximum number of indicator species per division was seven, and the maximum level of divisions was four, but large clusters with more than 30 samples were further divided. The TWINSPAN classification (Fig. 2) was used to construct Table 2, which distinguishes frequency and abundance values. The frequency of occurrence of a species in a group of communities was set to constant classes: I: 0-20 %, II: 21-40 %, III: 41-60 %, IV: 61-80 %, V: 81-100 %. We refer to species in frequency class V as constant species, IV and III as (very) frequent, II as occasional and I as scarce. The abundance values for clusters were estimated as the "characteristic degree" of cover according to Malmer (1962a), which means that only the samples that include the particular species are taken into account (opposite to mean cover). A dominant species had a cover of 4, 5 or 6 (> 25 %), and the terms abundant (cover 2 and 3) and sparse (cover 1) were used for species with less cover. Characteristic species were more or less (exclusively or preferentially) restricted to one community. Differential species were more or less confined to one or some communities compared to others. Indicator species were used as defined in Hill & Šmilauer (2005); they are highly preferential species in each TWINSPAN division.

Ordination

Ordinations were run using CANOCO for Windows 4.5 (ter Braak & Šmilauer 2002). DCA with detrending by segments was chosen, and no species were excluded. Analyses with and without downweighting of species were carried out on the same data set as for the TWINSPAN classification. Ordination plots (Fig. 3) were drawn in CANODRAW 4.5.

Hay Crop

The term hay crop includes the above-ground biomass and the litter attached to living plants, but excludes the stubble left after mowing. Thus, hay crop differs from both above-ground biomass and above-ground standing crop (e.g. Pearsall & Gorham 1956). However, the litter fraction amounts to 10-20 % of the hay crop in most communities and with most mowing frequencies, and the stubble, 2-4 cm in height, also amounts to about 10-20 % of the hay crop. Consequently, hay crop and above-ground biomass are often similar (Moen 1976, 1990, Aune et al. 1996).

Mowing was performed with a scythe in permanent plots in early August in all years. The mowing regimes were every year, every 2nd and every 4th year since 1974 at Sølendet, and every 2nd and every 4th year since 1973 at Tågdalen (Moen 1990). Note that a different set of criteria (see below) were used to select plots for the analyses of hay crop than for the multivariate analyses, hence the differences in included mowing regimes. The herbage was weighed in the field after mowing, and three representative samples were collected and frozen while fresh. These samples were weighed prior to and after drying (70 °C, 48 hours), and the hay crop (g/m^2) was estimated based on the percentage of dry matter. Decades of abandonment in both study areas had resulted in increased above-ground biomass and accumulation of litter. The harvested hay crop decreased the first years after mowing recommenced (Moen 1990: 356), and estimates of the hay crop were not considered valid until three cycles of a mowing treatment were completed. Few estimates of the hay crop from before 1982 met the selection criteria, and we omitted all data older than 1982 to make the data set as homogeneous as possible. A total of 902 separate hay crop measurements from 1982-2009 were included in the statistical analyses.

Two models were developed to explore the relationships between the hay crop, study areas, mowing regimes and vegetation. The first concerns differences in the hay crop between Sølendet and Tågdalen with the mowing regimes mowed every 2nd and 4th years in three groups of plant communities (hereafter called community groups). The community groups were fen carpet (C), fen lawn (L) and fen margin (M). Fen carpet incorporates vegetation clusters 1-3, fen lawn comprises clusters 4-7, and fen margin encompasses clusters 8-10 (see Fig. 2). Mowing every year was present at Sølendet only, and a separate model to ascertain the effect of mowing regimes in this study area was developed. The modelling approach was in both cases generalised linear mixed models (GLMM, Zuur et al. 2009). The estimates of hay crop were collected over 28 years from 82 plots that were nested in 37 localities. Consequently, we treated locality, plot and year as random factors in the GLMM's. The minimal adequate (i.e. most parsimonious) models were identified through stepwise exclusion of factors and interactions between factors (starting with full models) based on deviance tests (e.g. Jongman et al. 1995). The structure of the part of the model with random factors was determined first, followed by the structure of the fixed factor part. The response variable (hay crop (g/m^2)) was log-transformed to attain an approximate normal distribution. The statistical analyses of the hay crop were conducted in the R statistical environment (R Development Core Team 2008), making especial use of the packages "gplots" (Warnes), "lattice" (Sarkar 2008) and "lme4" (Bates et al. 2008).

Results

TWINSPAN Classification in Clusters and Plant Communities

The structure of the TWINSPAN divisions is shown in Fig. 2, and the output from the TWINSPAN classification is summarised for both a plant community hierarchy and a species hierarchy in Table 2. There are 121 entries in Table 2, 119 species and *Betula nana* and *B. pubescens* occurring in both layers B and C. 115 of these species were present in at least five of the 134 samples, while four species occurred in fewer than five samples but were included because they were important differential species for small clusters. Consult the Electronic Supplementary Material for the total TWINSPAN table (134 samples and 200 species).

The first dichotomy (Fig. 2) divided the data set into two nearly equally sized groups; 73 samples (65 from Tågdalen and 8 from Sølendet), with *Andromeda polifolia* and *Drosera anglica* as indicator species, and 61 samples (53 from Sølendet and 8 from Tågdalen) with five indicator species, among them the typical, extremely rich upland/continental fen species *Equisetum variegatum* and *Pedicularis oederi*, both of which are absent from Tågdalen. The first group (left in Fig. 2) was divided into a subgroup of the eight samples from Sølendet (further subdivided into clusters 1 and 2) with indicator species *Eleocharis quinqueflora*, and a subgroup of the 65 samples from Tågdalen (clusters 3-5). The second group (right in Fig. 2) was divided into a large subgroup of 50 samples (two from Tågdalen), with *Pedicularis oederi*, *Campylium stellatum* (pseudospecies level 4) and *Scorpidium cossonii* as indicator species, and a subgroup of 11 samples (a mix from the two study areas) with *Galium boreale* and *Geranium sylvaticum* as indicator species. The third level of division separated the latter subgroup in cluster 9 with 6 samples from Tågdalen (with indicator species *Andromeda polifolia*) and cluster 10 with 5 samples from Sølendet. Clusters 1, 2, 9 and 10 had few samples, and were small clusters defined after the third level of division. At the same level, cluster 3 (with ten samples, all from Tågdalen) was separated from the large cluster with indicator species *Scorpidium cossonii.* Cluster 8 (with 18 samples, only one from Tågdalen) had 6 fen margin/grassland species like *Crepis paludosa*, *Leontodon autumnalis* and *Deschampsia cespitosa* as indicator species. The central clusters after level 3 were large, with 55 samples in clusters 4 and 5 (all from Tågdalen), and 32 samples in clusters 6 and 7 (31 from Sølendet) included. On the left (Tågdalen) side of the principal dichotomy, division 4 separated 30 samples into cluster 4 (*Drosera anglica* as indicator species) and 25 samples into cluster 5 (six indicator species, e.g. *Saussurea alpina*, *Succisa pratensis* and *Thalictrum alpinum).* On the right (Sølendet) side, the fourth division separated the group of 32 samples into the equally sized clusters 6 (*Barbilophozia rutheana*, *Pedicularis palustris* and *Carex rostrata* as indicator species) and 7 (no indicator species). The ten clusters and the 16 species groups including 121 species are presented in Table 2.

Six plant communities and ten clusters

Community I: Eleocharis quinqueflora-Cinclidium *carpet community*

Clusters 1 (two samples) and 2 (six samples); all from Sølendet.

Eleocharis quinqueflora and *Cinclidium stygium* were characteristic species of the community and altogether eight species were constants in both clusters (e.g. *Triglochin palustre* and *Scorpidium cossonii* (very common)). Both clusters had an average of 32 species per plot, and 21 and 17 constants, respectively. Cluster 1, with only two samples from the same spring-influenced fen, had a number of characteristic species (e.g. *Utricularia minor*, *Carex heleonastes*, *Calliergon giganteum* and *Meesia triquetra*). Cluster 2 was a drier carpet community that included a number of differential species to cluster 1 (e.g. *Andromeda polifolia*, *Trichophorum cespitosum* and *Gymnocolea borealis*), species which also occur in lawn communities II-IV.

Community II: Drosera anglica-Scorpidium scorpioides *carpet community*

Cluster 3 (ten samples); all from Tågdalen.

Dactylorhiza incarnata and *Scheuchzeria palustris* were characteristic species, and *Drosera anglica* was a differential species towards community I. The constants *Menyanthes trifoliata*, *Carex limosa* and *Scorpidium scorpioides* (dominant) were differential species towards clusters 4-10. Altogether 13 species were constants (e.g. the abundant species *Trichophorum cespitosum*, *Campylium stellatum* and *Scorpidium cossonii*). Cluster 3 had an average of 29 species per plot which was the lowest of all clusters.

Community III: Eriophorum latifolium-Campylium *lawn community*

Clusters 4 and 5, with 30 and 25 samples; all from Tågdalen.

This community had no exclusive characteristic species, but a number of species were differential towards communities I, II, IV, V and cluster 10 of community VI. These typical Tågdalen species (lacking at Sølendet) included *Narthecium ossifragum*, *Schoenus ferrugineus* (dominant in some plots in cluster 4) and *Scapania degenii*. In addition, *Carex hostiana*, *Eriophorum latifolium* and *Trichophorum alpinum* had main occurrences in this community. *Campylium stellatum* was a dominant, and *Molinia caerulea*, *Trichophorum cespitosum* and *Scorpidium cossonii* were abundant constants. There were 14 additional constant species in both clusters: *Parnassia palustris*, *Potentilla erecta*, *Selaginella selaginoides*, *Thalictrum alpinum*, *Tofieldia pusilla*, *Carex dioica*, *C. panicea*, *Eriophorum angustifolium* and *Gymnocolea borealis.* Clusters 4 and 5 were separated at level four in the TWINSPAN classification, and they were rather closely related, with an average number of species of 30 and 38, and 16 and 22 constants, respectively. Cluster 4 was closest to the carpet communities I and II, as shown by higher frequencies of typical carpet and fen expanse species like *Drosera anglica* and *Scorpidium cossonii*. Cluster 5 was a somewhat drier sloping fen community, with more frequent occurrences of lawn and fen margin species like *Saussurea alpina*, *Succisa pratensis* and *Carex capillaris.*

Community IV: Equisetum variegatum-Thalictrum-Campylium *lawn community*
Clusters 6 and 7 with 16 samples each, all from Sølendet except one in cluster 7.
The community was not separated from the other communities by characteristic species, and had most of the dominant and abundant constants in common with communities II, III and/or V (e.g. *Thalictrum alpinum*, *Molinia caerulea, Trichophorum cespitosum*, *Campylium stellatum* and *Scorpidium cossonii*). A number of Sølendet species that were lacking or rare in fens at Tågdalen were differential species towards communities II and III: *Betula nana*, *Dactylorhiza cruenta*, *Equisetum variegatum*, *Pedicularis oederi*, *Kobresia simpliciuscula* and *Tomentypnum nitens. Carex rostrata*, *Eriophorum latifolium* and *Scorpidium cossonii* (abundance only) were differential species towards community V, but there were generally few and rather weak differential species between communities IV and V. Clusters 6 and 7 had on average 36 and 37 species and 22 and 21 constants per plot, and the clusters were separated at level 4 in the TWINSPAN classification. Cluster 6 represents the typical sloping fen at Sølendet where the field layer was moderately tall and included large occurrences of low-growing, rich fen species like *Saxifraga aizoides*, *Thalictrum alpinum*, *Carex capillaris* and *Kobresia simpliciuscula.* Cluster 7 had a field layer of tall-growing species like

Pedicularis palustris, *Carex lasiocarpa* and *C. rostrata*, with *Fissidens adianthoides* and *Barbilophozia rutheana* in the bottom layer.

Community V: Gymnadenia-Succisa-Campylium *fen margin community*
Cluster 8 with 18 samples, all except one from Sølendet.
The community was separated from IV by a number of fen margin species that occurred as constants (e.g. *Bartsia alpina*, *Crepis paludosa*, *Gymnadenia conopsea*, *Leontodon autumnalis*, *Saussurea alpina*, *Succisa pratensis* (abundant), *Deschampsia cespitosa* and *Molinia caerulea* (abundant)). Some species of open fens were differential towards community VI (e.g. *Pedicularis oederi*, *Scorpidium cossonii*, *Gymnocolea borealis*). *Campylium stellatum* was the only dominant constant, but additional abundant constants were *Thalictrum alpinum*, *Carex panicea* and *Trichophorum cespitosum*. The community was species-rich with a mean of 50 species and 25 species as constants.

Community VI: Galium boreale-Molinia-Hylocomiastrum pyrenaicum *fen margin community*
Cluster 9 with six samples from Tågdalen and cluster 10 with five samples from Sølendet.
This fen margin community was separated from the other communities by fen margin/grassland species like *Filipendula ulmaria*, *Galium boreale*, *Geranium sylvaticum* and *Hylocomiastrum pyrenaicum*. Plots that were not mowed included shrubs like *Betula nana*, *B. pubescens*, *Salix glauca* and *S. myrsinifolia*. *Saussurea alpina* and *Molinia caerulea* were constants, and both species were abundant in cluster 10. The clusters were separated at the third level. Cluster 9 included samples from two localities in Tågdalen, while all the plots in cluster 10 were from the same locality at Sølendet. The two clusters were rather different, with many differential species like *Betula pubescens* (as a shrub), *Equisetum palustre*, *Tofieldia pusilla*, *Carex flava*, *C. panicea* and *Callergonella cuspidata* in cluster 9, and *Betula nana* and *Tomentypnum nitens* as the only dominant differential species for cluster 10. Cluster 9 included the most species-rich samples and had a mean of 56 species and 36 constants, while cluster 10 had 39 species as a mean, and only 13 constants.

DCA Ordination, the Main Gradients

The data set used for the analyses comprised 134 samples and 200 species. Eigenvalues and gradient lengths for the first four axes of the DCA ordinations, with and without downweighting of rare species, are presented in Table 3. All values, including total inertia, were lower in the analysis with downweighting of rare species. However, the first four axes with downweighting explained 29 % of the total variation in the floristic data (ETIR) compared to 21 % in the analysis without downweighting. In both ordinations, the values of the first axis were much larger than the second, which in turn were much larger than the third. The length of the first DCA axis was 3.0 and 3.4, respectively, for the ordinations with and without downweighting of rare species. Figure 3 shows the outcome of the DCA analysis with downweighting of rare species.

On the first axis, the samples of cluster 10 had the lowest score, with the very lowest values noted in two samples dominated by *Betula nana* in the shrub layer, and that have been unmowed for 50 years. The samples of cluster 10 were followed by those of clusters 8 and 9. At the other end of axis 1, the samples of cluster 3 had the highest values, followed by those of clusters 2, 4 and 1. A majority of the samples from Tågdalen had high values. Shrubs (*Betula* spp., *Salix* spp.) and a number of fen margin and grassland species like *Geum rivale, Pyrola minor* and *Anthoxanthum odoratum* had low values, while fen expanse species like *Dactylorhiza incarnata*, *Carex limosa, Schoenus ferrugineus* and *Scorpidium scorpioides* had high values. The species and sample ordination thus indicated a fen margin/dry fen – fen carpet gradient.

On the second axis, the samples of cluster 1 had the lowest values, followed by samples of clusters 2, 6, 7 and 3. Samples of cluster 9 had the highest scores, and thereafter some samples of clusters 4 and 5. Low species scores were found in, for example, *Carex heleonastes*, *Eleocharis quinqueflora*, *Calliergon giganteum* and *Meesia triquetra*, and high values were found for both the shrubs *Betula pubescens* and *Salix* spp. and other fen margin species like *Luzula sudetica* and *Calliergonella cuspidata*. However, a number of extremely rich fen species like *Equisetum variegatum*, *Leontodon autumnalis* and *Kobresia simpliciuscula* associated with thin peat have low values. The species and sample ordination indicated a gradient from spring fen/fen carpet to (overgrown) fen margin, and the Sølendet samples and clusters had low values compared to the parallels from Tågdalen.

The third axis (species ordination not shown) had the lowest scores for the samples of cluster 1, and rather low scores for a majority of samples from clusters 2, 7 and 9. The highest scores were found in samples from cluster 6 and to some extent cluster 8. The axis separated the two clusters (6 and 7) of community IV well. Samples from Tågdalen were generally grouped close to the middle of the axis. Species mainly occurring in cushions, including *Aulacomnium palustre*, *Tomentypnum nitens*, all nine *Sphagnum* spp., and a large number of hepatics (e.g. four out of five *Scapania* species), had negative scores on the third axis. Negative scores for some shrubs indicate the initial development of low hummocks and possibly some overgrowing. Indicators of extremely rich vegetation like *Gymnadenia conopsea*, *Saxifraga aizoides*, *Carex hostiana* and *Kobresia simpliciuscula* had high scores on the third axis. Axis three certainly is complex, with a tendency to a cushion (low hummock initials) – dry margin fen gradient. A number of low-growing species mainly occurring in rich, damp grasslands and species on thin peat or spring-influenced fens were found with high scores. Thus, there were also elements of poor – rich and fen expanse – fen margin gradients in axis 3.

Hay Crop

The hay crop in rich fen vegetation mowed every 2nd year was very similar in the two study areas, with a mean of 109.2 g/m^2 at Tågdalen and 109.3 g/m^2 at Sølendet (Fig. 4). Mowing every 4th year compared to every 2nd year yielded higher hay crops in both areas ($|t| > 2$), and the response between the two areas was identical (Fig. 4, $|t| = 0.213$). The yield was lower for all three community groups in plots mowed every 2nd year than in those mowed every 4th year (Fig. 5), but was demonstrably lower ($|t| > 2$) only in carpet and margin vegetation. The yields in the lawn and margin community groups (L and M in Fig. 5) were similar for both mowing regimes, but differed from the yield in carpet vegetation mowed every 2nd year. The lowest yield was recorded in carpet mowed every 2nd year (70.7 g/m^2), and this differed ($|t| > 2$) from all the other categories except margin mowed every 2nd year ($|t| = 1.916$). The hay crop in carpet mowed every 4th year was about as large as that in lawn and margin mowed every 2nd year. It also appeared to be substantially lower than in fen lawn and margin mowed every 4th year, but this was not demonstrated unambiguously ($|t| = 1.988$). Interestingly, the yield did not vary among the same community groups in the two study areas. The interaction between these factors was part of the full model, but was excluded during model selection.

Analysis of the hay crop at Sølendet obtained by mowing every year revealed a reduction ($|t| > 2$) compared to longer mowing frequencies (Fig. 6), and the overall yield (64.6 g/m^2) was about 60 % compared to mowing every 2nd year (109.3 g/m^2). Carpet vegetation gave a yield of 76.0 g/m^2 compared to 100.9 and 99.6 g/m^2 in lawn and margin, respectively. The two latter community groups were similar, but differed from the carpet vegetation (Table 6). There was no interaction between mowing regime and community group at Sølendet, indicating a uniform response in hay crop to mowing in the represented rich fen vegetation communities.

Discussion

Extremely Rich Fen

The terminology of the poor – rich fen gradient is mainly developed in Sweden with a separation of poor fen, intermediate fen, moderately rich fen and extremely rich fen (Sjörs 1948, Du Rietz 1949, Sjörs 1983). The units along the gradient are characterised by the species (lists of species in e.g. Sjörs (1983) and Rydin et al. (1999)), and the ecological factors behind the gradient are correlated to the pH and the mineral concentration (conductivity) in fen water and peat. This system has been adopted in many studies (e.g. Persson 1962, Moen 1990, Økland 1990, Wheeler & Proctor 2000, Rydin & Jeglum 2006). The limits of extremely rich fen have been discussed, and Hájek et al. (2006) separated rich fen, extremely rich fen and calcareous fen based on studies in central European fens. In addition to differences in species occurrences, the extremely rich fens should be peat-forming and the calcareous fens tufa-forming with extremely high pH and conductivity. Most of the characteristic species for extremely rich fens (including calcareous fens) are common in Europe (e.g. Wheeler 1988, Rydin et al. 1999), but there are also differences. For instance, Hájek et al. (2006) lists 25 species that are typical of calcareous fens in central Europe, including nine that are common in our boreal rich fens. Two of these species (*Dactylorhiza incarnata* and *Parnassia palustris*) are, however, common in both moderately and extremely rich fens in Norway (Moen 1990). There are small areas of calcareous fens (sensu Hájek et al. 2006) in Norway, mainly occurring in spring-influenced fens. The *Eleocharis quinqueflora-Cinclidium* carpet community (cluster 1, pH in water 7.1-7.3 (Moen 1990)) seems to be closest to the calcareous fen of the fen communities described here. The group of species exclusive to extremely rich fens in boreal Norway comprises 23 species (Moen 1990:197, Fremstad 1997). 21 of these appeared in our data set, but four of them had few occurrences, and 17 are listed in Table 2. The most common species of extremely rich fen that occur in both study areas were *Dactylorhiza lapponica, Listera ovata, Carex capillaris, C. hostiana, Barbilophozia rutheana* and *Palustriella commutata*. *Equisetum variegatum* and *Kobresia simpliciuscula* only occurred at Sølendet, and *Schoenus ferrugineus* only at Tågdalen. Negative indicators for extremely rich fen, i.e. only occurring in poor to moderately rich fen, are lacking or scarce in our data set, also indicating extremely rich fen vegetation. However, in both cluster 2 in *Eleocharis quinqueflora-Cinclidium* carpet and cluster 3 in *Drosera anglica-Scorpidium scorpioides* carpet vegetation, a majority of the samples had no indicators of extremely rich fen vegetation, even in carpets occurring in mosaics with extremely rich lawn communities. There are, in general, few indicator species of extremely rich fen in boreal carpet vegetation that is not influenced by spring water (Sjörs 1983, Moen 1990). Therefore, the distinction between moderately and extremely rich fen vegetation is difficult, and may be artificial for this type of vegetation. A number of extremely rich fen species (e.g. *Palustriella commutata*) are found in common in spring-influenced carpets (spring fens) and rich spring vegetation.

The majority of plots (12.5 m^2) in the rich fens that were studied had on average 30-39 species (Table 2). However, the two most species-rich communities in fen margin had on average 50 and 56 species. These communities had a large number of species in common with fen margin/wet grassland and mire expanse. In general, base-rich communities with a moderate (intermediate) standing crop in the transition between different habitats are species-rich (Grime 2001). In addition, the margin communities that were studied included a number of species (e.g. low shrubs) that invaded the areas after traditional mowing ceased about 50 years ago. Simultaneously, most species associated with open, mowing-influenced vegetation were still found (e.g. long-lived, clonal species). There is, however, reason to believe that a number of these stress-tolerant, poor competitors will disappear over time. Such a development is known from a large number of studies of changes in the cultural landscape (e.g. Losvik 1988, Olff & Bakker 1991, Losvik 1999, Vandvik & Birks 2002a, b). This increase in species richness in margin communities can be regarded as being in accordance with the intermediate disturbance hypothesis of Connell (1978) or the humped-back model of species richness of Grime (2001). Under the latter model, “the greatest diversity occurs in the moderate or middle range of a physical gradient”.

The data set includes samples from plots analysed several times since 1967, both plots in abandoned areas and plots with different mowing intervals. Very few samples from the same plot were classified in different clusters, and the samples ended up rather close in the DCA diagrams. There does, however, seem to be a trend that unmowed plots are located more to the left and upwards in the DCA diagram compared to mowed plots (Fig. 3a). Fen margin communities occupy this part of the diagram, indicating a gradual shift in the vegetation of these unmowed plots; they are becoming more influenced by fen margin and damp grassland species. However, mowing in former hay fens in the upper boreal region has a limited impact on species occurrences over a time span of a few decades. A large majority of the species are long-lived and clonal (Sjörs 1948: 253), remaining in abandoned areas for a long time. The realisation that successional trends in boreal rich fens may be slower than expected is recent. As previous vegetation studies at Sølendet (Moen 1990, Aune et al. 1996) have shown, the wet, tall-herb birch woodland changes much faster (from tall-herbs to low-herbs) when regularly mowed. Our analysis hints at a pattern where abandonment affects local communities differently, and this is a topic suitable for further investigation.

Comparisons with Rich Fens

In the present study, we included samples from two different study areas representing the whole variation of rich hay fens from carpet via lawn to mire margin communities. However, 115 of the 134 samples in the areas were taken from the lawn and open margin hay fens, included in the alliances Caricion atrofuscae and Schoenion ferruginei (*Eriophorum latifolium-Campylium* lawn, *Equisetum variegatum-Thalictrum-Campylium* lawn and *Gymnadenia-Succisa-Campylium* margin, communities III-V in Table 2). In these communities, *Campylium stellatum* was the dominant, constant species, and *Thalictrum alpinum*, *Eriophorum latifolium*, *Molinia caerulea*, *Trichophorum cespitosum* and *Scorpidium cossonii* were abundant, constant species. In addition, *Pinguicula vulgaris*, *Potentilla erecta*, *Selaginella selaginoides*, *Tofieldia pusilla*, *Carex dioica*, *C. panicea*, *Eriophorum angustifolium*, *Fissidens adianthoides* and *Gymnocolea borealis* were constant species. *Fissidens adianthoides* is the only one of these 15 most common species in lawns and open margin communities that is classified as an extremely rich fen indicator in boreal Scandinavia.

Rich sloping fens similar to ours were described by Persson (1961, 1962) from northern Sweden and Havas (1961) from eastern Finland. Persson (1961) described *Campylium* vegetation in seven "associations", and the most common of these (the *Carex panicea* association) closely resembles our lawn and open margin communities (III-V, clusters 4-8 in Table 2). Of the 15 species mentioned above, as many as ten were listed as constant or common species by Persson (1961), while *Potentilla erecta*, *Eriophorum latifolium* and *Fissidens adianthoides* were more scarce. Only *Molinia caerulea* and *Gymnocolea borealis* are lacking completely in Persson's (1961) list, but the latter was described in 1980 (Frisvoll & Moen 1980) and may well be present in northern Sweden. The carpet communities (I and II, clusters 1-3) have parallels in the "*Scorpidium* association" and the fen margin community (VI, clusters 9 and 10) in the "*Carex dioica-Tomentypnum* association" of Persson (1961).

Havas (1961) described 11 "Siedlungsgruppen", four of which represent rich fen vegetation. The "*Carex flava-Trichophorum-Campylium stellatum*-Siedlungsgruppe" included 13 of the 15 constant or common species from our communities III-V (clusters

4-8), and only *Thalictrum alpinum* and *Gymnocolea borealis* are missing. The "Siedlungsgruppe *Carex flava-Filipendula ulmaria-Campylium stellatum"* is rather close to our lawn communities, particularly community IV (cluster 8). The "*Carex magellanica-Filipendula ulmaria-Sphagnum warnstorfii*-Siedlungsgruppe" is a parallel to community VI (clusters 9 and 10), and "Siedlungen des Rimpihorizonts" includes carpet vegetation resembling our communities I and II (clusters 1-3). In his monograph of mires in northern Finland, Ruuhijärvi (1960) described "*Campylium stellatum*-Braunmoore" (resembling our communities III-V), "*Drepanocladus revolvens*-Rimpibraunmoore" (resembling communities I and II) and "*Sphagnum warnstorfii*-Braunmoore" (resembling clusters 9 and 10). These units are part of the Finnish mire site type system used in a large number of publications, including rich fens (surveys in Ruuhijärvi (1983) and Ruuhijärvi & Lindholm (2006)).

Extremely rich fen vegetation is included in the monograph published by Booberg (1930), which described Gisselåsmyren in Jämtland, about 200 km from Sølendet. This mire has more of a lowland affinity with its location 320 m a.s.l., and no sloping fens were included. The *Schoenus ferrugineus* lawn communities do, however, have similarities to the *Schoenus* communities at Tågdalen. Tyler (1981) compared *Schoenus* communities in Fennoscandia and Estonia. Samples from Tågdalen (the same as in cluster 4) were included in her analyses, and were classified as the *Trichophorum-Schoenus ferrugineus* association, one of five associations described, including the *Schoenus* samples from Gisselåsmyren.

In Norway, the monographs of Nordhagen (1928, 1943) included communities resembling the rich fens described here. However, most of the rich fens described by Nordhagen are from the upper part of the northern boreal zone and the low alpine zone, and include more alpine species and fewer lowland species.

Phytosociological Classification

Based on the phytosociological, hierarchic classification system of Braun-Blanquet (1964), the Norwegian fens were classified by Nordhagen (1943) and Dahl (1957). Compared to the central European system (e.g. Dierssen 1982, 1996), the Norwegian system is based more on dominant and differential species, and less on character species. More recently, Rodwell et al. (2002) published an overview of the phytosociological system for European vegetation and its relationship to other classification systems (e.g. EUNIS habitats). Moen (1990) and Fremstad (1997) presented classification systems for Norwegian mires, and added a syntaxonomic system close to the central European system. Especially for the higher levels of the classification systems (classes, orders and alliances), there is much agreement between the different systems. To compare the communities and clusters described here, we mainly follow Moen (1990), with some comments on other systems, mainly Dierssen (1982, 1996) and Rodwell et al. (2002). Communities described here belong to the class Scheuchzerio-Caricetea nigra, and it is usually separated into two orders.

Order Scheuchzerietalia palustris

The community of cluster 1 (*Eleocharis quinqueflora-Cinclidium* carpet) seems to be closest to the Caricion lasiocarpae alliance. However, it is influenced by spring water and has a number of characteristic species (e.g. *Carex heleonastes* and *Meesia triquetra*). It is transitional to the spring alliance Cratoneurion commutati (in the Montio-Cardaminetea class). Similar carpets are described from various areas in the upper boreal and low alpine zones in Fennoscandia (references in Moen (1990: 227 ff)). Dierssen (1982) classified this community in the Caricetum heleonastes association of Caricion lasiocarpae. The other carpet communities (clusters 2 and 3) should be included in the Stygio-Caricion limosae alliance described by Nordhagen (1936), which corresponds to Rhynchosporion albae in the system of Dierssen (1982). These fen expanse communities of mud bottoms and carpets are widely distributed in flat fens in Fennoscandia (e.g. Havas 1961, Persson 1961, Singsaas 1989).

Order Caricetalia nigrae

The lawn and open margin communities (*Eriophorum latifolium-Campylium* lawn, *Equisetum variegatum-Thalictrum-Campylium* lawn and *Gymnadenia-Succisa-Campylium* lawn, clusters 4-8) are typical of extremely rich vegetation in Scandinavia and can be separated into the two alliances Caricion atrofuscae and Schoenion ferruginei (Nordhagen 1936). Dierssen (1982) used the names Caricion bicolorisatrofuscae and Caricion davalliane, and Rodwell et al. (2002) used the names Caricion atrofusco-saxatilis and Caricion davallianae (in the order Caricetalia davallianae). Both alliances include the lawn communities of extremely rich fens and are mainly distinguished by regional differences in species composition. Caricion atrofuscae occurs mainly in the northern boreal and low alpine zones, especially in mire margin communities with shallow peat. Schoenion ferruginei includes the lawn communities of extremely rich fens in the boreonemoral to middle boreal zones in Norway; it mostly occurs where the peat is deep. The Tågdalen rich fen lawns (community III) have some typical species of Schoenion ferruginei (e.g. *Schoenus ferrugineus*), and lack a number of the typical upland, rich fen species. The situation is the opposite in the open rich fens at Sølendet, which have a number of characteristic species for *Caricion atrofuscae,* like *Equisetum variegatum*, *Pedicularis oederi*, *Carex atrofusca* and *Kobresia simpliciuscula*. However, there is no sharp boundary between the alliances, and they meet in the upper part of the middle boreal vegetation zone in Scandinavia, as pointed out by Sjörs (1983).

The samples of the fen margin community (VI) lack most of the characteristic species of these two alliances and have a large number of fen margin species which also occur in grasslands (e.g. shrubs, *Galium boreale*, *Geranium sylvaticum* and *Hylocomiastrum pyrenaicum*). This community belongs to the alliance Sphagno-Tomenthypnion described by Dahl (1957).

Multivariate analyses

In the DCA analyses, the “outliers” of samples and species greatly influence the final result (Gauch 1982, Økland 1999). We omitted outlying samples to make the data set more homogeneous, but no species were omitted. Based on tests with different data sets, with and without downweighting of species, and on earlier experience from similar material (Moen 1990), we chose only to present DCA diagrams made after downweighting of rare species. The outcome of the DCA is, however, quite similar both with and without downweighting, and the length of the first DCA axis indicates a rather substantial turnover of species along the main floristic gradient in both ordinations. The axes were shorter and the eigenvalues lower when species were downweighted (see Table 2). This is in accordance with earlier studies (e.g. Eilertsen et al. (1990)).

Regional differences

The first TWINSPAN subdivision separated the majority of the samples from the two study areas, and this was also the case in the DCA diagrams of axes 1 and 2 where the Sølendet samples and clusters gave low values, and those from Tågdalen higher values. As a result, a large majority of the Sølendet samples and clusters in Fig. 3a were situated in the left lower part of the diagram, and the Tågdalen samples and clusters in the upper right part. The hay fens at Sølendet and Tågdalen have a majority of species in common, including most of the dominant and constant species. The local ecological conditions, pH and conductivity in fen water and peat, temperature in the growing season and productivity of the communities are similar in the two areas. However, there are differences in species occurrences that can be explained by differences in oceanity between the study areas, and it seems justifiable to place the lawn and open margin communities of Tågdalen and Sølendet in the different alliances Caricion atrofuscae and Schoenion ferruginei, respectively. Regional differences in mire vegetation have been widely studied. For instance, Damman (1995a) compared the mires in Norway and eastern North America, and a number of regional studies concerning ombrotrophic vegetation have been undertaken (e.g. Damman 1995b, Proctor & Maltby 1998, Wheeler & Proctor 2000). Differences in climate and the mineral content in the precipitation are important factors contributing to regional differences in bog vegetation. In extremely rich fens, the mineral nutrient content in the water is an important ecological factor explaining why there are fewer regional differences than in ombrotrophic bogs (Joosten & Clarke 2002). However, there are still distinct differences, as pointed out by Tyler (1981) regarding *Schoenus* communities in Fennoscandia and Estonia, and Hájková et al. (2008) regarding calcareous fens in the Carpathians and Bulgaria.

Hay Crop in Boreal Rich Fens

The effect of different forms of management (including mowing) on rich fens and other types of wetland in northern Sweden is described in several publications by Jan

Elveland and co-workers. These studies concentrated on the carpet vegetation of flat fens, and typical lawn communities of sloping fens are not included, but the results of mowing is akin to ours. For instance, *Carex lasiocarpa-C. rostrata* communities gave a hay yield of about 200-280 g/m^2 in the first year of mowing, and the yield dropped with repeated mowing the following years (Elveland 1978, Elveland & Sjöberg 1982). In our study areas, the first mowing after recommencement (after three decades) yielded 150-300 g/m^2 in most communities. With time, the yield in the annually mowed plots has been found to decrease to about one third of the first harvest, whereas it is about two thirds in plots mowed every 2nd year (Moen 1990, Aune et al. 1996). Our present analyses confirms these patterns in hay crop. Long-term mowing every year yielded a hay crop that was about 60 % of that recorded in plots mowed every 2nd year, i.e. the practice of traditional haymaking on outlying lands of upper boreal Norway. Mowing every 2nd year, in turn, yielded a substantially smaller hay crop than mowing every 4th year. Thus, the hay crop decreases as the mowing frequency increases, and while mowing every year was only performed at Sølendet, we believe this has validity in Tågdalen and other rich fen areas as well.

The hay yield in carpet vegetation was lower than that in lawn and margin, and this was in accordance with our expectations. Many fen carpet plots have a low degree of cover of vascular plants (Table 2), naturally resulting in low production in the field layer. In all communities mowing leads to reduced biomass (Aune et al. 1996), giving lower evapotranspiration and a higher water table, and waterlogged conditions in fen vegetation generally favour bryophytes, not vascular plants. Hence, fen carpet vegetation can be assumed to be more vulnerable to mowing. Elveland (1984) documented severe effects of mowing in mud bottom vegetation dominated by *Carex lasiocarpa*, where it was suggested that inundation of the stubble after mowing might explain the reduction in biomass. Inundation may occur in some plots in fen carpet, but is not likely to affect plots in the drier communities in our study areas. It may contribute to the differences in the hay yield between communities.

The hay yield was similar in fen carpet, lawn and margin at Sølendet and Tågdalen, and there was no interaction between study area and community group, indicating that production is similar in ecologically similar rich fen plant communities. This was what we expected since these communities were perceived to be ecologically quite similar, including summer warmth and with the dominant species in common. However, the vegetation samples in the two study areas were largely separated in the principal division in the TWINSPAN classification, indicating a fundamental vegetational difference that could have been reflected in the productivity of the communities. This was not the case, patterns strong enough to affect the classification of vegetation samples were too weak to influence hay yields. In addition, the most common species occurring in just one study area (see above) are rather small, and contribute little to the hay crop compared to many species present at both study areas.

Hay yields in plots mowed every 2nd year were, as expected, practically identical at Sølendet and Tågdalen (Fig. 4). Mowing every 2nd year is currently the most common of the experimental mowing regimes, with 57 plots subject to varying conditions along several ecological gradients, but the yield is uniform despite this environmental stochasticity. It has been shown that production in rich fen vegetation is limited by both nitrogen and phosphorus, and also that the availability of these macronutrients in the soil is not reduced by mowing. In some cases, the results even indicate that more nitrogen becomes available Thus, the reduction in production caused by mowing is interpreted as mainly a result of disturbance (Øien & Moen 2001, Øien 2004). The yields found at Sølendet match fairly well those obtained twenty years ago (Moen 1990), hence, there is no apparent decrease in productivity over this period. We conclude that long-term mowing represents a major disturbance of the plant cover that tends to equalise the biomass production in rich fens. We believe this finding applies to boreal rich fen systems in general, as long as macronutrients limit biomass production, and it may also be applicable to rich fens in other vegetational regions.

The hay crop in our study areas was substantially lower than that recorded in both mowed and unmowed rich fens in central Europe (Diemer et al. 2001, Hájková & Hájek 2003, Peintinger & Bergamini 2006, Rozbrojová & Hájek 2008). These authors all report a standing crop above 200 g/m^2 under mowed conditions (most common every year), reflecting the warmer climate and, at least in some cases, the higher macronutrient availability compared to central Norway. Our estimates were also lower than those found in unmowed, but otherwise similar, boreal, rich fen vegetation (Pearsall & Newbould 1957, Thormann & Bayley 1997). However, the estimates of hay crop in our lawn plots the first year after mowing recommenced (Moen 1990) are in the same range as those reported by the above authors. This discrepancy highlights the effect of long-term mowing on the hay crop compared with crop measurements after single mowing or cutting incidents.

The hay crop varies systematically from year to year, indicating that there may be temporal trends in the hay crop measurements, and further studies should address this. We also attempted to compare the hay crop in vegetation clusters, but the low sample size of some clusters, the lack of orthogonality and the spatial and temporal complexities of the design made this difficult. Interactions could not be examined, and lack of power in the tests meant we could not demonstrate differences even between clusters with substantially different yields (data not shown). The conclusions we were able to draw were that the carpet clusters 2 and 3 differed from lawn cluster 7 and the margin clusters 9 and 10. This is in accordance with the general pattern we have documented for community groups. A larger sample size in terms of hay crop measurements and independent plots from poorly represented vegetation clusters is needed to enable reliable conclusions regarding hay crop on the cluster level.

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Tables

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

	Sølendet	Tågdalen
Latitude (N)	62°40’	63°03’
Longitude (E)	11°50’	9°05’
Mean annual precipitation (mm)	637	1583
Mean July temperature (°C)	10.5	11.2
Mean January temperature (°C)	-9.5	-2.7
Altitude (m a.s.l.)	700-800	380-490
Area (ha)	306	146

Table 2 TWINSPAN table of the 134 samples classified in six communities and ten clusters. Relative frequency (I-V, IV and V in bold) and relative abundance (1-5, 4 and 5 in bold) are given for 121 species. Species included were either present in five or more samples (115 species) or were characteristic species for small clusters. Horizontal lines and numbers to the right show the species classification in 16 groups. The proportion of species displayed in the table is given for each species group. ER = characteristic species of extremely rich fen in central Norway. Consult Appendix 1 for a list of species names and abbreviations.

Community	**I**		**II**	**III**		**IV**		**V**	**VI**		
Cluster	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	
G Scap deg	-	-	-	II/1	**IV**/3	-	-	-	**IV**/1	-	**1**
D Trie eur	-	-	I/1	I/1	I/1	-	-	-	-	-	9/23
D Plat bif	-	-	-	I/1	I/1	-	-	-	I/1	-	
D Nart oss	-	-	II/1	II/1	**IV**/1	-	I/1	-	**IV**/1	-	
F Spha pla	-	-	I/1	I/**4**	I/1	-	-	-	-	-	
F Spha pap	-	-	-	I/1	-	-	-	-	-	-	
E Scho fer ER	-	-	I/1	II/**4**	-	-	-	-	-	-	
D Dros ang	-	-	**V**/1	**IV**/1	II/1	-	-	-	-	-	
C Eric tet	-	-	II/1	I/1	I/1	-	-	-	-	-	
F Warn sar	-	I/1	II/1	I/1	-	-	-	-	-	-	**2**
D Sche pal	-	-	**IV**/1	-	-	-	-	-	-	-	10/15
D Dact inc	-	II/1	**IV**/1	II/1	I/1	-	I/1	-	-	-	
F Scor sco	**V**/1	**IV/4**	**V/4**	I/1	-	I/2	-	-	-	-	
E Care lim	**V**/1	III/2	**V**/1	II/1	II/1	I/1	-	-	-	-	
D Meny tri	**V**/3	**IV**/2	**V**/1	II/1	II/1	I/1	I/2	I/1	III/1	-	
F Mees tri	**V**/1	I/2	-	-	-	-	-	-	-	-	
F Call gig	**V**/3	I/1	-	-	-	-	I/1	-	-	-	
E Care hel	**V**/1	I/1	-	-	-	-	-	-	-	-	
D Utri min	**V**/1	III/1	II/1	I/1	-	-	-	-	-	-	
E Care hos ER	-	-	III/1	**IV**/2	**IV**/2	**IV**/1	-	I/1	-	-	**3**
D List ova ER	-	-	-	II/1	III/1	I/1	-	II/1	**IV**/1	III/1	10/12
D Hupe sel	-	-	I/1	I/1	I/1	-	-	-	II/1	-	
F Spha con	-	-	I/1	I/1	II/1	-	-	I/1	II/1	-	
F Loes bad	-	I/1	II/1	III/1	III/1	I/1	I/1	I/1	III/1	-	
E Tric alp	-	III/1	III/1	**IV**/1	**V**/1	I/1	II/1	II/1	**V**/1	-	
E Care ros	-	**IV**/1	**V**/1	**IV**/1	**IV**/1	I/1	**V**/1	-	-	-	
D Parn pal	-	I/1	**IV**/1	**V**/1	**V**/1	-	II/1	III/1	**V**/1	II/1	
C Andr pol	-	**V**/1	**IV**/1	**V**/1	**IV**/1	I/1	II/1	II/1	**V**/1	-	
E Erio lat	**V**/1	**V**/1	**IV**/1	**V**/2	**V**/2	**V**/1	**IV**/2	III/1	II/3	-	
F Pseu tri	III/1	**V**/1	**V**/1	II/1	I/1	**IV**/1	I/1	I/1	-	-	**4**
E Eleo qui	**V**/1	**V**/2	-	-	-	I/1	I/1	I/1	-	-	2/5
G Trit pol	-	**IV**/1	II/1	II/1	I/1	I/1	III/1	II/1	-	-	**5**
G Barb rut ER	III/2	**V**/1	I/1	**IV**/1	**IV**/1	I/1	**V**/1	II/1	-	-	7/8
F Scor cos	**V/4**	**V/4**	**V**/3	**V**/3	**V**/2	**V**/3	**V**/3	**V**/1	I/1	-	
G Gymn bor	-	**IV**/1	**V**/1	**V**/1	**V**/1	**V**/1	**V**/1	**IV**/1	-	-	
E Tric ces	-	**V**/3	**V**/3	**V**/3	**V**/3	**V**/3	**V**/3	**V**/2	**V**/2	III/2	
E Care dio	**V**/1	**V**/1	**V**/1	**V**/1	**V**/1	**V**/2	**V**/1	**V**/1	**V**/1	I/1	
D Euph wet	-	**IV**/1	II/1	**IV**/1	**IV**/1	**IV**/1	III/1	II/1	I/1	-	
G Aneu pin	III/1	**V**/1	**IV**/1	III/1	**V**/1	III/1	**IV**/1	**IV**/1	**V**/1	**IV**/1	**6**
E Erio ang	**V**/1	**V**/1	**V**/1	**V**/1	**V**/1	**V**/1	**V**/1	**V**/1	**V**/1	III/2	4/4
D Tofi pus	-	III/1	**IV**/1	**V**/1	**V**/1	**V**/1	III/1	**IV**/1	**V**/1	-	
D Ping vul	-	**IV**/1	**IV**/1	**V**/1	**V**/1	**V**/1	III/1	**V**/1	**V**/1	I/1	

Table 2 (cont.)

Community	**I**		**II**	**III**		**IV**		**V**	**VI**		
Cluster	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	
E Junc alp	-	-	-	I/2	I/1	-	I/1	I/1	-	-	**7**
D Dact mac	-	-	-	-	I/1	-	-	II/1	-	-	6/9
D Bart alp	-	I/1	-	III/1	**V**/1	II/1	II/1	**V**/1	**V**/1	I/1	
E Nard str	-	-	I/1	I/1	**IV**/1	-	I/1	**IV**/1	**V**/1	-	
E Care ech	-	-	I/1	I/1	II/1	-	I/1	II/2	-	III/2	
F Hylo pyr	-	-	-	I/1	II/1	I/1	I/1	I/1	**IV**/2	**V**/1	
F Palu com ER	-	I/1	-	I/3	I/2	I/1	II/2	II/1	-	-	**8**
F Camp ste	III/2	**V/4**	**V**/3	**V/4**	**V/4**	**V/5**	**V/5**	**V/4**	**V**/3	**V**/1	11/12
E Care pan	III/2	**V**/1	**IV**/2	**V**/1	**V**/1	**V**/2	**V**/1	**V**/2	**V**/3	III/1	
D Sela sel	-	III/1	**V**/1	**V**/1	**V**/1	**V**/1	**V**/1	**V**/1	**V**/1	**IV**/1	
D Equi pal	**V**/1	**V**/1	I/1	II/1	**IV**/1	**V**/1	**V**/1	**IV**/1	**V**/1	-	
F Fiss adi ER	-	II/1	-	III/1	**V**/2	III/1	**V**/2	**V**/1	**V**/2	III/1	
E Moli cae	-	**IV**/1	**V**/1	**V**/2	**V**/2	**V**/2	**V**/2	**V**/3	**V**/3	**V**/3	
E Care fla	**V**/1	I/1	II/1	III/1	**V**/1	**IV**/1	**V**/1	**IV**/2	**V**/2	-	
D Pote ere	-	II/1	III/1	**V**/1	**V**/2	**V**/1	**V**/2	**V**/1	**V**/3	**V**/1	
D Dact lap ER	-	-	-	III/1	III/1	**IV**/1	II/1	**IV**/1	II/1	-	
D Succ pra	-	I/1	-	**IV**/1	**V**/2	**IV**/1	III/1	**V**/3	**V**/3	**V**/1	
C Vacc uli	-	-	I/1	I/1	I/1	-	-	I/1	II/1	-	**9** 1/2
F Hylo spl	-	-	-	I/1	I/1	-	-	I/1	II/1	**IV**/1	**10**
F Dicr bon	-	-	-	I/1	II/1	-	-	I/1	**IV**/2	II/1	5/9
D Gali bor	-	-	-	-	II/1	-	I/1	II/1	**V**/1	**V**/1	
D Viol pal	III/1	-	-	I/1	I/1	-	I/1	I/1	**IV**/1	-	
C Betu pub	-	-	I/1	I/1	II/1	II/1	I/1	II/1	**V**/2	I/1	
F Ditr fle	-	-	-	I/1	I/1	III/1	I/1	II/1	-	-	**11**
E Care fxh ER	-	-	I/1	I/1	I/1	**IV**/1	-	I/1	-	I/1	3/3
D Thal alp	III/1	**V**/1	**IV**/1	**V**/1	**V**/2	**V**/3	**V**/2	**V**/3	**V**/1	**V**/2	
F Cinc sty	**V**/3	**V**/1	-	-	-	I/1	III/1	I/1	-	-	**12**
E Care las	-	**V**/1	I/1	II/2	**IV**/1	I/2	**V**/3	III/1	**V**/1	II/1	4/6
D Trig pal	**V**/1	**IV**/1	II/1	I/1	I/1	**IV**/1	III/1	II/1	-	III/1	
D Pedi pal	**V**/1	**V**/1	-	I/1	I/1	I/1	**V**/1	I/1	-	-	
F Rhiz pse	-	-	-	-	I/1	-	-	I/1	III/1	II/1	**13**
E Luzu sud	-	-	-	-	-	-	-	I/1	**V**/1	I/1	12/29
C Sali myf	-	-	-	-	-	-	-	-	**IV**/1	II/1	
B Betu pub	-	-	-	I/1	I/1	-	-	-	**V**/3	-	
F Rhyt squ	-	-	-	I/1	I/1	-	-	-	**IV**/1	II/1	
F Call cus	-	-	-	-	II/1	-	-	I/**5**	**V**/3	-	
D Ranu acr	-	-	-	-	-	-	-	II/1	III/1	I/1	
D Gera syl	-	-	-	-	-	-	-	II/1	**V**/1	**V**/1	
D Fili ulm	-	-	-	-	-	-	-	II/1	**V**/1	II/1	
D Alch sp.	-	-	-	-	-	-	-	I/1	**IV**/1	I/1	
C Sali gla	-	-	-	-	I/1	-	I/1	II/1	**V**/1	II/1	
G Scap irr	-	-	-	-	-	-	I/1	I/1	III/1	I/1	

Table 2 (cont.)

Community	**I**		**II**	**III**		**IV**		**V**	**VI**		
Cluster	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	
F Plag ela	-	-	-	-	I/1	-	I/1	II/1	**IV**/1	-	**14**
E Care cho	-	-	I/1	I/1	-	-	-	I/1	-	III/1	8/8
D Saus alp	-	I/1	-	I/1	**IV**/1	**V**/1	**V**/1	**V**/1	**V**/1	**V**/2	
F Spha war	III/1	-	-	I/**4**	I/1	I/1	**IV**/1	II/2	**V**/1	-	
F Bryu pse	**V**/1	**IV**/1	-	I/1	I/1	**V**/1	**V**/1	**V**/1	**V**/3	**IV**/1	
E Care nig	III/1	III/1	I/1	I/1	I/1	-	III/1	**IV**/1	**IV**/2	I/1	
G Barb qua	-	-	-	I/1	III/1	II/1	III/1	**IV**/1	III/1	II/1	
E Care cap ER	-	-	-	I/1	**IV**/1	**V**/1	II/1	**V**/1	**V**/1	**IV**/1	
G Trit qui	-	-	-	-	-	-	I/1	III/1	I/1	**IV**/1	**15**
G Plag por	-	-	-	-	I/1	-	-	III/1	-	III/1	18/35
G Loph b/g	-	-	-	-	I/1	I/3	-	III/1	II/1	I/1	
D Soli vir	-	-	-	-	-	-	-	II/1	I/1	II/1	
D Crep pal	-	-	-	-	-	I/1	I/1	**V**/1	**V**/1	**IV**/1	
B Betu nan	-	-	-	-	-	-	-	I/1	-	II/**4**	
E Fest ovi	-	-	-	-	-	III/1	II/1	**IV**/1	I/1	**V**/1	
E Desc ces	-	I/1	-	-	-	II/1	-	**V**/1	**IV**/1	**V**/1	
D Bist viv	**V**/1	I/1	-	-	I/1	II/1	**V**/1	**V**/1	**V**/1	**V**/1	
C Betu nan	III/1	I/1	-	-	-	**IV**/1	II/1	III/2	-	**IV**/3	
F Call ric	-	-	-	-	-	-	I/1	II/1	-	-	
F Brei pra	-	-	-	-	-	-	-	II/1	-	-	
E Care vag	-	-	-	-	-	I/1	-	**IV**/1	-	**IV**/1	
E Care atr ER	-	-	-	-	-	-	I/2	III/1	-	-	
D Leon aut	-	-	-	-	-	II/1	-	**V**/1	-	II/1	
D Ange syl	-	-	-	-	-	I/1	I/1	**IV**/1	-	II/1	
F Tome nit	-	-	-	-	-	I/1	**IV**/1	**IV**/2	-	**V**/1	
D Gymn con ER	-	-	-	-	-	II/1	II/1	**V**/1	-	III/1	
E Kobr sim ER	-	I/1	-	-	-	**V**/1	II/1	III/1	-	-	**16**
E Junc tri ER	-	I/1	-	-	-	II/1	II/1	II/1	-	-	11/20
D Saxi aiz ER	-	-	-	-	-	**V**/1	I/1	III/1	-	-	
D Pedi oed	-	-	-	-	-	**V**/1	III/1	**V**/1	-	I/1	
D Ante dio	-	-	-	-	-	III/1	-	I/1	-	-	
C Juni com	-	-	-	-	-	I/1	-	II/1	-	-	
E Erio vag	-	-	-	-	I/1	III/1	II/1	II/1	-	-	
D Equi var ER	**V**/1	III/1	-	-	-	**V**/1	**V**/1	**V**/1	-	III/1	
F Fiss osm ER	-	I/1	-	-	I/1	II/1	-	I/1	-	-	
E Care bux	III/3	-	-	-	-	I/1	III/1	I/1	II/1	-	
D Dact cru ER	**V**/1	III/1	-	-	-	III/1	**IV**/1	II/1	-	-	
Mean no. of species	**32**	**32**	**29**	**30**	**38**	**36**	**37**	**50**	**56**	**39**	121/200
No. of samples	**2**	**6**	**10**	**30**	**25**	**16**	**16**	**18**	**6**	**5**	

Table 3 Results from DCA ordination of 134 samples and 200 active species of rich fen vegetation. Eigenvalues and gradient lengths for the DCA analyses with (A) and without (B) downweighting of rare species. Total inertia is 1.884 for A and 4.051 for B.

DCA analysis		First axis	Second axis	Third axis	Fourth axis
A	Eigenvalue	0.264	0.145	0.082	0.050
	Gradient length	2.989	2.417	1.622	1.428
B	Eigenvalue	0.337	0.228	0.168	0.115
	Gradient length	3.423	2.963	2.631	2.008

Table 4 Characteristics of two minimal adequate models (GLMM, normal distribution) exploring the relationship between hay crop (ln(g/m^2)), study area, mowing regime and community group. The first model has two levels of mowing regime and applies to both study areas, the second includes mowed every year as a third mowing regime and applies to Sølendet alone. Contrasts between levels of fixed factors (both models) and interactions between fixed factors (first model alone) are summarised with estimates and accompanying t-values. The estimate for the intercept of the first model is the scenario fen carpet mowed every 4th year at Tågdalen, the intercept of the second model is similar but excludes study area. T = Tågdalen, S = Sølendet, 0.25 = mowed every 4th year, 0.5 = mowed every 2nd year, 1 = mowed every year, C = fen carpet, L = fen lawn, M = fen margin.

Study area	n	Random factors	Fixed factors	Contrast	Estimate	t
Sølendet and Tågdalen	702	Locality, plot and year	Intercept	-	4.68	22.65
			Study area	T – S	-0.04	-0.27
			Mowing regime	0.25 - 0.5	-0.68	-5.38
			Community group	C – L	0.15	0.74
				C – M	0.55	1.99
			Study area : mowing regime	T:0.5 – S:0.5	0.23	1.85
			Community group : mowing regime	C:0.5 – L:0.5	0.34	2.59
				C:0.5 – M:0.5	-0.02	-0.09
Sølendet	654	Locality and year	Intercept	-	4.59	33.01
			Mowing regime	0.25 - 0.5	-0.27	-3.79
				0.25 - 1	-0.71	-9.13
			Community group	C - L	0.37	2.78
				C - M	0.34	2.46

Table 5 Differences in hay crop (ln(g/m^2)) between levels of fixed factors, estimates from the minimal adequate model (GLMM) with interactions between study area and mowing regime and community group and mowing regime (|t| > 2 in bold, |t| = 1.99 in italics). T = Tågdalen, S = Sølendet, 0.25 = mowed every 4th year, 0.5 = mowed every 2nd year, C = fen carpet, L = fen lawn, M = fen margin.

Fixed factors	Levels	Δ levels	|t|
Study area : mowing regime	T:0.25 – T:0.5	0.68	**3.29**
	T:0.25 – S:0.25	0.04	0.21
	T:0.25 – S:0.5	0.49	**2.39**
	T:0.5 - S:0.25	0.64	**3.07**
	T:0.5 - S:0.5	0.18	0.89
	S:0.25 - S:0.5	0.45	**2.18**
Community group : mowing regime	C:0.25 – C:0.5	0.68	**3.29**
	C:0.25 – L:0.25	0.15	0.71
	C:0.25 – L:0.5	0.19	0.92
	C:0.25 – :0.25	0.55	*1.99*
	C:0.25 – M:0.5	0.15	0.54
	C:0.5 - L:0.25	0.83	**4.00**
	C:0.5 - L:0.5	0.49	**2.37**
	C:0.5 - M:0.25	1.23	**4.45**
	C:0.5 - M:0.5	0.53	1.92
	L:0.25 - L:0.5	0.34	1.63
	L:0.25 - M:0.25	0.40	1.46
	L:0.25 - M:0.5	0.30	1.07
	L:0.5 - M:0.25	0.74	**2.68**
	L:0.5 - M:0.5	0.04	0.15
	M:0.25 - M:0.5	0.70	**2.53**

Table 6 Differences in hay crop ($\ln(g/m^2)$) between levels of fixed factors at Sølendet, estimates from the minimal adequate model (GLMM) with mowing regime and community group (|t| > 2 in bold). S = Sølendet, 0.25 = mowed every 4th year, 0.5 = mowed every 2nd year, 1 = mowed every year, C = fen carpet, L = fen lawn, M = fen margin.

Fixed factors	Levels	Δ levels	|t|
Mowing regime	0.25 - 0.5	0.27	**3.79**
	0.25 - 1	0.71	**9.13**
	0.5 - 1	0.44	**5.63**
Community group	C - L	0.37	**2.78**
	C - M	0.34	**2.46**
	L - M	0.03	0.25

Figures

Fig. 1 The location of Sølendet and Tågdalen nature reserves.

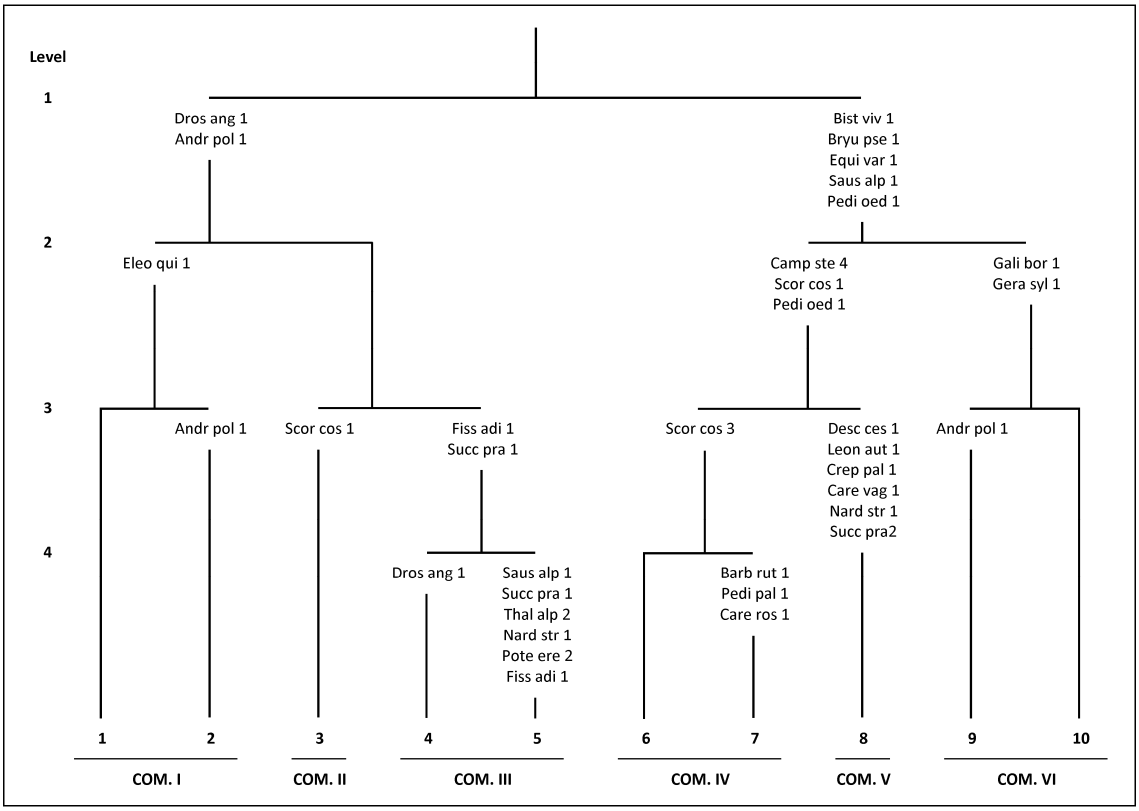
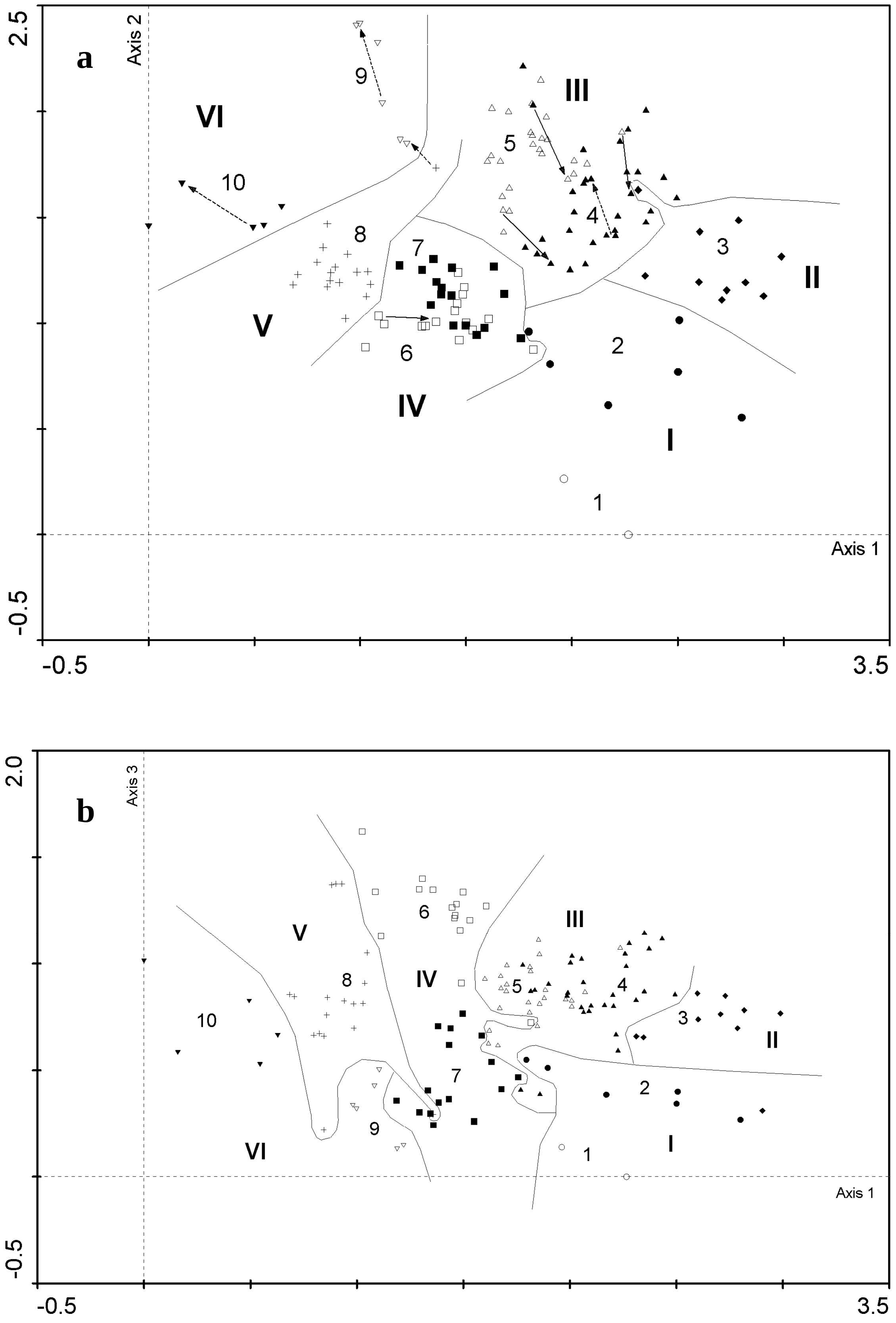


Fig. 2 TWINSPAN tree of 134 samples classified into ten clusters at level 5; the number of samples in each end cluster is given in Table 2. The clusters are combined into six communities (I-VI). The indicator species (with pseudospecies level) for each division are shown. The full names of the species are given in Appendix 1.


a
2.5
-0.5
-0.5
3.5
Axis 1
Axis 2
I
II
III
IV
V
VI
1
2
3
4
5
6
7
8
9
10
b
2.0
-0.5
-0.5
3.5
Axis 1
Axis 3
I
II
III
IV
V
VI
1
2
3
4
5
6
7
8
9
10

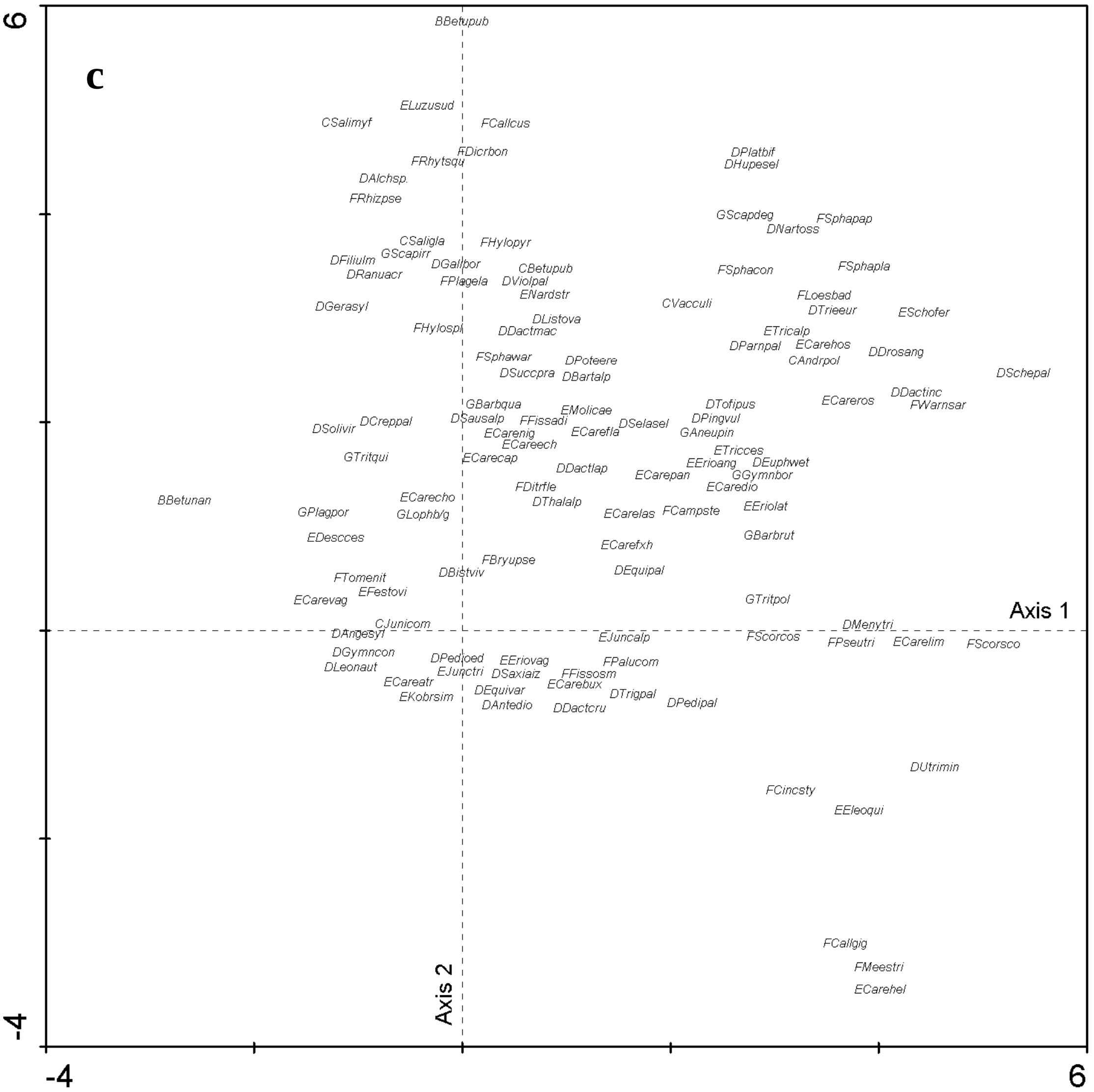


Fig. 3 DCA ordination of the full data set of 134 samples. **a** Sample ordination, axes 1 and 2. Arrows with a solid line indicate larger displacement of plots that were re-analysed after 30 years of mowing, while arrows with a dashed line indicate larger displacement of plots that were re-analysed after continued abandonment. **b** Sample ordination axes 1 and 3. The symbols in A and B represent the six communities (different symbol forms) and the ten clusters (forms and open/filled symbols) of the TWINSPAN classification. **c** The species ordination of axes 1 and 2 with the 121 most frequent species shown (as in Table 3). The full names of the species are given in Appendix 1.

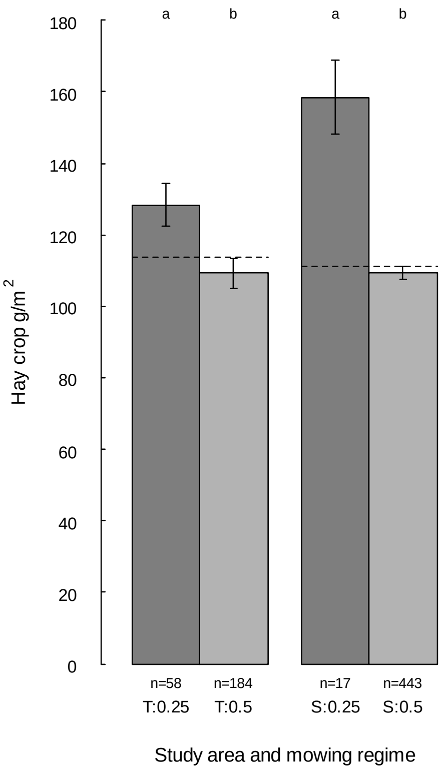


Fig. 4 Hay crop (g/m^2) ± se for plots mowed every 4th (0.25) and 2nd (0.5) year at Sølendet (S) and Tågdalen (T). The mean hay crop in the study areas is shown with dashed lines, the number of observations are indicated on the x axis, and groups that differ significantly are indicated with the letters a and b at the top.

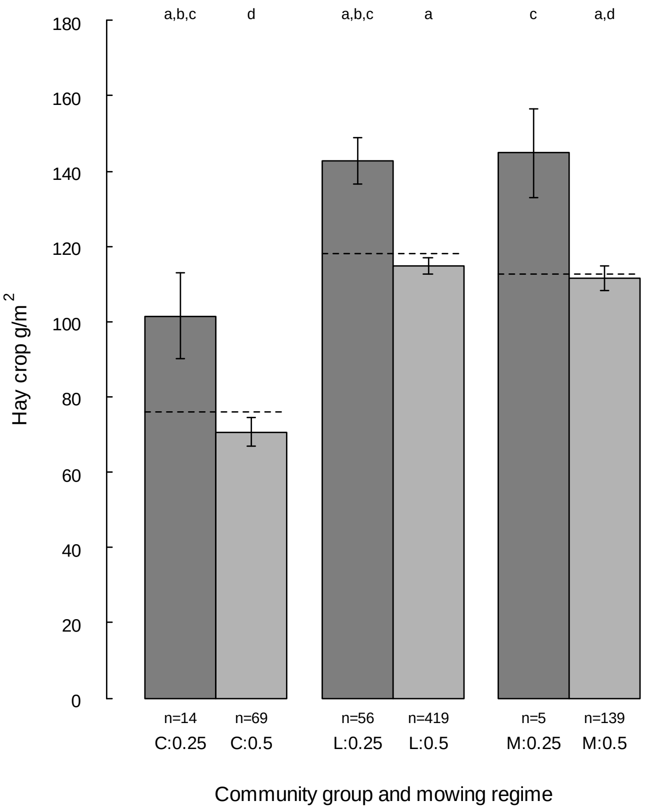


Fig. 5 Hay crop (g/m^2) ± se for plots mowed every 4th (0.25) and 2nd (0.5) year in the community groups fen carpet (C), fen lawn (L) and fen margin (M). The mean hay crop per community group is shown with dashed lines, the number of observations is indicated on the x axis, and groups that differ significantly are indicated with the letters a, b, c and d at the top.

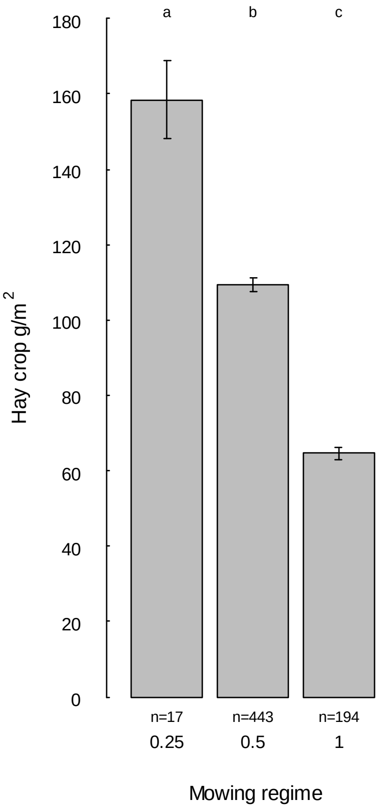


Fig. 6 Hay crop (g/m^2) ± se at Sølendet for plots mowed every 4th (0.25), every 2nd (0.5) and every (1) year. The number of observations is indicated on the x axis, and groups that differ significantly are indicated with the letters a, b and c at the top.

Appendix 1. Species list with abbreviations

The 200 species (= taxa) included in the multivariate analyses of rich fen vegetation in Sølendet and Tågdalen nature reserves with vegetation layers, scientific names and the abbreviations used in Table 2 and Figs. 2 and 3. B = shrub layer, C = field layer, woody plants, D = field layer, herbs, E = field layer, graminoids, F = bottom layer, mosses, G = bottom layer, liverworts (hepatics) and H = bottom layer, macrolichens.

Layer	Species	Abbreviation
B	*Alnus incana* - B	BAlnuinc
B	*Betula nana* - B	BBetunan
B	*Betula pubescens* - B	BBetupub
B	*Salix glauca* - B	BSaligla
B	*Salix myrsinifolia* coll. - B	BSalimyf
C	*Alnus incana*	CAlnuinc
C	*Andromeda polifolia*	CAndrpol
C	*Betula nana*	CBetunan
C	*Betula pubescens*	CBetupub
C	*Calluna vulgaris*	CCallvul
C	*Empetrum nigrum* coll.	CEmpenig
C	*Erica tetralix*	CErictet
C	*Juniperus communis*	CJunicom
C	*Oxycoccus microcarpus*	COxycmic
C	*Salix glauca*	CSaligla
C	*Salix hastata*	CSalihas
C	*Salix lapponum*	CSalilap
C	*Salix myrsinifolia* coll.	CSalimyf
C	*Salix phylicifolia*	CSaliphy
C	*Salix reticulata*	CSaliret
C	*Sorbus aucuparia*	CSorbauc
C	*Vaccinium uliginosum*	CVacculi
C	*Vaccinium vitis-idaea*	CVaccvit
D	*Alchemilla* sp.	DAlchsp.

Appendix 1. Species list with abbreviations

Layer	**Species**	**Abbreviation**
D	*Anemone nemorosa*	DAnemnem
D	*Angelica sylvestris*	DAngesyl
D	*Antennaria dioica*	DAntedio
D	*Bartsia alpina*	DBartalp
D	*Bistorta vivipara*	DBistviv
D	*Caltha palustris*	DCaltpal
D	*Cirsium palustre*	DCirspal
D	*Coeloglossum viride*	DCoelvir
D	*Comarum palustre*	DComapal
D	*Corallorhiza trifida*	DCoratri
D	*Crepis paludosa*	DCreppal
D	*Dactylorhiza cruenta*	DDactcru
D	*Dactylorhiza incarnata*	DDactinc
D	*Dactylorhiza lapponica*	DDactlap
D	*Dactylorhiza maculata*	DDactmac
D	*Drosera anglica*	DDrosang
D	*Drosera rotundifolia*	DDrosrot
D	*Epilobium palustre*	DEpilpal
D	*Equisetum palustre*	DEquipal
D	*Equisetum scirpoides*	DEquisci
D	*Equisetum variegatum*	DEquivar
D	*Erigeron boreale*	DErigbor
D	*Euphrasia wettsteinii*	DEuphwet
D	*Filipendula ulmaria*	DFiliulm
D	*Galium boreale*	DGalibor
D	*Geranium sylvaticum*	DGerasyl
D	*Geum rivale*	DGeumriv
D	*Gymnadenia conopsea*	DGymncon
D	*Huperzia selago*	DHupesel
D	*Leontodon autumnalis*	DLeonaut
D	*Listera ovata*	DListova
D	*Melampyrum pratense*	DMelapra
D	*Melampyrum sylvaticum*	DMelasyl
D	*Menyanthes trifoliata*	DMenytri
D	*Narthecium ossifragum*	DNartoss
D	*Parnassia palustris*	DParnpal

Layer	**Species**	**Abbreviation**
D	*Pedicularis oederi*	DPedioed
D	*Pedicularis palustris*	DPedipal
D	*Pinguicula vulgaris*	DPingvul
D	*Platanthera bifolia*	DPlatbif
D	*Potentilla erecta*	DPoteere
D	*Pyrola minor*	DPyromin
D	*Pyrola rotundifolia*	DPyrorot
D	*Ranunculus acris*	DRanuacr
D	*Rumex acetosa*	DRumeace
D	*Saussurea alpina*	DSausalp
D	*Saxifraga aizoides*	DSaxiaiz
D	*Scheuchzeria palustris*	DSchepal
D	*Selaginella selaginoides*	DSelasel
D	*Solidago virgaurea*	DSolivir
D	*Succisa pratensis*	DSuccpra
D	*Thalictrum alpinum*	DThalalp
D	*Tofieldia pusilla*	DTofipus
D	*Trientalis europaea*	DTrieeur
D	*Triglochin palustre*	DTrigpal
D	*Utricularia minor*	DUtrimin
D	*Viola palustris/epipsila*	DViolpal
E	*Agrostis capillaris*	EAgrocap
E	*Anthoxanthum odoratum*	EAnthodo
E	*Calamagrostis stricta*	ECalastr
E	*Carex atrofusca*	ECareatr
E	*Carex buxbaumii*	ECarebux
E	*Carex capillaris*	ECarecap
E	*Carex capitata*	ECarecap
E	*Carex chordorrhiza*	ECarecho
E	*Carex dioica*	ECaredio
E	*Carex echinata*	ECareech
E	*Carex flava*	ECarefla
E	*Carex flava* x *hostiana*	ECarefxh
E	*Carex flava* x *tumidicarpa*	ECarefxt
E	*Carex heleonastes*	ECarehel

Appendix 1. Species list with abbreviations

Layer	Species	Abbreviation
E	*Carex hostiana*	ECarehos
E	*Carex lasiocarpa*	ECarelas
E	*Carex limosa*	ECarelim
E	*Carex nigra*	ECarenig
E	*Carex panicea*	ECarepan
E	*Carex pauciflora*	ECarepau
E	*Carex rostrata*	ECareros
E	*Carex saxatilis*	ECaresax
E	*Carex vaginata*	ECarevag
E	*Deschampsia cespitosa*	EDescces
E	*Eleocharis quinqueflora*	EEleoqui
E	*Eriophorum angustifolium*	EErioang
E	*Eriophorum latifolium*	EEriolat
E	*Eriophorum vaginatum*	EEriovag
E	*Festuca ovina*	EFestovi
E	*Festuca vivipara*	EFestviv
E	*Hierochloe odorata*	EHierodo
E	*Juncus alpinoarticulatus*	EJuncalp
E	*Juncus castaneus*	EJunccas
E	*Juncus triglumis*	EJunctri
E	*Kobresia simpliciuscula*	EKobrsim
E	*Luzula sudetica*	ELuzusud
E	*Molinia caerulea*	EMolicae
E	*Nardus stricta*	ENardstr
E	*Schoenus ferrugineus*	ESchofer
E	*Trichophorum alpinum*	ETricalp
E	*Trichophorum cespitosum*	ETricces
F	*Aulacomnium palustre*	FAulapal
F	*Brachythecium reflexum*	FBracref
F	*Brachythecium turgidum*	FBractur
F	*Breidleria pratensis*	FBreipra
F	*Bryum pseudotriquetrum*	FBryupse
F	*Calliergon giganteum*	FCallgig
F	*Calliergon richardsonii*	FCallric
F	*Calliergonella cuspidata*	FCallcus

Layer	Species	Abbreviation
F	*Calliergonella lindbergii*	FCalllin
F	*Campylium stellatum*	FCampste
F	*Cinclidium stygium*	FCincsty
F	*Ctenidium molluscum*	FCtenmol
F	*Dicranum bonjeanii*	FDicrbon
F	*Ditrichum flexicaule*	FDitrfle
F	*Fissidens adianthoides*	FFissadi
F	*Fissidens osmundoides*	FFissosm
F	*Hylocomiastrum pyrenaicum*	FHylopyr
F	*Hylocomiastrum umbratum*	FHyloumb
F	*Hylocomium splendens*	FHylospl
F	*Hypnum bambergeri*	FHypnbam
F	*Loeskypnum badium*	FLoesbad
F	*Meesia triquetra*	FMeestri
F	*Paludella squarrosa*	FPalusqu
F	*Palustriella commutata*	FPalucom
F	*Philonotis fontana/tomentella*	FPhilf/t
F	*Plagiomnium elatum*	FPlagela
F	*Plagionmium ellipticum*	FPlagell
F	*Plagiothecium denticulatum*	FPlagden
F	*Pleurozium schreberi*	FPleusch
F	*Polytrichastrum formosum*	FPolyfor
F	*Pseudocalliergon trifarium*	FPseutri
F	*Racomitrium lanuginosum*	FRacolan
F	*Rhizomnium pseudopunctatum*	FRhizpse
F	*Rhytidiadelphus squarrosus/subpinnatus*	FRhytsqu
F	*Rhytidiadelphus triquetrus*	FRhyttri
F	*Sanionia uncinata*	FSaniunc
F	*Scorpidium cossonii*	FScorcos
F	*Scorpidium scorpioides*	FScorsco
F	*Sphagnum auriculatum* s.lat.	FSphaaur
F	*Sphagnum contortum*	FSphacon
F	*Sphagnum lindbergii*	FSphalin
F	*Sphagnum papillosum*	FSphapap
F	*Sphagnum platyphyllum*	FSphapla
F	*Sphagnum subnitens*	FSphasub

Appendix 1. Species list with abbreviations

Layer	**Species**	**Abbreviation**
F	*Sphagnum subsecundum*	FSphasub
F	*Sphagnum teres*	FSphater
F	*Sphagnum warnstorfii*	FSphawar
F	*Straminergon stramineum*	FStrastr
F	*Tomentypnum nitens*	FTomenit
F	*Tortella tortuosa*	FTorttor
F	*Warnstorfia sarmentosa*	FWarnsar
G	*Aneura pinguis*	GAneupin
G	*Barbilophozia floerkei*	GBarbflo
G	*Barbilophozia lycopodioides*	GBarblyc
G	*Barbilophozia quadriloba* coll.	GBarbqua
G	*Barbilophozia rutheana*	GBarbrut
G	*Calypogeia sphagnicola*	GCalysph
G	*Cephalozia lunulifolia* coll.	GCephlun
G	*Cephaloziella* sp.	GCephsp.
G	*Chiloscyphus pallescens/polyanthos*	GChilpal
G	*Cladopodiella fluitans*	GCladflu
G	*Fossombronia foveolata*	GFossfov
G	*Gymnocolea borealis*	GGymnbor
G	*Lophozia bantriensis/gillmanii*	GLophb/g
G	*Moerckia hibernica*	GMoerhib
G	*Odontoschisma elongatum*	GOdonelo
G	*Pellia neesiana*	GPellnee
G	*Plagiochila porelloides*	GPlagpor
G	*Ptilidium ciliare*	GPtilcil
G	*Riccardia multifida*	GRiccmul
G	*Scapania degenii*	GScapdeg
G	*Scapania irrigua*	GScapirr
G	*Scapania paludicola*	GScappal
G	*Scapania paludosa*	GScappal
G	*Scapania undulata*	GScapund
G	*Tritomaria polita*	GTritpol
G	*Tritomaria quinquedentata*	GTritqui
H	*Cetraria islandica*	HCetrisl

Paper II

Opposite effects of mowing on size of *Eriophorum latifolium* ramets in rich fen carpet and lawn communities

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Abstract

Question: How does mowing affect the size of vegetative and flowering ramets of *Eriophorum latifolium* along a wet – dry gradient in boreal rich fen vegetation?

Location: Central Norway.

Methods: Seven size parameters of individually marked ramets (n = 683-895) were surveyed over a four year period in 32 plots with a range of mowing regimes in rich fen carpet (one study area) and lawn vegetation (two study areas). Generalised linear models and generalised linear mixed models were applied to analyse possible differences caused by mowing regime, vegetation, study area and year.

Results: Mowing reduced the length, width and number of leaves in rosettes of *E. latifolium* in carpet in one study area and lawn in the other study area, but increased the same size parameters in lawn in the first area. The width of leaves was not reduced by extensive mowing (every 8th year), only by mowing every 3rd year, while the length and number of leaves had a gradual response to increased mowing intensity. Flowering ramets had more stalk leaves and spikelets in unmowed plots, whereas there was no clear effect of mowing on the height of flowering stalks. Flowering stalks were taller in carpet than lawn vegetation, while the number of spikelets was lower in carpet than lawn (one study area).

Conclusions: The same mowing regime had opposite effects on size parameters in ramets in different types of fen vegetation in one study area, and similar mowing regimes in the two study areas had opposite effects on size parameters in the same type of vegetation. This study emphasises that a thorough assessment of both mowing regime and vegetation is necessary when management plans are implemented.

Keywords: Boreal region; Long-term management; Leaf length; Leaf width; Number of leaves; Flowering stalk; Central Norway

Introduction

Cessation of mowing in outlying lands has led to successional changes in European landscapes over the last century (Emanuelsson 2009). Low-growing species are encroached upon by shrubs, tall herbs and grasses, leading to changes in species abundance and composition in several grassland (Losvik 1988, Hansson & Fogelfors 2000) and fen vegetation types (Moen 1990, Diemer et al. 2001). Halting or reversing effects of encroachment is possible in fen vegetation when mowing is sustained or resumed, and species tolerant to disturbance maintain or regain their dominance (Güsewell et al. 1998, Moen et al. 1999, Billeter et al. 2003). In outlying lands, and in fens (sensu e.g. Sjörs (1948) and Rydin & Jeglum (2006)) in particular, nutrient availability is often very low (Øien & Moen 2001), favouring stress tolerant species (Grime 2001), at least if the disturbance (Crawley 1997) is moderate. Mowing affects individual plants through disturbance, and the level of disturbance is determined by the intensity and frequency of mowing. The intensity can be assessed by how much stubble is left after mowing, and the frequency by the interval between mowing incidents. Mowing favours plants that either avoid or are resilient to the mowing treatment. Low-growing plants (often with rosettes) and plants reproducing early in the season can avoid being mowed, and plants with low positioning of meristems and clonal growth are often resilient to mowing (e.g. Klimešová et al. 2008).

There seems to be consistency in the positive effects of mowing on the number of leaves per plant, but contradictory results regarding leaf size and height of the flowering stalk. Overgrowing decreases the number of rosette leaves in *Succisa pratensis* in fen vegetation but does not affect the height of flowering stalks, and it increases vegetative shoot height in both *Carex davalliana* and *S. pratensis* (Billeter et al. 2003). Mowing increases the number of leaves in the rosette but decreases the leaf area of *Viola palustris* in wet meadow vegetation (Jensen & Meyer 2001). Similarly, mowing increases the number of leaves while length of leaves and biomass decrease in *Cnidium dubium* in a riparian floodplain (Geissler & Gzik 2008). On the other hand, mowing increases leaf area in *Dactylorhiza majalis* in wet meadow vegetation (Janečková et al. 2006). Syrjänen & Lehtilä (1993) studied the effects of removal of flowering stalks and complete defoliation in *Primula veris* in deciduous forest, and the first treatment may be comparable to mowing. These authors found that removal of flowering stalks increases the height of flowering stalks, leaf area and to some extent number of leaves next year, but they also documented temporal variation and differences between populations. The tall-growing graminoid *Carex lasiocarpa* tolerates mowing rather badly, but the reduction of e.g. height and above-ground biomass is higher in wet fen (mud bottom) than in drier fen lawn (Elveland 1984, Moen 1990). This suggests a more severe effect of mowing in wet vegetation in some species, possibly because flooding of the stubble hinders oxygen uptake and transport (Moen 1990).

Eriophorum latifolium Hoppe (Cyperaceae) is a rosette-forming, clonal graminoid common in boreal rich fens. The aim of this paper is to establish how mowing affects the size of ramets in *E. latifolium* under field conditions, and to see if the outcome varies along a wet – dry gradient in fen vegetation. Ramets in unmowed compared to mowed areas are expected to have longer and wider but fewer leaves in the rosette, and taller flowering stalks with more stalk leaves and spikelets. A larger impact is expected with shorter mowing interval for all size parameters, and mowing is expected to affect ramets in the same way in two study areas with similar rich fen vegetation. *E. latifolium* is most abundant in open fen lawn vegetation, and it is expected to tolerate mowing better in fen lawn than fen carpet. The effects of long-term mowing on size parameters in ramets of *E. latifolium* were examined in Sølendet and Tågdalen nature reserves in the period 2006-09. Differences due to vegetation, mowing regime, study area and year was examined with generalised linear models and generalised linear mixed models.

Material and methods

Study species

Eriophorum latifolium is a rich fen and spring graminoid growing in areas with base-rich peat with pH most often in the range 5.5-7.5 and electrical conductivity in surface water mostly above 100 µS (Kutschera et al. 1982, Moen 1990, Petraglia & Tomaselli 2003). It is widely distributed throughout Europe (Hultén & Fries 1986), reaches 2100 m a.s.l. in the Alps (Jäger et al. 1965), and 1120 m a.s.l. in Norway (Elven 2005). In Norway it can be found in boreal areas up to the climatic forest limit, and may be locally abundant or dominant in open lawn communities of sloping fens formerly used for hay making. It does not tolerate stagnant water well, and is absent in mud bottom vegetation (Moen 1990, Fremstad 1997).

Vegetative ramets form rosettes with normally three to five rather slender leaves, while flowering ramets produce an elongated flowering stalk lacking a basal rosette. See Table 1 for size attributes of *E. latifolium*. In general, apical meristems are transformed and consumed when ramets in monocarpic (sensu de Kroon & van Groenendael 1997) species flower (Jónsdóttir & Watson 1997), and ramets of *E. latifolium* also die after flowering. New rhizomes emerge from below-ground leaf axils (Raunkiær 1895), the rhizome is short, and the new ramet typically remains within 5 cm from its mother ramet. Each mother ramet can give rise to between one and four daughter ramets, resulting in the formation of loose tufts of potentially integrated ramets. Roots are mostly 10-20 cm long, and in rich fen in Fennoscandia they normally extend down to 10 cm, and occasionally down to 20 cm (Metsävainio 1931). The density of *E. latifolium* ramets is higher in mowed than unmowed fen lawn vegetation (92 m^{-2} and 35 m^{-2} respectively), and this pattern is also seen for above-ground biomass (21.3 and 14.7 g/m^2) and below-ground biomass (29.1 and 24.4 g/m^2) (Aune et al. 1996). Thus, total biomass and root/shoot (biomass) ratio is higher in mowed than unmowed areas, but the weight of individual ramets should on average be lower in mowed areas.

Study areas

The study was conducted at Sølendet and Tågdalen nature reserves which are situated 145 km apart in central Norway (Table 2, Fig. 1). Extremely rich fen vegetation (sensu Sjörs 1948, 1952) formerly used for haymaking covers substantial areas in both nature reserves, a type of vegetation considered near threatened in Norway due to overgrowing (Fremstad & Moen 2001). Mowing is currently implemented as a management tool in both areas to prevent encroachment. The study areas lie at the transition between the middle boreal and northern boreal vegetation zones (Moen 1999). Tågdalen has an oceanic climate, while Sølendet has a more continental climate, and precipitation is markedly higher at Tågdalen than at Sølendet (Table 2). The growing season is short, normally from late May until late August. Both Sølendet and Tågdalen hold large populations of *E. latifolium*.

Experimental design

Size parameters in *E. latifolium* ramets were studied in 32 sample plots of 0.25 m^2 (0.5 x 0.5 m), 15 at Sølendet and 17 at Tågdalen. At Sølendet, the sample plots were placed independently in 15 permanent plots (4 m^2, from here on referred to as plots), whereas at Tågdalen, the 17 sample plots were nested within 12.5 m^2 plots, which again were nested in localities. Locality here refers to spatially congregated groups of plots. The vegetation within plots was homogeneous, and the treatments were applied at the plot level in both study areas. The plots in Tågdalen were located along a 1 km stretch with fens in a small valley, and the plots at Sølendet were located up to 500 m apart in a largely open fen area. The mowing intervals at Sølendet were: mowed every 3rd year (five plots), extensively mowed (every 8th year on average, range 4-12 years, six plots) or unmowed (four plots), and a motorised mower was used. The plots mowed every 3rd year have been mowed ten times between 1979 and 2006, and the extensively mowed plots have been mowed three or four times between 1979 and 2001. The mowing at Tågdalen was carried out using a scythe, and the mowing regimes were every 2nd year (three plots, eight sample plots) and unmowed (four plots, nine sample plots). Mowing commenced in 1973, 1983 and 1985 in the three mowed plots, and has been performed biennially since.

Vegetation

Three local vegetation gradients in mire vegetation are recognised and used in the Fennoscandian tradition (e.g Tuomikoski 1942, Sjörs 1948, Du Rietz 1949, Ruuhijärvi 1960, Persson 1961, Eurola 1962, Malmer 1962, Moen 1990, Rydin & Jeglum 2006). The poor – rich gradient reflects pH and mineral concentration, the mire expanse – mire margin gradient (often) reflects peat depth, and the hummock – mud bottom gradient reflects groundwater level. In this paper the mire expanse – mire margin and hummock – mud bottom gradients are combined in a wet – dry gradient. The rich fen vegetation at Sølendet and Tågdalen was described and classified into six plant communities and ten vegetation clusters based on 134 vegetation samples (A. Lyngstad, A. Moen & D.-I. Øien unpubl.), and resembled the vegetation of sloping rich fens described from northern Sweden (Persson 1961, 1962) and eastern Finland (Havas 1961). There was little variation along the poor – rich gradient, all plots had extremely rich fen vegetation. The 32 sample plots used in this study are shown superimposed on DCA-diagrams based on the 134 samples used in the aforementioned classification (Fig. 2). The wet – dry gradient was reflected in the first DCA-axis for both study areas, and the sample plots fall into four (out of ten possible) vegetation clusters. Table 3 gives an overview of the four represented clusters, the plant communities they belong to, and their relative location along the wet – dry gradient. The fen carpet community (cluster 2) is dominated by *Scorpidium* spp. in the bottom layer, and the lawn communities (clusters 4-6) by *Campylium stellatum*. The lawn communities have the dominant species in common, and the separation between the study areas is caused by occurrences of some oceanic and lowland species at Tågdalen, and some continental and alpine species at Sølendet (A. Lyngstad, A. Moen & D.-I. Øien unpubl.).

Size measurements

Ramets of *E. latifolium* were identified and marked with numbered plastic sticks, using the sample plots as coordinate systems. All ramets were marked in sample plots containing up to 20 ramets (nine sample plots), and when the number of ramets exceeded 20, all ramets within a smaller area in the sample plots were marked (23 sample plots). The exact size of this area was noted to avoid ambiguity concerning ramet identity or descent. The length of the longest leaf was measured to the nearest cm from the bottom layer to the tip of the leaf (Bedford et al. 1988). This was recorded for all vegetative ramets, as was also the width of the widest leaf (measured to the nearest mm), number of mature leaves (> 2 cm long, from here on referred to as number of leaves) and number of emerging leaves (< 2 cm long). The height of the stalk (measured to the nearest cm), number of stalk leaves and number of spikelets was recorded in flowering ramets. Censuses were carried out once a year between 2006 and 2009, in August and September in 2006, and between mid-July and early August the other years.

Statistical analysis

The experimental design at Tågdalen was nested with sample plots within plots within localities, while that at Sølendet was not nested. Separate modelling approaches were therefore used, generalised linear models (GLM) on data from Sølendet, and generalised linear mixed models (GLMM, McCulloch & Searle 2001, Zuur et al. 2009) on data from Tågdalen, with locality, plot and sample plot as random factors (Crawley 2007). The data was not transformed prior to analysis. The minimal adequate models (i.e. most parsimonious) for all size parameters were identified through step-wise exclusion of factors and interactions between factors (starting with full models) based on deviance tests (e.g. Jongman et al. 1995). For the GLMM's the structure of the random part of the model was determined first, then the structure of the part with fixed factors. The fixed factors considered for both study areas were mowing regime, vegetation cluster and year. Overparameterisation and unbalanced data was an issue in some models, and complexity was generally reduced by leaving out interactions rather than factors. Appendix S1 contains an overview of the minimal adequate models for each size parameter. Statistical analyses were conducted in the R statistical environment (R Development Core Team 2008), making use of the packages "gplots" (Warnes) and "lme4" (Bates et al. 2008).

Results

Typical ramet size

Table 1 gives an overview of the size parameters measured in *E. latifolium*. Maximum, minimum and mean (+/- se) values are shown summarised over four years for each study area. The average vegetative rosette had three mature leaves and one emerging leaf, and the longest and widest leaves were on average 10 cm long and 3 mm wide. The average flowering ramet was 40 cm tall with three stalk leaves and four spikelets in the inflorescence. Three ramets that subsequently survived until next year lacked both mature and emerging leaves, and were registered with no leaves.

Length of leaves

Leaves were generally longer in fen carpet than in fen lawn vegetation at Sølendet (Fig. 3). Mowing every 3rd year and mowing extensively reduced the length of the leaves in fen carpet vegetation compared to unmowed plots. Contrastingly, in fen lawn vegetation the leaf length increased under the mowing treatments compared to the unmowed plots, albeit significantly so only in plots mowed every 3rd year. As a result, the mowing reduced and eventually evened out differences in leaf length attributable to differences in vegetation. At Sølendet, leaves were longer in 2006 than in 2008 and 2009 ($p = 0.011$, $p < 0.001$), longer in 2007 than in 2009 ($p < 0.001$), and longer in 2008 than in 2009 ($p = 0.002$). The length did not differ between 2006 and 2007 or between 2007 and 2008 ($p > 0.05$). At Tågdalen, mowing every 2nd year reduced the length of the leaves compared to no mowing (Fig. 4). The leaves in mowed plots were shorter in 2006 compared to the other years, while leaf length in unmowed plots seemed to decrease gradually from 2006 to 2009. Note that only 2009 differed significantly from the other years in this respect. Leaves were longer in vegetation cluster 5 than 4, but the difference decreased from 2006 to 2008, and the length was not shown to differ in 2008 (Fig. 5). Leaf length was at its longest in cluster 5 in 2006, and a steady decrease followed in this cluster while an increase was seen in cluster 4. This pattern was disrupted by the decrease in 2009, where the shortest leaf lengths were recorded for both clusters. Consult Tables S1-S21 in Appendix S2 for further details concerning the differences between estimates of levels of fixed factors and the accompanying |t|- or p-values for the seven size parameters.

Width of leaves

Leaves were wider in fen carpet than fen lawn vegetation in the unmowed plots at Sølendet (Fig. 6), and while this pattern also seemed to be present in extensively mowed plots, the clusters were not significantly different. Leaf width was similar in fen carpet and lawn in plots mowed every 3rd year. Mowing generally increased leaf width in fen lawn, and mowing every 3rd year reduced leaf width in fen carpet. The leaves were narrower in 2007 than in 2006 ($p = 0.001$), 2009 ($p = 0.045$) and likely also 2008 ($p = 0.051$), and there were no differences between the other three years at Sølendet ($p > 0.05$). Mowing every 2nd year generally reduced the width of the leaves compared to unmowed plots at Tågdalen (Fig. 7), and the effect of mowing regimes differed in all years except 2008. The width decreased steadily from 2006 to 2008 in unmowed plots, while no temporal effects were shown in plots mowed every 2nd year.

Number of leaves

More frequent mowing lowered the number of leaves per rosette in fen carpet at Sølendet, whereas the number of leaves in fen lawn increased (Fig. 8). Thus, the highest number of leaves in fen carpet was found in unmowed plots, and in fen lawn in the plots mowed every 3rd year. An increase in number of leaves was seen in unmowed plots from 2006 to 2009 at Sølendet, but only the years 2006 and 2009 differed significantly ($p = 0.045$). Rosettes in plots mowed every 3rd year had fewer leaves than rosettes in unmowed and extensively mowed plots in 2007 ($p = 0.001$ in both cases), and fewer leaves than rosettes in unmowed plots in 2008 and 2009 ($p < 0.001$ in both cases). Rosettes in extensively mowed plots had fewer leaves than rosettes in unmowed plots in 2009 ($p = 0.002$). The number of leaves was higher in rosettes in plots mowed every 3rd year in 2006 than in the subsequent years ($p < 0.01$ in all cases). Mowing every 2nd year at Tågdalen reduced the number of leaves per rosette compared to the unmowed plots (Fig. 9). The rosettes had more leaves in 2007 than in other years, fewer leaves in 2008 and 2009 than in other years, while 2006 held a middle position ($|t| > 2$ in all cases). 2008 and 2009 were similar ($|t| = 1.65$).

Number of emerging leaves

Rosettes in unmowed plots in fen lawn at Sølendet had more emerging leaves than rosettes in unmowed fen carpet ($p = 0.002$) and in lawn and carpet mowed every 3rd year ($p < 0.001$ in both cases). The number of emerging leaves varied little among other combinations of the factors mowing regime and vegetation cluster. There were more emerging leaves registered in 2006 than in the other years, and the years 2007-09 did not differ at Sølendet (Table S8, Appendix S2). A similar pattern was seen at Tågdalen, but in addition to more emerging leaves in 2006, there were fewer emerging leaves in 2008 than in other years (Table S19, Appendix S2).

Height of the flowering stalk

The tallest flowering stalks at Sølendet were recorded in the unmowed plots in 2006, and the shortest stalks were recorded in extensively mowed plots in 2007 and 2008 (Fig. 10). The height varied less between years in plots mowed every 3rd year than in the other mowing regimes, and the height of the stalks was similar in all mowing regimes in 2009. The mean height was close to 40 cm for both fen carpet and fen lawn in all years, the exceptions being fen carpet in 2006 (48 cm) and fen lawn in 2008 (31 cm). The former was significantly higher ($p < 0.05$) than for all vegetation and year combinations except fen lawn in 2007 ($p = 0.186$), the latter lower ($p < 0.05$) than for all vegetation and year combinations except fen carpet in 2009 ($p = 0.070$). Flowering stalks at Tågdalen seemed to be shorter in plots mowed every 2nd year than in unmowed plots in all years except 2007, but this was demonstrated clearly only for 2006 and 2008 (Fig. 11).

Number of stalk leaves

Flowering ramets had more stalk leaves in unmowed plots than in mowed plots at Sølendet ($p = 0.005$, $p = 0.002$). None of the explanatory variables included affected the number of stalk leaves at Tågdalen.

Number of spikelets

Each inflorescence had more spikelets in fen lawn than fen carpet at Sølendet, and there were more spikelets per inflorescence in 2008 than 2009 in this study area (Fig. 12). Mowing regime did not affect the number of spikelets at Sølendet, but was the only factor affecting the number of spikelets at Tågdalen where mowing every 2nd year reduced the number of spikelets compared to no mowing (Fig. 12).

Discussion

Vegetative ramets

The response to mowing in vegetative ramets of *E. latifolium* at Sølendet varied with both mowing regime and vegetation cluster. In fen carpet, leaf numbers and sizes were generally larger in unmowed than in mowed plots, and leaves became shorter before they became narrower as the mowing frequency increased. Contrastingly, rosettes in fen lawn had more and larger leaves in mowed plots, both length and number of leaves increased with increasing mowing frequency, whereas the width of leaves peaked under extensive mowing. Thus, the hypothesis of longer and wider leaves in unmowed areas was confirmed for rosettes of *E. latifolium* in fen carpet, but refuted in fen lawn vegetation. Number of leaves per rosette showed the same pattern of decrease or increase as the length of leaves, and the hypothesis of fewer leaves in unmowed areas holds in fen lawn but not fen carpet. Length and number of leaves responded gradually to increased mowing frequency as hypothesised, but leaf width did not follow this pattern. The length seemed to be reduced before the width of leaves as the disturbance from mowing increased. This is an adequate response, as it reduces the proportion of the above-ground biomass likely to be removed during mowing (e.g. Aune et al. 1996), and may contribute to the competitiveness of *E. latifolium* under mowed conditions. The increasing ramet size in fen lawn at Sølendet demonstrated the beneficial effects of mowing on *E. latifolium* in this type of vegetation. Hájková et al. (2009) finds that *E. latifolium* is among the species most restricted by abandonment in rich fens in the Czech Republic, and increased competition from *Molinia caerulea* is a major cause of the decline noted by these authors. *M. caerulea* is an abundant species in fen lawn vegetation that does not tolerate mowing very well (Moen 1990, Hájková et al. 2009), and mowing in fen lawn may therefore benefit *E. latifolium* through reduced competition. The increased size of *E. latifolium* in mowed fen lawn is contrasted by the reduced size in mowed fen carpet. Inundation of the stubble after scything is posed as an explanation to the more severe effect of mowing on *Carex lasiocarpa* in mud bottom than fen lawn (Elveland 1984, Moen 1990). The fen carpet communities studied here have a low water table compared to the mud bottom communities studied by Elveland (1984), and the negative impact is not nearly as pronounced. While inundation may play a role, it is likely not a sufficient explanation. *E. latifolium* has a narrow range on the wet – dry gradient in fen where it performs well (Moen 1990), and it is in fen carpet close to its upper tolerance limit along this gradient. Mowing tends to lower the distance to the water table in fens (A. Moen, unpubl.), and may therefore have a more negative effect in fen carpet. Some tall-growing species, particularly *C. lasiocarpa* and *C. rostrata*, are more abundant in fen carpet than fen lawn (A. Lyngstad, A. Moen & D.-I. Øien unpubl.). Light may become a limiting resource (Tilman 1997) for rosette plants like *E. latifolium* in the absence of mowing as litter accumulates and plants grow taller. Specific leaf area (leaf surface area/biomass ratio) increases under shading (Reich et al. 2003), implying a larger investment in photosynthetic tissue when light becomes scarce. Elongation of leaves is a possible way for plants to avoid shading (Janečková et al. 2006), and the particularly long (and relatively narrow) leaves registered in *E. latifolium* in unmowed fen carpet may be a result of elongation. Leaves were shown to reach widths of 8-9 mm (Table 1), considerably wider than the average width of 3-3.5 mm in unmowed fen carpet, suggesting that plasticity in leaf width was not limiting in this case. Thus, it may be that a larger proportion of the resources available to ramets in fen carpet were invested in above-ground structures, resulting in a larger relative impact of mowing. In addition, ramets of *E. latifolium* tended to grow more upright in fen carpet than in fen lawn vegetation (pers. obs.), this would further increase susceptibility to mowing.

The response to mowing in vegetative ramets at Tågdalen was more straightforward than the response at Sølendet. Leaves were longer in vegetation cluster 4 than 5 regardless of mowing regime, whereas the other size parameters pertaining to vegetative ramets were unaffected by vegetation cluster. This may be because both vegetation clusters at Tågdalen belonged to the same fen lawn vegetation community, and were more similar than the vegetation clusters at Sølendet. Mowing every 2nd year reduced the length, width and number of leaves regardless of vegetation cluster; this was similar to the response to mowing in fen carpet at Sølendet. This result fitted with the expectations of longer and wider leaves in unmowed plots, but not regarding number of leaves per rosette. The different response to mowing in fen lawn at Tågdalen and Sølendet is intriguing, and not in accordance with the expectations. Mowing was performed with a scythe every 2nd year at Tågdalen as opposed to every 3rd year with a motorised mower at Sølendet. The scythe leaves shorter stubble, and ramets are less likely to avoid being cut. In addition, each plot at Tågdalen has (as of 2009) been mowed between 13 and 19 times, whereas the plots at Sølendet have been mowed ten times. Both the number of mowing incidents, intensity and frequency of mowing are therefore higher at Tågdalen, and comparisons between mowing treatments should be made with caution. Unmowed plots are not affected by this uncertainty. The length, width and number of leaves in rosettes in unmowed fen lawn at Tågdalen match the values registered in unmowed fen carpet at Sølendet rather well, and better than it matches the values in fen lawn at Sølendet. Thus, the differences in mowing regime may account for some, but not all of the dissimilar responses to mowing in ramets in ecologically equivalent fen vegetation in the study areas. This topic is suitable for further investigation.

Flowering ramets

The root/shoot biomass ratio in *E. latifolium* is lower in unmowed than mowed plots, and the weight of individual ramets is higher in unmowed plots (Aune et al. 1996). Ramets in unmowed areas can be expected to utilise their larger resource storage and invest more when they flower. Hence, flowering stalks were hypothesised to be taller with more stalk leaves and spikelets in unmowed plots. This was the case for stalk leaves in unmowed plots at Sølendet and for spikelets in unmowed plots at Tågdalen, whereas stalk leaves at Tågdalen and spikelets at Sølendet were unaffected by mowing regime. Flowering stalks were often taller in unmowed than mowed plots in both study areas, but the statistical analyses had low power due to few observations. Temporal variation confounded the picture further, and whether flowering stalks are taller in unmowed areas remains uncertain. There were indications that flowering stalks were taller in fen carpet than fen lawn vegetation at Sølendet. This fits well with the pattern seen in vegetative ramets, which were also larger on average in fen carpet than fen lawn. Competition from tall-growing species (see above) may be higher in fen carpet than fen lawn, and taller flowering stalks may be necessary to ensure efficient seed dispersal. Interestingly, the number of spikelets was lower in fen carpet than fen lawn, suggesting a possible trade-off between the vegetative and generative structures in flowering ramets. A trade-off between vegetative growth and reproduction has been demonstrated in several clonal species (e.g. Delph et al. 1993, Sun et al. 2001, Jongejans et al. 2006), but examples of the opposite are not uncommon either (Lord 1998, Thiele et al. 2009). Sun et al. (2001) found that higher shoots produced more seeds in *Scirpus mariqueter*; this seems to contradict the results for *E. latifolium*. However, the sizes of spikelets are presently unknown, and it may be that the lower number of spikelets in the taller flowering ramets was compensated by more flowers or larger seed weight per spikelet.

Temporal variation

Size measurements vary between years at both study areas, but temporal variation seemed to be more important at Tågdalen. Climatic conditions vary substantially between years, and is a source of environmental stochasticity that can affect populations uniformly (Lande et al. 2003). The oceanic climate at Tågdalen is more variable than that at continental Sølendet, and it has been shown that climatic factors are more important in determining flowering density in *E. latifolium* at Tågdalen than at Sølendet (A. Lyngstad, A. Moen & B. Pedersen unpubl.). It is reasonable to assume that this may be the case also for size parameters, both in vegetative and flowering ramets. Climatic variation may suffice as an explanation to yearly variations in the cases where year is not part of an interaction with mowing regime, but such interactions were found for several size parameters. Climate may still be an important factor in these cases, but the lack of effect of some mowing regimes suggests the influence of additional factors. As demonstrated by Hik et al. (2003), handling plants can lower above-ground biomass, and the decreasing length and width of leaves in unmowed plots at Tågdalen (Figs. 4 and 7) may be caused by disturbance from the sampling procedure. The vegetation in mowed plots is accustomed to repeated disturbance, but this is not the case in unmowed plots, and this may explain the decrease.

Young leaves in *Carex bigelowii* over-winter and resume growth in spring (Jónsdóttir & Watson 1997), and *E. latifolium* may follow a similar strategy. Ramets were revisited in September 2007, and many had developed new emerging leaves since the census in July same year (pers. obs.). Thus, leaves seem to be formed continuously in *E. latifolium*-

rosettes during the growing season. This implies that the late census of 2006 compared to 2007-09 can account for the higher number of emerging leaves registered in 2006 in both study areas, and maybe also the higher number of leaves in plots mowed every 3rd year at Sølendet in 2006. Flowering stalks at Sølendet were tallest in 2006, the year with highest registered flowering density (9.9 m^{-2}) in this study area in the period 1982-2008 (A. Lyngstad, A. Moen & B. Pedersen unpubl.). The conditions that triggered flowering in a large proportion of ramets can reasonably be expected to have been favourable for the height of flowering stalks as well. In addition, flowering stalks may have continued to elongate after the censuses in late July in 2007-09, this possible elongation would have been registered in the late census of 2006. There was, however, no such difference in height of flowering stalks between 2006 and the other years at Tågdalen, suggesting that census period did not influence the results of height measurements.

Management implications and concluding remarks

This study demonstrates different responses to mowing in size parameters of *E. latifolium* ramets growing in quite similar types of vegetation. The same mowing regime had opposite effects on vegetative ramets in fen carpet and fen lawn within one study area, and this underscores the need for a thorough assessment of vegetation when management plans are adopted, especially if they target declining species. Most size parameters are affected by any mowing regime, but the width of leaves responded to the shortest mowing intervals only. This may be an adaptation to mowing in *E. latifolium*, contributing to its long-term competitiveness under mowed conditions. The different impact of similar mowing intervals in similar vegetation in the two study areas may be explained by the use of a scythe in one area and a motorised mower in the other. The scythe is known to leave shorter stubble, and the intensity of disturbance is therefore higher when a scythe is used. There are often financial and practical reasons to implement mechanised mowing, but this may alter the effects of mowing on both individual ramets and, eventually, populations as a whole.

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I want to thank Ane Fremstedal, Eva Ulvan and Dag-Inge Øien for help with the field work. Lester Rocha has given helpful statistical advice. This study is part of a PhD project under the supervision of Asbjørn Moen and Bård Pedersen, and was funded by the Norwegian University of Science and Technology.

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Tables

Table 1. Maximum, minimum, mean (+/- se) and number of observations of size measurements in *E. latifolium* (2006-09). Length of leaves, width of leaves, number of leaves and number of emerging leaves were registered in vegetative ramets. Height of stalk, number of stalk leaves and number of spikelets were registered in flowering ramets.

	Sølendet					Tågdalen				
	Max	Min	Mean	se	n	Max	Min	Mean	se	n
Length of leaves (cm)	27	1	10.8	0.09	1435	20	1	9.2	0.08	1519
Width of leaves (mm)	8	1	3.0	0.03	1435	7	0.5	2.8	0.03	1518
Number of leaves	9	0	3.1	0.03	1455	6	1	3.2	0.03	1518
Number of emerging leaves	3	0	0.8	0.01	1141	3	0	1.1	0.01	1517
Height of stalk (cm)	77	3	41.0	1.15	104	60	9	37.4	1.37	57
Number of stalk leaves	5	2	3.3	0.07	104	4	2	2.8	0.07	57
Number of spikelets	7	2	4.7	0.17	43	5	2	3.9	0.13	32

Table 2. Characteristics of Sølendet and Tågdalen nature reserves. *ETS* = effective temperature sum (Laaksonen 1979).

	Sølendet	Tågdalen
Latitude (N)	62°40’	63°03’
Longitude (E)	11°50’	9°05’
Mean annual precipitation (mm)	637	1583
Mean annual *ETS* (day degrees)	578	639
Mean July temperature (°C)	10.5	11.2
Mean January temperature (°C)	-9.5	-2.7
Altitude (m a.s.l.)	700-800	380-490
Area (ha)	306	146

Table 3. The rich fen plant communities and vegetation clusters represented at each study area with their relative positioning along a wet – dry gradient (within study area) and number of sample plots.

Study area	Plant community	Vegetation cluster	Relative wet - dry gradient	Number of sample plots
Sølendet	*Eleocharis quinqueflora-Cinclidium* carpet community	Cluster 2	Wet	6
	Equisetum variegatum-Thalictrum-Campylium lawn community	Cluster 6	Dry	9
Tågdalen	*Eriophorum latifolium-Campylium* lawn community	Cluster 4	Wet	10
		Cluster 5	Dry	7

Figures

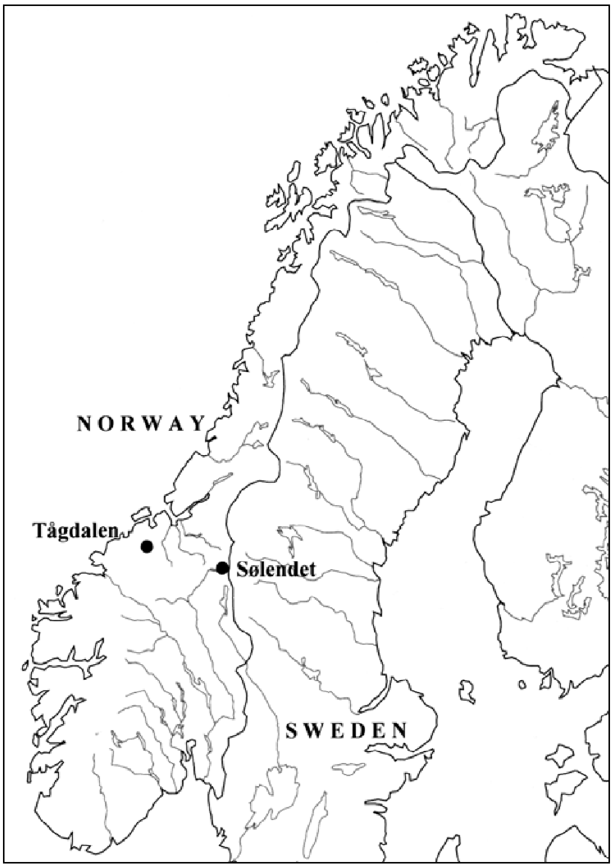

Fig. 1. The location of Sølendet and Tågdalen nature reserves.

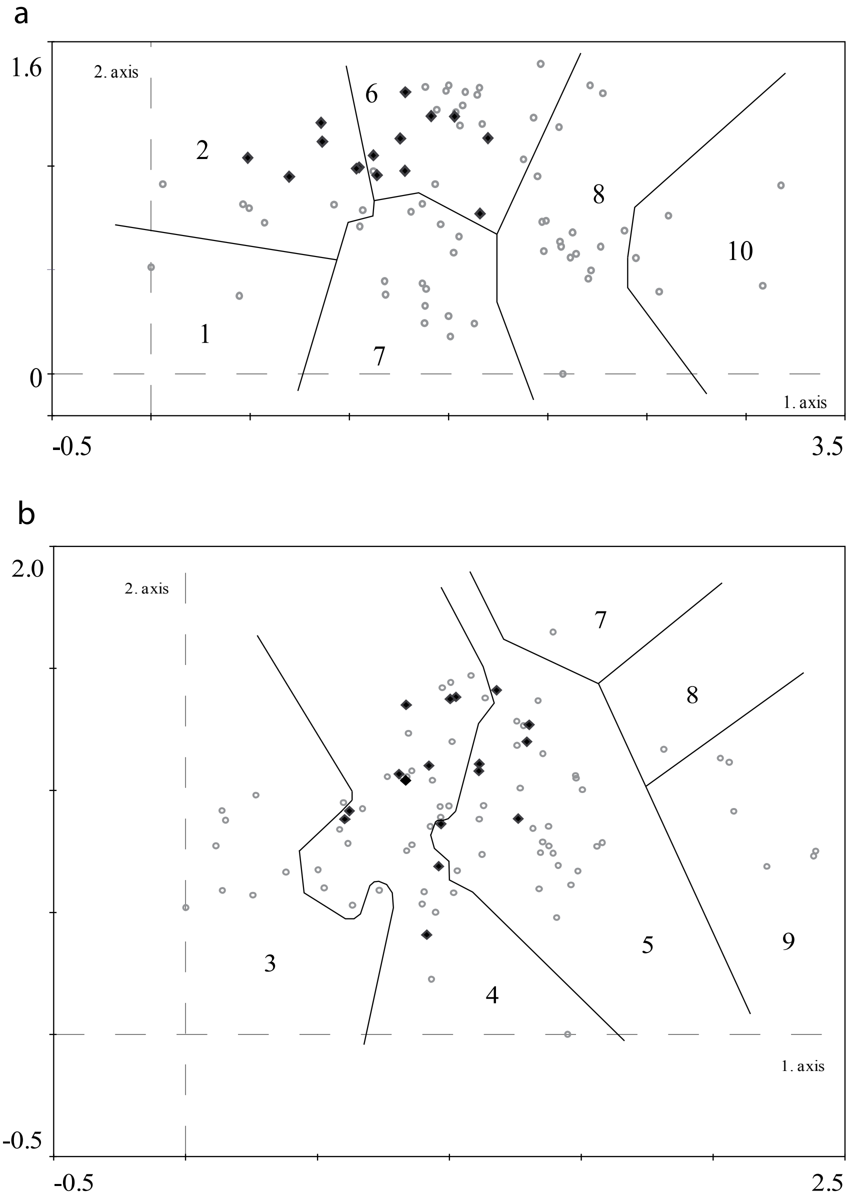

Fig. 2. DCA-ordination (axes 1 and 2) based on (a) 61 vegetation samples from Sølendet, and (b) 73 samples from Tågdalen (open circles) used to describe and classify the rich fen vegetation of the study areas (A. Lyngstad, A. Moen & D.-I. Øien unpubl.). The separation of plant communities and vegetation clusters 1-10 is based on this classification. Axis 1 reflects a wet – dry gradient (left to right) in both (a) and (b). The sample plots utilised in this paper are shown superimposed (black diamonds) and belong to fen carpet (cluster 2) and fen lawn (cluster 6) at Sølendet and fen lawn (clusters 4 and 5) at Tågdalen. Note the differences in scale.

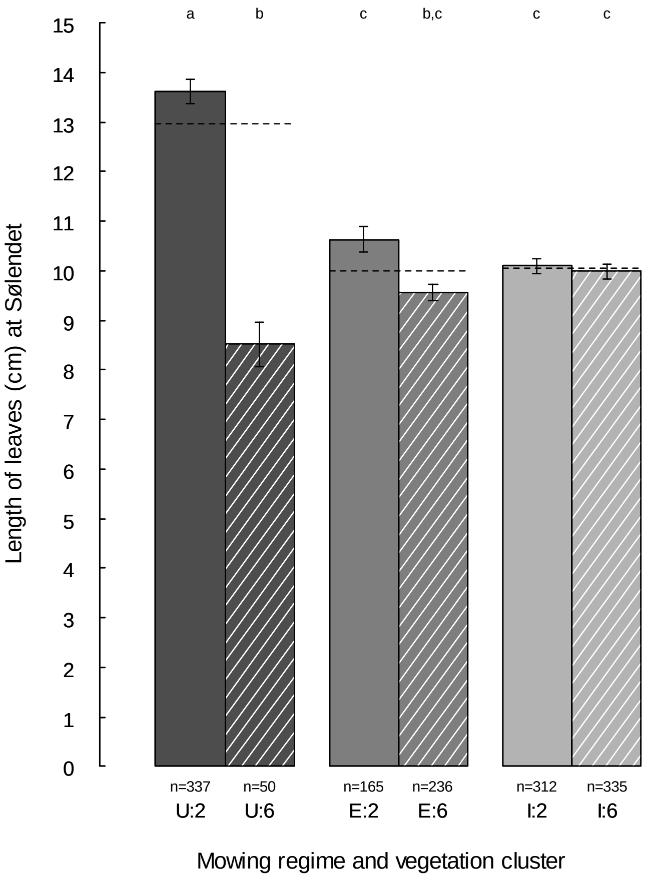

Fig. 3. Length of the longest leaves (+/- se) at Sølendet grouped by mowing regime and vegetation clusters 2 and 6. Differences ($p < 0.05$) between groups are indicated with the letters a, b and c at the top. The number of observations is shown below the bars, and the dashed lines indicate the average length of leaves per mowing regime. U = unmowed, E = mowed extensively and I = mowed every 3rd year.

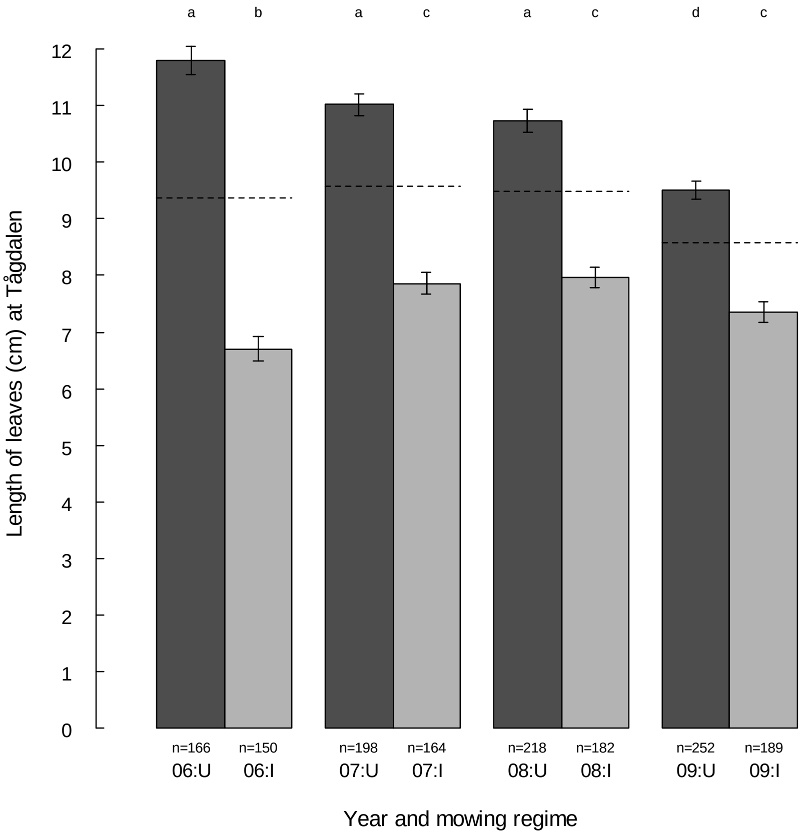

Fig. 4. Length of the longest leaves (+/- se) at Tågdalen grouped by year (2006-09) and mowing regime. Differences (|t| > 2) between groups are indicated with the letters a, b, c and d at the top. The number of observations is shown below the bars, and the dashed lines indicate the average length of leaves per year. U = unmowed and I = mowed every 2nd year.

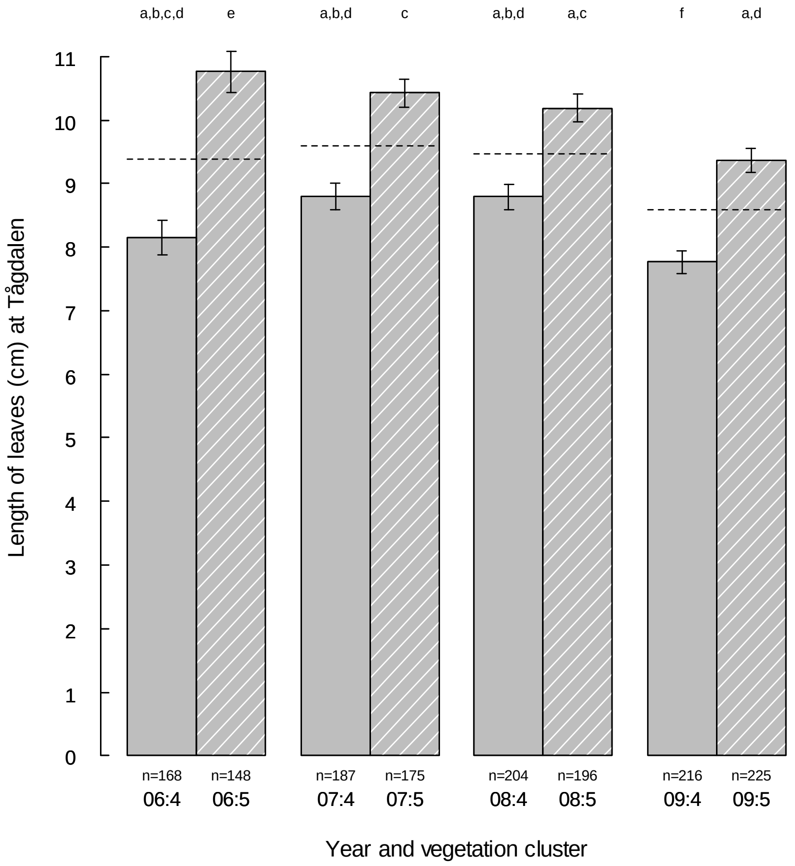

Fig. 5. Length of the longest leaves (+/- se) at Tågdalen grouped by year (2006-09) and vegetation clusters 4 and 5. Differences (|t| > 2) between groups are indicated with the letters a-f at the top. The number of observations is shown below the bars, and the dashed lines indicate the average length of leaves per year.

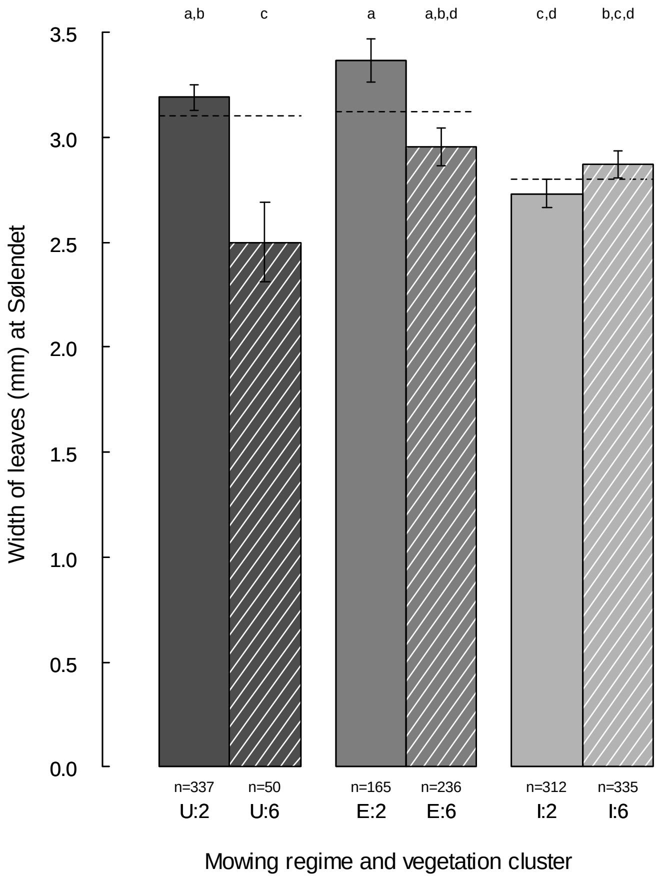

Fig. 6. Width of the widest leaves (+/- se) at Sølendet grouped by mowing regime and vegetation clusters 2 and 6. Differences ($p < 0.05$) between groups are indicated with the letters a, b, c and d at the top. The number of observations is shown below the bars, and the dashed lines indicate the average width of leaves for each mowing regime. U = unmowed, E = mowed extensively and I = mowed every 3rd year.

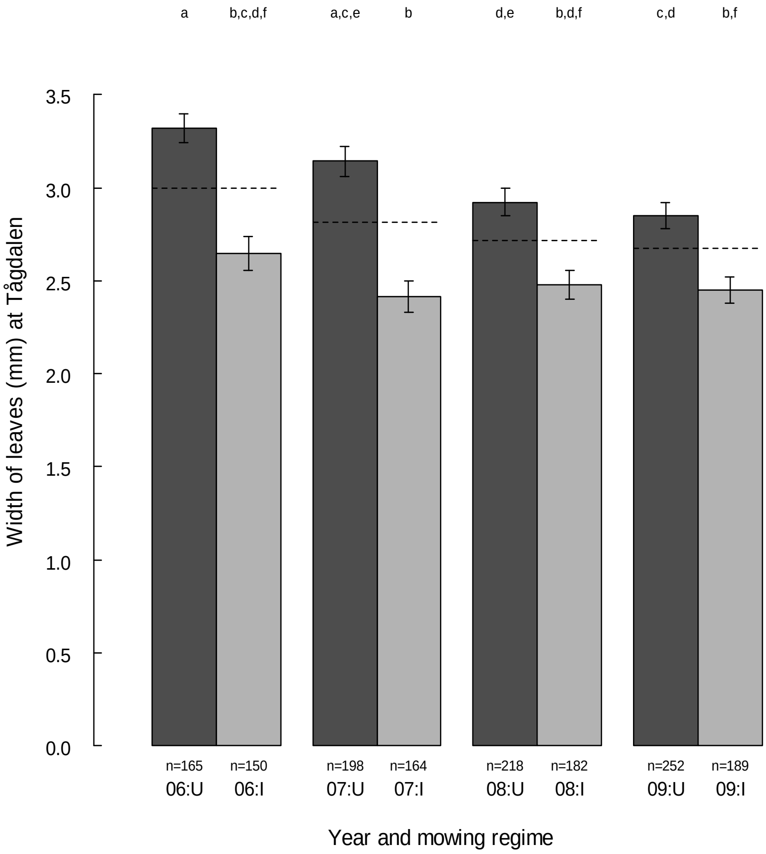

Fig. 7. Width of the widest leaves (+/- se) at Tågdalen grouped by year (2006-09) and mowing regime. Differences (|t| > 2) between groups are indicated with the letters a-f at the top. The number of observations is shown below the bars, and the dashed lines indicate the average width of leaves per year. U = unmowed and I = mowed every 2nd year.

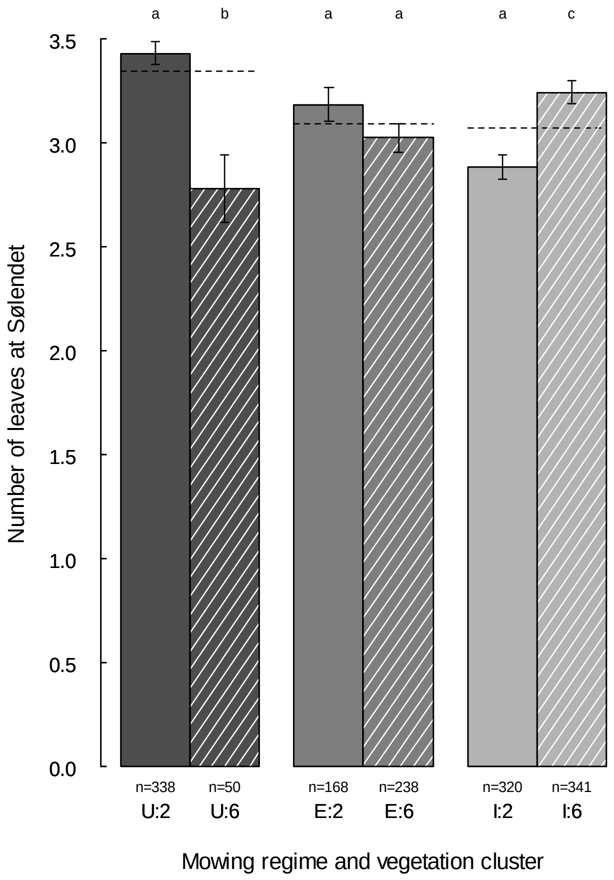

Fig. 8. Number of leaves (+/- se) per rosette at Sølendet grouped by mowing regime and vegetation clusters 2 and 6. Differences ($p < 0.05$) between groups are indicated with the letters a, b and c at the top. The number of observations is shown below the bars, and the dashed lines indicate the average number of leaves for each treatment. U = unmowed, E = mowed extensively and I = mowed every 3rd year.

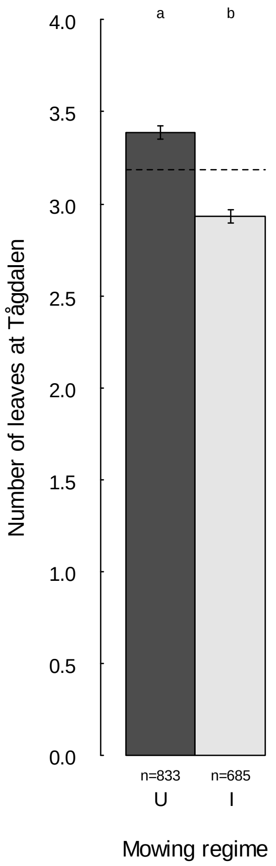

Fig. 9. Number of leaves (+/- se) per rosette in plots unmowed and mowed every 2nd year at Tågdalen. Differences (|t| > 2) between groups are indicated with the letters a and b, the number of observations is shown below the bars, and the dashed lines indicate the average number of leaves at Tågdalen.

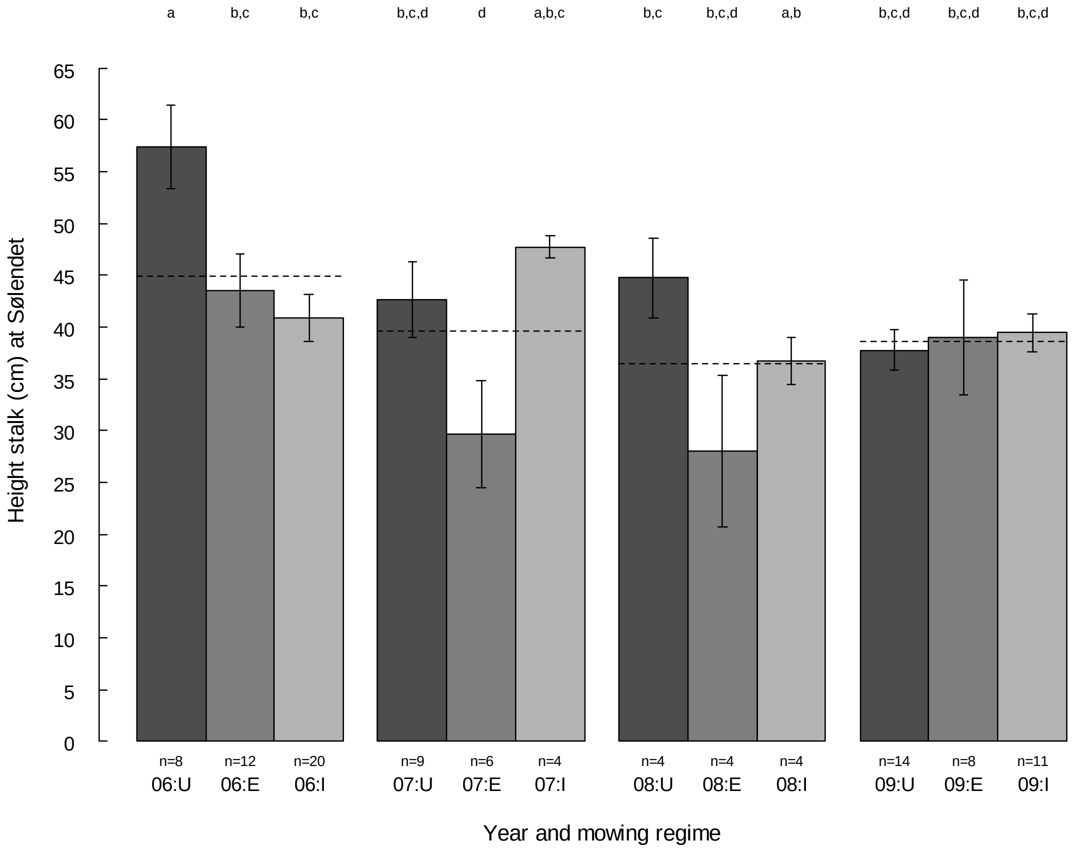

Fig. 10. Height of flowering stalks (+/- se) at Sølendet grouped by year (2006-09) and mowing regime. Differences ($p < 0.05$) between groups are indicated with the letters a-d at the top. The number of observations is shown below the bars, and the dashed lines indicate the average height of flowering stalks per year. U = unmowed, E = mowed extensively and I = mowed every 3rd year.

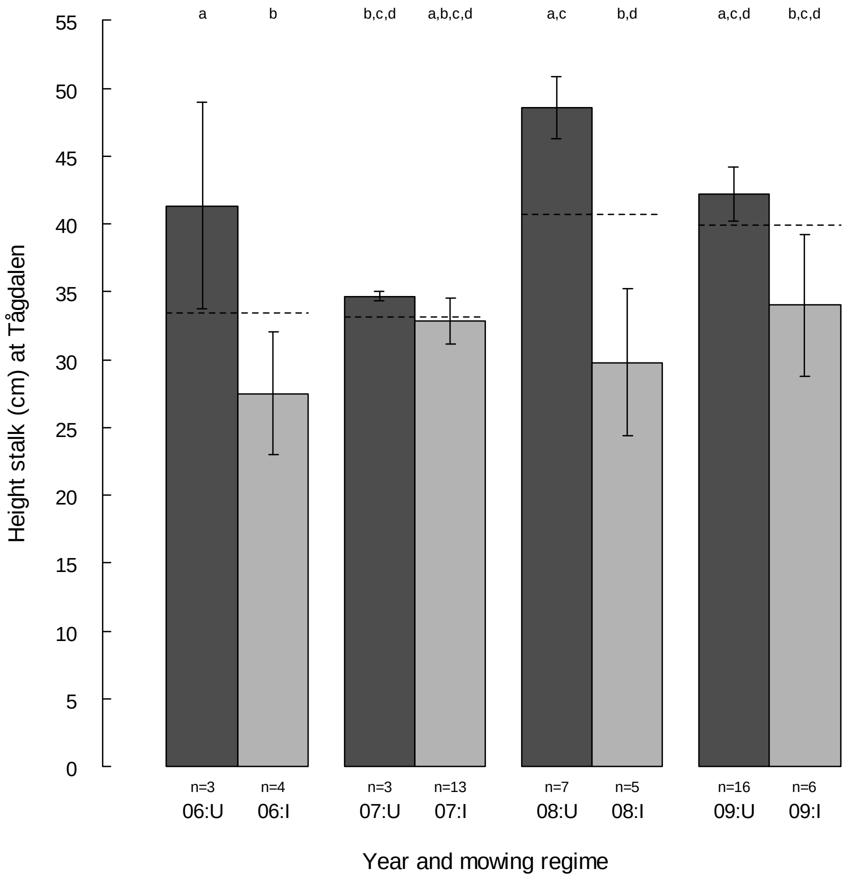

Fig. 11. Height of flowering stalks (+/- se) at Tågdalen grouped by year (2006-09) and mowing regime. Differences (|t| > 2) between groups are indicated with the letters a-d at the top. The number of observations is shown below the bars, and the dashed lines indicate the average height of flowering stalks per year. U = unmowed and I = mowed every 2nd year.

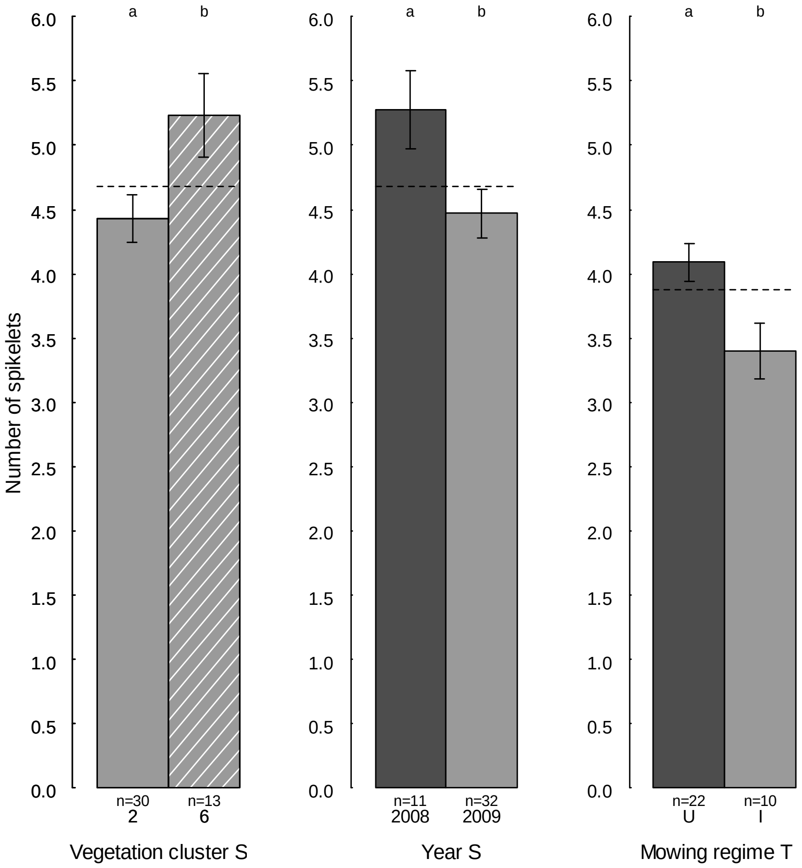

Fig. 12. The number of spikelets (+/- se) per inflorescence for vegetation cluster 2 and 6 at Sølendet (left), year (2008-09) at Sølendet (middle), and mowing regime at Tågdalen (right). Differences ($p < 0.05$ at Sølendet, $|t| > 2$ at Tågdalen) are indicated with the letters a and b at the top. The number of observations is shown below the bars, and the dashed lines indicate the average number of spikelets at Sølendet and Tågdalen respectively. U = unmowed, I = mowed every 2nd year, S = Sølendet and T = Tågdalen.

Appendix S1. Minimal adequate models for size parameters in *Eriophorum latifolium*

Characteristics of the minimal adequate models exploring how mowing regime, vegetation cluster and year (2006-09) affect size in ramets of *E. latifolium* in two study areas. The seven size parameters are length of leaves, width of leaves, number of leaves, number of emerging leaves in vegetative ramets, and height of stalk, number of stalk leaves and number of spikelets in flowering ramets. Generalised linear models (GLM, no random factors) were applied at Sølendet, and GLMM's with sample plot as random factor were applied at Tågdalen. The mowing regimes at Sølendet were unmown (U), mown extensively = every 8th year (E) and mown every 3rd year (I), and at Tågdalen unmown (U) and mown every 2nd year (I). Fen carpet vegetation cluster 2 and lawn cluster 6 were found at Sølendet and lawn clusters 4 and 5 were found at Tågdalen. The contrasts between levels of fixed factors and interactions between fixed factors are summarised with estimates and accompanying |t|- and p-values (when provided). Intercept varies between models, but is the combination of those levels of the factors that are listed first in the column "Contrast" for each model.

Size parameter	**Study area**	**n**	**Fixed factors**	**Contrast**	**Estimate**	**|t|**	**p**
Length of leaves	Sølendet	1435	Intercept	-	14.17	58.56	<0.001
			Mowing regime	U - E	-3.01	9.81	<0.001
				U - I	-3.49	13.73	<0.001
			Vegetation cluster	6 - 2	-5.07	10.34	<0.001
			Year	2006 - 2007	-0.24	0.89	0.372
				2006 - 2008	-0.59	2.25	0.025
				2006 - 2009	-1.27	4.96	<0.001
			Mowing regime : vegetation cluster	U:6 - E:2	4.02	6.82	<0.001
				U:6 - I:2	4.23	7.41	<0.001
	Tågdalen	1519	Intercept	-	11.33	24.99	-
			Mowing regime	U - I	-5.33	8.46	-
			Vegetation cluster	4 - 5	0.90	1.42	-
			Year	2006 - 2007	-0.58	2.04	-
				2006 - 2008	-0.65	2.34	-
				2006 - 2009	-2.35	8.66	-
			Mowing regime : year	U:2006 - I:2007	2.31	5.70	-
				U:2006 - I:2008	2.96	7.47	-
				U:2006 - I:2009	3.30	8.47	-
			Vegetation cluster : year	4:2006 - 5:2007	-0.95	2.29	-
				4:2006 - 5:2008	-1.63	4.06	-
				4:2006 - 5:2009	-0.32	0.82	-

Appendix S1. Minimal adequate models

Size parameter	**Study area**	**n**	**Fixed factors**	**Contrast**	**Estimate**	**|t|**	**p**
Width of leaves	Sølendet	1435	Intercept	-	3.33	36.12	<0.001
			Mowing regime	U - E	0.18	1.52	0.128
				U - I	-0.46	4.71	<0.001
			Vegetation cluster	6 - 2	-0.69	3.71	<0.001
			Year	2006 - 2007	-0.33	3.28	0.001
				2006 - 2008	-0.13	1.31	0.192
				2006 - 2009	-0.10	1.03	0.302
			Mowing regime : vegetation cluster	U:6 - E:2	0.28	1.24	0.214
				U:6 - I:2	0.81	3.72	<0.001
Width of leaves	Tågdalen	1518	Intercept	-	3.28	28.01	-
			Mowing regime	U - I	-0.64	3.79	-
			Year	2006 - 2007	-0.18	1.67	-
				2006 - 2008	-0.40	3.74	-
				2006 - 2009	-0.48	4.65	-
			Mowing regime : year	U:2006 - I:2007	-0.04	0.24	-
				U:2006 - I:2008	0.25	1.61	-
				U:2006 - I:2009	0.30	1.95	-
Number of leaves	Sølendet	1455	Intercept	-	3.27	30.27	<0.001
			Mowing regime	U - E	0.04	0.25	0.799
				U - I	0.16	1.06	0.289
			Vegetation cluster	6 - 2	-0.66	4.29	<0.001
			Year	2006 - 2007	0.07	0.44	0.658
				2006 - 2008	0.25	1.71	0.087
				2006 - 2009	0.29	2.01	0.044
			Mowing regime : vegetation cluster	U:6 - E:2	0.50	2.75	0.006
				U:6 - I:2	1.05	5.93	<0.001
			Mowing regime : year	U:2006 - E:2007	0.05	0.25	0.803
				U:2006 - I:2007	-0.84	4.23	<0.001
				U:2006 - E:2008	-0.49	2.41	0.016
				U:2006 - I:2008	-0.84	4.28	<0.001
				U:2006 - E:2009	-0.67	3.32	0.001
				U:2006 - I:2009	-1.02	5.38	<0.001
	Tågdalen	1518	Intercept	-	3.47	37.49	-
			Mowing regime	U - E	-0.43	3.71	-
			Year	2006 - 2007	0.15	2.13	-
				2006 - 2008	-0.21	2.98	-
				2006 - 2009	-0.33	4.73	-

Size parameter	**Study area**	**n**	**Fixed factors**	**Contrast**	**Estimate**	**|t|**	**p**
Number of emerging leaves	Sølendet	1141	Intercept	-	2.50	7.72	<0.001
			Mowing regime	U - E	-0.50	0.88	0.379
				U - I	-1.31	3.86	<0.001
			Vegetation cluster	6 - 2	0.25	3.16	0.002
			Year	2006 - 2007	-1.61	4.91	<0.001
				2006 - 2008	-1.79	5.45	<0.001
				2006 - 2009	-1.75	5.36	<0.001
			Mowing regime : vegetation cluster	U:6 - E:2	-0.25	2.67	0.008
				U:6 - I:2	-0.07	0.80	0.425
			Mowing regime : year	U:2006 - E:2007	0.46	0.81	0.420
				U:2006 - I:2007	1.27	3.67	0.000
				U:2006 - E:2008	0.61	1.08	0.282
				U:2006 - I:2008	1.29	3.74	<0.001
				U:2006 - E:2009	0.57	1.01	0.313
				U:2006 - I:2009	1.19	3.46	0.001
Number of emerging leaves	Tågdalen	1517	Intercept	-	0.47	10.55	<0.001
			Year	2006 - 2007	-0.53	7.60	<0.001
				2006 - 2008	-0.69	9.64	<0.001
				2006 - 2009	-0.50	7.66	<0.001
Height stalk	Sølendet	104	Intercept	-	58.19	16.19	<0.001
			Mowing regime	U - E	-14.15	3.08	0.003
				U - I	-12.38	2.77	0.007
			Vegetation cluster	6 - 2	-6.55	1.58	0.118
			Year	2006 - 2007	-15.53	3.16	0.002
				2006 - 2008	-13.44	2.17	0.033
				2006 - 2009	-20.84	4.63	<0.001
			Vegetation cluster : year	6:2006 - 2:2007	12.95	1.10	0.275
				6:2006 - 2:2008	-22.78	1.85	0.068
				6:2006 - 2:2009	12.54	1.96	0.054
			Mowing regime : year	U:2006 - E:2007	0.08	0.01	0.991
				U:2006 - I:2007	17.05	2.11	0.038
				U:2006 - E:2008	4.73	0.53	0.599
				U:2006 - I:2008	36.46	2.40	0.019
				U:2006 - E:2009	13.54	2.06	0.043
				U:2006 - I:2009	14.74	2.25	0.027
	Tågdalen	57	Intercept	-	45.06	8.79	-
			Mowing regime	U - I	-22.10	3.28	-
			Year	2006 - 2007	-12.77	2.17	-
				2006 - 2008	-2.29	0.39	-
				2006 - 2009	-3.77	0.75	-
			Mowing regime : year	U:2006 - I:2007	20.75	2.89	-
				U:2006 - I:2008	5.69	0.76	-
				U:2006 - I:2009	10.91	1.63	-

Appendix S1. Minimal adequate models

Size parameter	Study area	n	Fixed factors	Contrast	Estimate	|t|	p
Number of stalk leaves	Sølendet	104	Intercept	-	0.11	32.23	<0.001
			Mowing regime	U - E	-0.47	2.84	0.006
				U - I	-0.53	3.20	0.002
	Tågdalen	57	Intercept	-	2.84	28.20	-
Number of spikelets	Sølendet	43	Intercept	-	5.06	14.55	<0.001
			Vegetation cluster	6 - 2	1.24	2.93	0.006
			Year	2008 - 2009	-0.82	2.12	0.042
	Tågdalen	32	Intercept	-	4.09	27.87	-
			Mowing regime	U - I	-0.69	2.63	-

Appendix S2. Summarising statistical analyses of factors affecting size parameters

Statistical analyses were performed to determine which factors affected size parameters in ramets of *Eriophorum latifolium* at the study areas Sølendet (GLM, Tables S1-S13) and Tågdalen (GLMM, Tables S14-S21). The response variables were: length of the longest leaf (Tables S1, S2, S14 and S15), width of the widest leaf (Tables S3, S4 and S16), number of leaves (Tables S5, S6, S17 and S18), number of small (emerging) leaves (Tables S7, S8 and S19), height of the flowering stalk (Tables S9, S10 and S20), number of stalk leaves per flowering stalk (Table S11) and number of spikelets per inflorescence (Tables S12, S13 and S21). The fixed factors were mowing regime, vegetation cluster and year, but only factors or interactions remaining in the minimal adequate models were considered. The tables summarise the differences (pairwise comparisons) between levels of fixed factors (Δ levels) when no interactions were present, and between groups of levels of fixed factors when interactions were found. Significant differences are indicated in bold ($|t| > 2$ or $p < 0.05$) and italics ($0.1 > p > 0.05$).

Table S1. The length of leaves in *E. latifolium* at Sølendet. Differences between estimates for the levels (Δ levels) of year (2006-09) with p-values.

Fixed factor	Levels		Δ levels	p
Year	2006	2007	0.35	0.152
	2006	2008	0.62	**0.011**
	2006	2009	1.38	**<0.001**
	2007	2008	0.26	0.284
	2007	2009	1.03	**<0.001**
	2008	2009	0.77	**0.002**

Appendix S2. Summarising statistical analyses

Table S2. The length of leaves in *E. latifolium* at Sølendet. Differences between estimates for groups of levels (Δ levels) of mowing regime and vegetation clusters 2 and 6 with p-values. U = unmowed, E = mowed extensively and I = mowed every 3rd year.

Interaction	Levels		Δ levels	p
Mowing regime : vegetation cluster	U:2	U:6	5.06	**<0.001**
	U:2	E:2	3.01	**<0.001**
	U:2	E:6	4.06	**<0.001**
	U:2	I:2	3.49	**<0.001**
	U:2	I:6	3.62	**<0.001**
	U:6	E:2	2.05	**<0.001**
	U:6	E:6	1.01	*0.084*
	U:6	I:2	1.58	**0.001**
	U:6	I:6	1.45	**0.008**
	E:2	E:6	1.05	*0.072*
	E:2	I:2	0.47	0.119
	E:2	I:6	0.60	0.267
	E:6	I:2	0.57	0.323
	E:6	I:6	0.44	0.416
	I:2	I:6	0.13	0.809

Table S3. The width of leaves in *E. latifolium* at Sølendet. Differences between estimates for the levels (Δ levels) of year (2006-09) with p-values.

Fixed factor	Levels		Δ levels	p
Year	2006	2007	0.30	**0.001**
	2006	2008	0.12	0.199
	2006	2009	0.11	0.211
	2007	2008	0.18	*0.051*
	2007	2009	0.19	**0.045**
	2008	2009	0.01	0.955

Table S4. The width of leaves in *E. latifolium* at Sølendet. Differences between estimates for groups of levels (Δ levels) of mowing regime and vegetation clusters 2 and 6 with p-values. U = unmowed, E = mowed extensively and I = mowed every 3rd year.

Interaction	Levels		Δ levels	p
Mowing regime : vegetation cluster	U:2	U:6	0.69	**<0.001**
	U:2	E:2	0.18	0.128
	U:2	E:6	0.24	0.292
	U:2	I:2	0.45	**<0.001**
	U:2	I:6	0.32	0.131
	U:6	E:2	0.87	**<0.001**
	U:6	E:6	0.46	**0.041**
	U:6	I:2	0.24	0.203
	U:6	I:6	0.38	*0.072*
	E:2	E:6	0.41	*0.065*
	E:2	I:2	0.63	**<0.001**
	E:2	I:6	0.49	**0.018**
	E:6	I:2	0.22	0.325
	E:6	I:6	0.08	0.700
	I:2	I:6	0.14	0.505

Table S5. The number of leaves in *E. latifolium* at Sølendet. Differences between estimates for groups of levels (Δ levels) of mowing regime and vegetation clusters 2 and 6 with p-values. U = unmowed, E = mowed extensively and I = mowed every 3rd year.

Interaction	Levels		Δ levels	p
Mowing regime : vegetation cluster	U:2	U:6	0.66	**<0.001**
	U:2	E:2	0.04	0.800
	U:2	E:6	0.11	0.545
	U:2	I:2	0.13	0.377
	U:2	I:6	0.48	**0.005**
	U:6	E:2	0.70	**<0.001**
	U:6	E:6	0.54	**0.003**
	U:6	I:2	0.78	**<0.001**
	U:6	I:6	1.14	**<0.001**
	E:2	E:6	0.15	0.409
	E:2	I:2	0.08	0.594
	E:2	I:6	0.44	**0.010**
	E:6	I:2	0.24	0.198
	E:6	I:6	0.59	**0.001**
	I:2	I:6	0.36	**0.038**

Table S6. The number of leaves in *E. latifolium* at Sølendet. Differences between estimates for groups of levels (Δ levels) of year (2006-09) and mowing regime with p-values. U = unmowed, E = mowed extensively and I = mowed every 3rd year.

Interaction	Levels		Δ levels	p
Year : mowing regime	2006:U	2006:E	0.04	0.800
	2006:U	2006:I	0.13	0.377
	2006:U	2007:U	0.07	0.658
	2006:U	2007:E	0.16	0.444
	2006:U	2007:I	0.56	**0.003**
	2006:U	2008:U	0.25	*0.088*
	2006:U	2008:E	0.20	0.328
	2006:U	2008:I	0.40	**0.031**
	2006:U	2009:U	0.29	**0.045**
	2006:U	2009:E	0.34	*0.092*
	2006:U	2009:I	0.63	**0.001**
	2006:E	2006:I	0.08	0.594
	2006:E	2007:U	0.03	0.870
	2006:E	2007:E	0.12	0.569
	2006:E	2007:I	0.60	**0.002**
	2006:E	2008:U	0.21	0.186
	2006:E	2008:E	0.24	0.240
	2006:E	2008:I	0.44	**0.017**
	2006:E	2009:U	0.25	0.119
	2006:E	2009:E	0.38	*0.059*
	2006:E	2009:I	0.67	**<0.001**
	2006:I	2007:U	0.06	0.696
	2006:I	2007:E	0.03	0.872
	2006:I	2007:I	0.68	**<0.001**
	2006:I	2008:U	0.13	0.392
	2006:I	2008:E	0.33	0.112
	2006:I	2008:I	0.53	**0.005**
	2006:I	2009:U	0.16	0.255
	2006:I	2009:E	0.47	**0.021**
	2006:I	2009:I	0.75	**<0.001**
	2007:U	2007:E	0.09	0.657
	2007:U	2007:I	0.63	**0.001**
	2007:U	2008:U	0.18	0.220
	2007:U	2008:E	0.27	0.192
	2007:U	2008:I	0.47	**0.012**
	2007:U	2009:U	0.22	0.140
	2007:U	2009:E	0.41	**0.044**
	2007:U	2009:I	0.69	**<0.001**
	2007:E	2007:I	0.72	**0.001**
	2007:E	2008:U	0.09	0.656
	2007:E	2008:E	0.36	*0.084*
	2007:E	2008:I	0.56	**0.007**
	2007:E	2009:U	0.13	0.531
	2007:E	2009:E	0.50	**0.016**
	2007:E	2009:I	0.79	**<0.001**

Table S6. (cont.)

Interaction	Levels		Δ levels	p
Year : mowing regime	2007:I	2008:U	0.81	**<0.001**
	2007:I	2008:E	0.36	*0.080*
	2007:I	2008:I	0.16	0.409
	2007:I	2009:U	0.85	**<0.001**
	2007:I	2009:E	0.22	0.281
	2007:I	2009:I	0.07	0.719
	2008:U	2008:E	0.45	**0.027**
	2008:U	2008:I	0.65	**<0.001**
	2008:U	2009:U	0.04	0.798
	2008:U	2009:E	0.59	**0.003**
	2008:U	2009:I	0.88	**<0.001**
	2008:E	2008:I	0.20	0.323
	2008:E	2009:U	0.49	**0.017**
	2008:E	2009:E	0.14	0.492
	2008:E	2009:I	0.43	**0.037**
	2008:I	2009:U	0.69	**<0.001**
	2008:I	2009:E	0.06	0.761
	2008:I	2009:I	0.22	0.227
	2009:U	2009:E	0.63	**0.002**
	2009:U	2009:I	0.92	**<0.001**
	2009:E	2009:I	0.29	0.157

Table S7. The number of small leaves in *E. latifolium* at Sølendet. Differences between estimates for groups of levels (Δ levels) of mowing regime and vegetation clusters 2 and 6 with p-values. U = unmowed, E = mowed extensively and I = mowed every 3rd year.

Interaction	Levels		Δ levels	p
Mowing regime : vegetation cluster	U:2	U:6	0.25	**0.002**
	U:2	E:2	0.50	0.380
	U:2	E:6	0.50	0.376
	U:2	I:2	1.32	**<0.001**
	U:2	I:6	1.19	**<0.001**
	U:6	E:2	0.75	0.187
	U:6	E:6	0.75	0.184
	U:6	I:2	1.57	**<0.001**
	U:6	I:6	1.44	**<0.001**
	E:2	E:6	0.00	0.994
	E:2	I:2	0.83	0.142
	E:2	I:6	0.70	0.217
	E:6	I:2	0.82	0.144
	E:6	I:6	0.69	0.219
	I:2	I:6	0.13	0.699

Table S8. The number of small leaves in *E. latifolium* at Sølendet. Differences between estimates for groups of levels (Δ levels) of year (2006-09) and mowing regime with p-values. U = unmowed, E = mowed extensively and I = mowed every 3rd year.

Interaction	Levels		Δ levels	p
Year : mowing regime	2006:U	2006:E	0.50	0.380
	2006:U	2006:I	1.32	**<0.001**
	2006:U	2007:U	1.61	**<0.001**
	2006:U	2007:E	1.65	**0.004**
	2006:U	2007:I	1.64	**<0.001**
	2006:U	2008:U	1.79	**<0.001**
	2006:U	2008:E	1.67	**0.003**
	2006:U	2008:I	1.82	**<0.001**
	2006:U	2009:U	1.75	**<0.001**
	2006:U	2009:E	1.68	**0.003**
	2006:U	2009:I	1.86	**<0.001**
	2006:E	2006:I	0.83	0.142
	2006:E	2007:U	1.11	**0.049**
	2006:E	2007:E	1.15	**0.042**
	2006:E	2007:I	1.14	**0.043**
	2006:E	2008:U	1.29	**0.022**
	2006:E	2008:E	1.18	**0.038**
	2006:E	2008:I	1.33	**<0.001**
	2006:E	2009:U	1.26	**0.026**
	2006:E	2009:E	1.18	**0.036**
	2006:E	2009:I	1.37	**0.016**
	2006:I	2007:U	0.28	0.402
	2006:I	2007:E	0.32	0.568
	2006:I	2007:I	0.31	0.362
	2006:I	2008:U	0.46	0.174
	2006:I	2008:E	0.35	0.538
	2006:I	2008:I	0.50	0.149
	2006:I	2009:U	0.43	0.204
	2006:I	2009:E	0.36	0.529
	2006:I	2009:I	0.54	0.118
	2007:U	2007:E	0.04	0.945
	2007:U	2007:I	0.03	0.930
	2007:U	2008:U	0.18	0.589
	2007:U	2008:E	0.06	0.910
	2007:U	2008:I	0.21	0.536
	2007:U	2009:U	0.15	0.656
	2007:U	2009:E	0.07	0.899
	2007:U	2009:I	0.25	0.461
	2007:E	2007:I	0.01	0.987
	2007:E	2008:U	0.14	0.808
	2007:E	2008:E	0.02	0.965
	2007:E	2008:I	0.17	0.759
	2007:E	2009:U	0.11	0.850
	2007:E	2009:E	0.03	0.954
	2007:E	2009:I	0.21	0.705

Table S8. (cont.)

Interaction	Levels		Δ levels	p
Year : mowing regime	2007:I	2008:U	0.15	0.670
	2007:I	2008:E	0.03	0.952
	2007:I	2008:I	0.18	0.596
	2007:I	2009:U	0.12	0.736
	2007:I	2009:E	0.04	0.941
	2007:I	2009:I	0.22	0.517
	2008:U	2008:E	0.11	0.842
	2008:U	2008:I	0.04	0.917
	2008:U	2009:U	0.03	0.925
	2008:U	2009:E	0.11	0.853
	2008:U	2009:I	0.08	0.824
	2008:E	2008:I	0.15	0.793
	2008:E	2009:U	0.08	0.885
	2008:E	2009:E	0.01	0.989
	2008:E	2009:I	0.19	0.738
	2008:I	2009:U	0.07	0.846
	2008:I	2009:E	0.14	0.803
	2008:I	2009:I	0.04	0.906
	2009:U	2009:E	0.07	0.896
	2009:U	2009:I	0.11	0.755
	2009:E	2009:I	0.18	0.748

Table S9. The height of the stalk in *E. latifolium* at Sølendet. Differences between estimates for groups of levels (Δ levels) of year (2006-09) and vegetation clusters 2 and 6 with p-values.

Interaction	Levels		Δ levels	p
Year : vegetation cluster	2006:2	2006:6	9.04	**0.020**
	2006:2	2007:2	15.84	**0.002**
	2006:2	2007:6	11.68	0.186
	2006:2	2008:2	13.75	**0.026**
	2006:2	2008:6	43.09	**0.001**
	2006:2	2009:2	20.92	**<0.001**
	2006:2	2009:6	18.12	**0.002**
	2006:6	2007:2	6.80	0.164
	2006:6	2007:6	2.64	0.764
	2006:6	2008:2	4.72	0.442
	2006:6	2008:6	34.05	**0.006**
	2006:6	2009:2	11.88	**0.009**
	2006:6	2009:6	9.08	0.114
	2007:2	2007:6	4.16	0.637
	2007:2	2008:2	2.08	0.734
	2007:2	2008:6	27.25	**0.026**
	2007:2	2009:2	5.08	0.298
	2007:2	2009:6	2.28	0.690
	2007:6	2008:2	2.07	0.814
	2007:6	2008:6	31.41	**0.011**
	2007:6	2009:2	9.24	0.295
	2007:6	2009:6	6.44	0.465
	2008:2	2008:6	29.33	**0.017**
	2008:2	2009:2	7.16	0.244
	2008:2	2009:6	4.36	0.477
	2008:6	2009:2	22.17	*0.070*
	2008:6	2009:6	24.97	**0.042**
	2009:2	2009:6	2.80	0.624

Table S10. The height of the stalk in *E. latifolium* at Sølendet. Differences between estimates for groups of levels (Δ levels) of year (2006-09) and mowing regime with p-values. U = unmowed, E = mowed extensively and I = mowed every 3rd year.

Interaction	Levels		Δ levels	p
Year : mowing regime	2006:U	2006:E	14.25	**0.002**
	2006:U	2006:I	13.14	**0.004**
	2006:U	2007:U	15.84	**0.002**
	2006:U	2007:E	29.53	**<0.001**
	2006:U	2007:I	11.79	0.128
	2006:U	2008:U	13.75	**0.026**
	2006:U	2008:E	23.17	**0.010**
	2006:U	2008:I	7.58	0.594
	2006:U	2009:U	20.92	**<0.001**
	2006:U	2009:E	20.55	**0.002**
	2006:U	2009:I	20.58	**0.001**
	2006:E	2006:I	1.12	0.807
	2006:E	2007:U	1.59	0.745
	2006:E	2007:E	15.28	**0.033**
	2006:E	2007:I	2.46	0.750
	2006:E	2008:U	0.50	0.935
	2006:E	2008:E	8.92	0.316
	2006:E	2008:I	21.83	0.126
	2006:E	2009:U	6.67	0.145
	2006:E	2009:E	6.30	0.331
	2006:E	2009:I	6.33	0.316
	2006:I	2007:U	2.70	0.579
	2006:I	2007:E	16.39	**0.022**
	2006:I	2007:I	1.34	0.862
	2006:I	2008:U	0.62	0.920
	2006:I	2008:E	10.04	0.259
	2006:I	2008:I	20.71	0.147
	2006:I	2009:U	7.78	*0.083*
	2006:I	2009:E	7.42	0.253
	2006:I	2009:I	7.44	0.239
	2007:U	2007:E	13.69	*0.055*
	2007:U	2007:I	4.04	0.600
	2007:U	2008:U	2.08	0.734
	2007:U	2008:E	7.33	0.409
	2007:U	2008:I	23.42	0.101
	2007:U	2009:U	5.08	0.298
	2007:U	2009:E	4.72	0.467
	2007:U	2009:I	4.74	0.452
	2007:E	2007:I	17.74	**0.023**
	2007:E	2008:U	15.78	**0.028**
	2007:E	2008:E	6.36	0.474
	2007:E	2008:I	37.11	**0.010**
	2007:E	2009:U	8.61	0.225
	2007:E	2009:E	8.98	0.206
	2007:E	2009:I	8.95	0.208

Table S10. (cont.)

Interaction	Levels		Δ levels	p
Year : mowing regime	2007:I	2008:U	1.96	0.799
	2007:I	2008:E	11.38	0.201
	2007:I	2008:I	19.37	0.174
	2007:I	2009:U	9.12	0.237
	2007:I	2009:E	8.76	0.257
	2007:I	2009:I	8.78	0.255
	2008:U	2008:E	9.42	0.290
	2008:U	2008:I	21.33	0.135
	2008:U	2009:U	7.16	0.244
	2008:U	2009:E	6.80	0.295
	2008:U	2009:I	6.82	0.280
	2008:E	2008:I	30.75	**0.032**
	2008:E	2009:U	2.25	0.800
	2008:E	2009:E	2.62	0.768
	2008:E	2009:I	2.59	0.770
	2008:I	2009:U	28.50	**0.047**
	2008:I	2009:E	28.13	**0.050**
	2008:I	2009:I	28.16	**0.050**
	2009:U	2009:E	0.36	0.955
	2009:U	2009:I	0.34	0.957
	2009:E	2009:I	0.02	0.997

Table S11. The number of stalk leaves in *E. latifolium* at Sølendet. Differences between estimates for the levels (Δ levels) of mowing regime with p-values. U = unmowed, E = mowed extensively and I = mowed every 3rd year.

Fixed factor	Levels		Δ levels	p
Mowing regime	U	E	0.47	**0.005**
	U	I	0.47	**0.002**
	E	I	0.01	0.975

Table S12. The number of spikelets in *E. latifolium* at Sølendet. The difference (Δ levels) between vegetation clusters 2 and 6 with p-values.

Fixed factor	Levels		Δ levels	p
Vegetation cluster	2	6	0.74	**0.034**

Table S13. The number of spikelets in *E. latifolium* at Sølendet. The difference (Δ levels) between the years 2008 and 2009 with p-values.

Fixed factor	Levels		Δ levels	p
Year	2008	2009	0.74	**0.043**

Table S14. The length of leaves in *E. latifolium* at Tågdalen. Differences between estimates for groups of levels (Δ levels) of year (2006-09) and mowing regime with |t|-values. U = unmowed and I = mowed every 2nd year.

Interaction	Levels		Δ levels	|t|
Year : mowing regime	2006:U	2006:I	4.85	**9.76**
	2006:U	2007:U	0.35	0.84
	2006:U	2007:I	3.30	**6.64**
	2006:U	2008:U	0.53	1.26
	2006:U	2008:I	3.04	**6.13**
	2006:U	2009:U	1.94	**4.66**
	2006:U	2009:I	3.73	**7.52**
	2006:I	2007:U	4.49	**9.05**
	2006:I	2007:I	1.55	**3.12**
	2006:I	2008:U	4.32	**8.70**
	2006:I	2008:I	1.80	**3.63**
	2006:I	2009:U	2.90	**5.85**
	2006:I	2009:I	1.11	**2.24**
	2007:U	2007:I	2.95	**5.93**
	2007:U	2008:U	0.17	0.42
	2007:U	2008:I	2.69	**5.42**
	2007:U	2009:U	1.59	**3.81**
	2007:U	2009:I	3.38	**6.81**
	2007:I	2008:U	2.77	**5.58**
	2007:I	2008:I	0.25	0.51
	2007:I	2009:U	1.35	**2.73**
	2007:I	2009:I	0.44	0.88
	2008:U	2008:I	2.52	**5.07**
	2008:U	2009:U	1.42	**3.39**
	2008:U	2009:I	3.21	**6.46**
	2008:I	2009:U	1.10	**2.22**
	2008:I	2009:I	0.69	1.39
	2009:U	2009:I	1.79	**3.61**

Table S15. The length of leaves in *E. latifolium* at Tågdalen. Differences between estimates for groups of levels (Δ levels) of year (2006-09) and vegetation clusters 4 and 5 with |t|-values.

Interaction	Levels		Δ levels	|t|
Year : vegetation cluster	2006:4	2006:5	2.04	**4.07**
	2006:4	2007:4	0.35	0.84
	2006:4	2007:5	0.83	1.66
	2006:4	2008:4	0.53	1.26
	2006:4	2008:5	0.43	0.87
	2006:4	2009:4	1.94	**4.66**
	2006:4	2009:5	0.74	1.47
	2006:5	2007:4	2.39	**4.77**
	2006:5	2007:5	1.21	**2.41**
	2006:5	2008:4	2.56	**5.12**
	2006:5	2008:5	1.60	**3.20**
	2006:5	2009:4	3.98	**7.95**
	2006:5	2009:5	2.77	**5.54**
	2007:4	2007:5	1.18	**2.36**
	2007:4	2008:4	0.17	0.42
	2007:4	2008:5	0.79	1.57
	2007:4	2009:4	1.59	**3.81**
	2007:4	2009:5	0.38	0.77
	2007:5	2008:4	1.36	**2.71**
	2007:5	2008:5	0.39	0.79
	2007:5	2009:4	2.77	**5.54**
	2007:5	2009:5	1.56	**3.12**
	2008:4	2008:5	0.96	1.92
	2008:4	2009:4	1.42	**3.39**
	2008:4	2009:5	0.21	0.42
	2008:5	2009:4	2.38	**4.75**
	2008:5	2009:5	1.17	**2.34**
	2009:4	2009:5	1.21	**2.41**

Table S16. The width of leaves in *E. latifolium* at Tågdalen. Differences between estimates for groups of levels (Δ levels) of year (2006-09) and mowing regime with |t|-values. U = unmowed and I = mowed every 2nd year.

Interaction	Levels		Δ levels	|t|
Year : mowing regime	2006:U	2006:I	0.64	**3.79**
	2006:U	2007:U	0.18	1.56
	2006:U	2007:I	0.86	**5.09**
	2006:U	2008:U	0.40	**3.42**
	2006:U	2008:I	0.79	**4.66**
	2006:U	2009:U	0.48	**4.14**
	2006:U	2009:I	0.82	**4.87**
	2006:I	2007:U	0.46	**2.71**
	2006:I	2007:I	0.22	1.30
	2006:I	2008:U	0.24	1.42
	2006:I	2008:I	0.15	0.88
	2006:I	2009:U	0.16	0.93
	2006:I	2009:I	0.18	1.08
	2007:U	2007:I	0.68	**4.01**
	2007:U	2008:U	0.22	1.87
	2007:U	2008:I	0.61	**3.59**
	2007:U	2009:U	0.30	**2.58**
	2007:U	2009:I	0.64	**3.79**
	2007:I	2008:U	0.46	**2.72**
	2007:I	2008:I	0.07	0.42
	2007:I	2009:U	0.38	**2.23**
	2007:I	2009:I	0.04	0.22
	2008:U	2008:I	0.39	**2.30**
	2008:U	2009:U	0.08	0.71
	2008:U	2009:I	0.42	**2.50**
	2008:I	2009:U	0.31	1.81
	2008:I	2009:I	0.03	0.20
	2009:U	2009:I	0.34	**2.01**

Table S17. The number of leaves in *E. latifolium* at Tågdalen. The difference between unmown plots (U) and plots mown every 2nd year (I) with |t|-value.

Fixed factor	Levels		Δ levels	|t|
Mowing regime	U	I	3.04	**3.71**

Table S18. The number of leaves in *E. latifolium* at Tågdalen. Differences between estimates for the levels (Δ levels) of year (2006-09) with |t|-values.

Fixed factor	Levels		Δ levels	|t|
Year	2006	2007	0.15	**2.13**
	2006	2008	0.21	**2.98**
	2006	2009	0.32	**4.73**
	2007	2008	0.36	**5.05**
	2007	2009	0.48	**6.67**
	2008	2009	0.12	1.65

Table S19. The number of small leaves in *E. latifolium* at Tågdalen. Differences between estimates for the levels (Δ levels) of year (2006-09) with |t|-values.

Fixed factor	Levels		Δ levels	|t|
Year	2006	2007	0.67	**17.93**
	2006	2008	0.81	**22.04**
	2006	2009	0.65	**18.11**
	2007	2008	0.14	**3.66**
	2007	2009	0.02	0.53
	2008	2009	0.16	**4.28**

Table S20. The height of the stalk in *E. latifolium* at Tågdalen. Differences between estimates for groups of levels (Δ levels) of year (2006-09) and mowing regime with |t|-values. U = unmowed and I = mowed every 2nd year.

Interaction	Levels		Δ levels	|t|
Year : mowing regime	2006:U	2006:I	22.10	**3.28**
	2006:U	2007:U	12.77	**2.17**
	2006:U	2007:I	14.12	1.97
	2006:U	2008:U	2.29	0.39
	2006:U	2008:I	18.70	**2.48**
	2006:U	2009:U	3.77	0.74
	2006:U	2009:I	14.96	**2.24**
	2006:I	2007:U	9.33	1.38
	2006:I	2007:I	7.98	1.11
	2006:I	2008:U	19.81	**2.94**
	2006:I	2008:I	3.40	0.45
	2006:I	2009:U	18.33	**2.72**
	2006:I	2009:I	7.14	1.06
	2007:U	2007:I	1.35	0.19
	2007:U	2008:U	10.48	1.77
	2007:U	2008:I	5.93	0.79
	2007:U	2009:U	9.00	1.53
	2007:U	2009:I	2.19	0.33
	2007:I	2008:U	11.83	1.65
	2007:I	2008:I	4.58	0.61
	2007:I	2009:U	10.35	1.44
	2007:I	2009:I	0.84	0.12
	2008:U	2008:I	16.41	**2.18**
	2008:U	2009:U	1.48	0.25
	2008:U	2009:I	12.67	1.89
	2008:I	2009:U	14.93	1.98
	2008:I	2009:I	3.74	0.50
	2009:U	2009:I	11.19	1.67

Table S21. The number of spikelets in *E. latifolium* at Tågdalen. The difference between unmown plots (U) and plots mown every 2nd year (I) with |t|-value.

Fixed factor	Levels		Δ levels	|t|
Mowing regime	U	I	0.69	**2.63**

Paper III

Population dynamics of *Eriophorum latifolium* in boreal rich fens vary with mowing regime and plant community

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Abstract

Management of formerly mowed outlying lands may affect local plant populations differently depending on mowing regime and plant community. The population dynamics of the clonal graminoid *Eriophorum latifolium* was studied in basicolous fens in two study areas in central Norway (2006-09, n = 683-895 ramets / 470-483 clonal fragments). A model was developed to clarify demographic processes affecting the transition of clonal fragments from year t to $t + 1$, and the population dynamics were analysed using transition population matrix models including elasticity analysis, and life table response experiment (LTRE) analysis. The perennial nature of *E. latifolium* was reflected in the high elasticity of survival probability in populations from all the studied rich fen communities, but clonal reproduction and fragmentation in addition to survival had high elasticity in a dry fen lawn community in the early stages of succession towards shrub-dominated fen margin vegetation. In one study area, mowing every 2nd year caused a decrease in population growth rate through lower growth and survival probabilities of clonal fragments, whereas in the other study area, mowing every 3rd year yielded an increase in population growth rate through a higher seedling establishment ratio, indicating that *E. latifolium* thrived with the latter level of disturbance. Flowering probability had low elasticity but explained much of the year-to-year variation in population growth rate, emphasising that vital rates with low elasticity can be of importance when they have high variability. The seedling establishment ratio was an important vital rate as it affected the population growth rate differently in the study areas. The recruitment phase is also the least known part of the life history in *E. latifolium*, and deserves future attention.

Keywords: Clonal growth, central Norway, demography, vital rates, matrix population models, LTRE

1. Introduction

Cessation of mowing in outlying lands has led to successional changes in European landscapes over the last century (Emanuelsson 2009). Low-growing species are encroached upon by litter accumulation and growing shrubs, tall herbs and grasses, leading to changes in species abundance and composition in several fen vegetation types (Moen 1990, Diemer et al. 2001). The majority of vascular plants found in boreal mires (including fens) are clonal (Sjörs 1948: 253), and plants with clonal growth are often resilient to mowing (e.g. Klimešová et al. 2008). Clonal growth in vascular plants is an especially common trait in wet, nutrient-poor, or cold habitats, reflecting benefits of clonality when nutrients are scarce and climate is harsh (Callaghan et al. 1997, Jónsdóttir & Watson 1997, Klimeš et al. 1997), both ecological conditions that apply to boreal fens. Clonal growth has been defined as ”the capacity of individual plants in nature to form ramets by vegetative means that are potentially independent” (de Kroon & van Groenendael 1997), and a clonal fragment is a demographic unit made up of physically interconnected ramets. Vegetative reproduction enables proliferation even if climatic conditions are unsuitable for sexual reproduction, and physiological integration in clonal fragments may alleviate unfavourable circumstances experienced by single ramets (Oborny & Cain 1997, Oborny et al. 2000, Oborny et al. 2001, Herben 2004).

Mowing is implemented as a management tool in rich fens in the nature reserves Sølendet and Tågdalen in central Norway, and flowering density of several rich fen species is monitored to ensure adequate management practices. The perennial, clonal graminoid *Eriophorum latifolium* Hoppe (Cyperaceae) is among the monitored species, and a correlation between flowering density and the performance of the populations is assumed. However, the relationship between flowering and population performance in clonal plants like *E. latifolium* may not be straightforward. The rosettes of *E. latifolium* die after flowering because the apical meristems are transformed and consumed when the ramets flower, a life history trait shared with other clonal monocarpic (sensu de Kroon & van Groenendael 1997) graminoids (Callaghan et al. 1997, Jónsdóttir & Watson 1997). A high proportion of flowering ramets has been shown to be followed by increased mortality in *Carex bigelowii* (Carlsson & Callaghan 1990), and an increased level of flowering has been shown to reduce population growth rate in some populations of *Cirsium dissectum* due to the combination of high post-flowering mortality and very low seedling establishment (Jongejans et al. 2008).

The probability of adult survival is often the vital rate most important to population growth rate in long lived species, while vital rates related to fecundity have little impact (Silvertown et al. 1993), and we expect this to be the case in *E. latifolium*. Physiological integration causes dependence between ramets in clonal fragments, and the vital rates of clonal fragments can be assumed to be more than the sum of the vital rates of single ramets (Fischer & van Kleunen 2001). In the present study we examine the effects of long-term mowing on demography and population growth rate in clonal fragments of *E. latifolium*. Our main aims are to determine which vital rates contribute the most to population growth rate, and to evaluate the relationships between mowing, flowering and performance of *E. latifolium*. Furthermore, we want to elucidate how different mowing regimes affect the demographic processes along a wet – dry gradient in boreal rich fens. We recorded the fates of clonal fragments of *E. latifolium* for four years (n = 701-895), and applied transition matrix population models (Caswell 2001) to the demographic data. Population growth rate was estimated for a range of combinations of the factors study area, vegetation, mowing regime and year. Elasticity analysis is a prospective technique showing how much a relative change in a matrix element or a vital rate affects the population growth rate (de Kroon et al. 1986, Zuidema et al. 2007). We calculated elasticities of vital rates (Franco & Silvertown 2004) to show their impact on population growth rate, and used life table response experiment (LTRE) analyses (retrospective technique) to explore the effects of study area, vegetation cluster, mowing regime and year on population growth rate (Caswell 1989, 2001, Zuidema et al. 2007).

2. Materials and methods

2.1. Study species

Eriophorum latifolium is a rich fen and spring species growing in areas with base-rich peat with pH most often in the range 5.5-7.5 and electrical conductivity in surface water mostly above 100 µS (Kutschera et al. 1982, Moen 1990, Petraglia & Tomaselli 2003). It is widely distributed throughout Europe (Hultén & Fries 1986), reaches 2100 m a.s.l. in the Alps (Jäger et al. 1965), and 1120 m a.s.l. in Norway (Elven 2005). In Norway it can be found in boreal areas almost up to the climatic forest limit (Moen 1999), and may be locally abundant or dominant in open lawn communities of sloping fens formerly used for hay production.

Vegetative ramets form rosettes with normally three to five slender leaves, while flowering ramets produce an elongated flowering stalk lacking a basal rosette (A. Lyngstad unpublished data). New rhizomes emerge from below-ground leaf axils (Raunkiær 1895), the rhizome is short, and the new ramet typically remains within 5 cm from its mother ramet. Each mother ramet can give rise to between one and four daughter ramets (Raunkiær 1895), resulting in the formation of loose tufts of potentially integrated ramets. Roots are mostly 10-20 cm long, and in rich fen in Fennoscandia they normally extend down to 10 cm, and occasionally down to 20 cm (Metsävainio 1931). The density of *E. latifolium* ramets is higher in mowed than unmowed fen areas (92 m^{-2} and 35 m^{-2} respectively), and this pattern is also seen for above-ground biomass (21.3 and 14.7 g/m^2) and below-ground biomass (29.1 and 24.4 g/m^2) (Aune et al. 1996). Thus, total biomass and root/shoot (biomass) ratio is higher in mowed than unmowed areas, but the weight of individual ramets is lower in mowed areas.

The seeds in *E. latifolium* are about 1.5 mm long with a 100-seed weight of 0.04 g (Kutschera et al. 1982), and have attached numerous, up to 25 mm long cotton-like bristles that facilitate wind dispersal (Tutin et al. 1980, Elven 2005). This trait is shared with the closely related *E. angustifolium*, which is among the wetland plants best adapted to wind dispersal, and in which seeds can travel several kilometres (Grime 2001, Soons 2006). Similar dispersal distances can be expected in *E. latifolium*. *E. latifolium* has a transient seed bank (Mika 1978, Thompson et al. 1997), and the germination of seeds is affected positively by chilling (Maas 1989).

2.2. Study areas

The study was conducted at Sølendet and Tågdalen nature reserves which are situated 145 km apart in central Norway (Table 1, Fig. 1). Extremely rich fen vegetation (sensu Sjörs 1948, 1952) formerly used for haymaking covers substantial areas in both nature reserves, a type of vegetation considered near threatened in Norway due to overgrowing (Fremstad & Moen 2001). Mowing is currently implemented as a management tool in both areas to prevent encroachment. The study areas lie at the transition between the middle boreal and northern boreal vegetation zones (Moen 1999). Tågdalen has an oceanic climate, while Sølendet has a more continental climate, and precipitation is markedly higher at Tågdalen than at Sølendet (Table 1). The growing season is short, normally from late May until late August. Both Sølendet and Tågdalen hold large populations of *E. latifolium*.

2.3. Vegetation

Three local vegetation gradients in mire vegetation are recognised and used in the Fennoscandian tradition of mire studies (e.g. Tuomikoski 1942, Sjörs 1948, Ruuhijärvi 1960, Malmer 1962, Moen 1990, Rydin & Jeglum 2006). The poor – rich gradient reflects the pH and the mineral concentration, the mire expanse – mire margin gradient (often) reflects the peat depth, and the hummock – mud bottom gradient reflects the groundwater level. In this paper, the mire expanse – mire margin and hummock – mud bottom gradients are combined in a wet – dry gradient. The rich fen vegetation at Sølendet and Tågdalen was described and classified into six plant communities and ten vegetation clusters based on 134 vegetation samples (A. Lyngstad, A. Moen & D.-I.

Øien unpublished data), and resembled the vegetation of sloping rich fens described from northern Sweden (Persson 1961, 1962) and eastern Finland (Havas 1961). There was little variation along the poor – rich gradient, and all samples had rich (mostly extremely rich) fen vegetation. The 32 sample plots used in this study are shown superimposed on DCA-diagrams based on the samples used in the aforementioned classification (Fig. 2). The wet – dry gradient was reflected in the first DCA-axis for both study areas, and the sample plots fall into four (out of ten possible) vegetation clusters. Table 2 gives an overview of the four represented clusters, the plant communities they belong to, and their relative location along the wet – dry gradient. The fen carpet community (cluster 2) is dominated by *Scorpidium* spp. in the bottom layer, and the lawn communities (clusters 4-6) by *Campylium stellatum*. The lawn communities share dominant species, and the separation between the study areas is caused by occurrences of some oceanic and lowland species at Tågdalen, and some continental and alpine species at Sølendet (A. Lyngstad, A. Moen & D.-I. Øien unpublished data).

2.4. Experimental design and demographic census

The demography of *E. latifolium* was surveyed in 32 sample plots of 0.25 m^2, 15 at Sølendet and 17 at Tågdalen. At Sølendet, the sample plots were placed independently in 15 permanent plots (4 m^2, from here on referred to as plots), whereas at Tågdalen, the 17 sample plots were nested within 12.5 m^2 plots, which again were nested in localities. Locality here refers to spatially congregated groups of plots. The vegetation within plots was homogeneous, and the treatments were applied at the plot level in both study areas. The plots in Tågdalen were located along a 1 km stretch with fens in a small valley, and the plots at Sølendet were located up to 500 m apart in a largely open fen area. The mowing intervals at Sølendet were: mowed every 3rd year (five plots), extensively mowed (every 8th year on average, range 4-12 years, six plots) or unmowed (four plots), and a motorised mower was used. The plots mowed every 3rd year have been mowed ten times between 1979 and 2006, and the extensively mowed plots have been mowed three or four times between 1979 and 2001. The mowing at Tågdalen was carried out using a scythe, and the mowing regimes were every 2nd year (three plots, eight sample plots) and unmowed (four plots, nine sample plots). Mowing commenced in 1973, 1983 and 1985 in the three mowed plots, and has been performed biennially since.

Ramets of *E. latifolium* (n = 683-895) were identified and marked with numbered plastic sticks, using the sample plots as coordinate systems. All ramets were marked in sample plots containing up to 20 ramets (nine sample plots), and when the number of ramets exceeded 20, all ramets within a smaller area in the sample plots were marked (23 sample plots). The exact size of this area was noted to avoid ambiguity concerning ramet identity or descent. Physical connection between ramets was recorded in the years 2007-09, making it possible to define clonal fragments (n = 470-483). An overview of number of ramets and clonal fragments registered per year in the two study areas is shown in Table 3. Censuses were carried out once a year between 2006 and 2009, in August and September in 2006, and between mid-July and early August the other years.

2.5. Vital rates

Fundamental aspects of the life-history of a clonal plant like *E. latifolium* are survival, fragmentation, growth, retrogression, flowering, and seedling establishment, survival and growth (de Kroon & van Groenendael 1997). A model was developed to clarify the demographic processes affecting the transition of clonal fragments from year t to $t + 1$, with separate pathways for seedlings, fragmented, and intact clonal fragments, because the probabilities of equivalent vital rates (e.g. survival (Endels et al. 2007)) are likely to be different in different parts of the life cycle (Fig. 3). Vital rates for clonal fragments that split (as opposed to remaining intact) were denoted with a $_d$, e.g. γ_d, the probability of growth in surviving and fragmented clonal fragments. The vital rates defined either the probabilities or the outcomes of demographic processes between t and $t + 1$ (see Table 4 for details), and were modelled separately for the study areas. Clonal fragments survived (σ) as long as one of the ramets remained alive, and clonal fragments with more than two ramets always survived. Fragmentation (κ) was defined as the division of a surviving clonal fragment into two or more new clonal fragments with at least one ramet each between year t and year $t + 1$. This could come about either through the physical splitting of a clonal fragment where all ramets remained alive or through the death of a ramet that connected other ramets (Jónsdóttir & Watson 1997). Growth (γ, γ_d) was defined as an increase in number of ramets in a clonal fragment from year t to year $t + 1$ (not to be confused with the population growth rate), and retrogression (ρ, ρ_d) was defined as a decrease in number of ramets in a clonal fragment from year t to year $t + 1$. Clonal fragments were considered flowering (φ, φ_d) when they contained at least one flowering ramet. All viable seeds were assumed to germinate within the first year after flowering, ramets emerging from seeds were assigned to the class seedling, and they stayed there for one year only. Seedling establishment (ε) was considered as the ratio number of seedlings m^{-2} at year $t + 1$ / number of flowering ramets m^{-2} at year t. This is referred to as the seedling establishment ratio from here on. No seedlings developed into clonal fragments with more than two ramets, and no seedlings entered flowering stage classes at year $t + 1$.

At Sølendet, where the experimental design was not nested, the binomially distributed vital rates defining the probabilities of demographic processes (σ_j, κ_j, γ_j, γ_{dj}, ρ_j, ρ_{dj}, φ_j, φ_{dj}, σ_s and γ_s) were analysed with GLM's (quasi-GLM for σ_j because of overdispersion) (Crawley 2007). At Tågdalen, where the design was nested (see section 2.4), the binomially distributed vital rates were analysed with GLMM's with locality, plot and sample plot as random factors (McCulloch & Searle 2001, Crawley 2007). The seedling establishment ratio (ε) was analysed with NB GLM at both study areas because of large overdispersion (Zuur et al. 2009). A small number of very high values of the seedling establishment ratio complicated the modelling process. Ratio values above 25 were considered outliers on the basis that they were further from the median ratio value than two standard deviations. These outliers were attributed the value 25 and included in the data set. Zero-truncated GLM's were applied in the analyses of the vital rates defining the outcome of demographic processes (π_j, ω_j, ω_{dj}, ν_j, ν_{dj} and τ_j), because zero was not a possible value for these otherwise Poisson distributed parameters (Zuur et al. 2009). Vital rates related to fragmentation for the transition 2006-07 were entered in the analysis as means of the two last transitions because fragmentation was not observed during the 2006-07 transition. At Sølendet, seedling growth (σ_s) and how much a split fragment grows (ω_{dj}) were not modelled, and at Tågdalen, mean number of flowering ramets in a fragment (τ_j), the probability of growth in a split fragment (γ_{dj}) and how much a split fragment grows (ω_{dj}) were not modelled, either because they were identical for all clonal fragments, or because they had too few observations to justify modelling. The minimal adequate models (i.e. most parsimonious) for each vital rate were identified through step-wise exclusion of factors and interactions between factors (starting with full models) based on deviance tests (e.g. Jongman et al. 1995). The fixed factors considered in the vital rates models were mowing regime, vegetation (cluster), year (transition), if the clonal fragment was flowering in year t or not, and how large the clonal fragment was in year t in terms of number of ramets. For the GLMM's the structure of the random part of the model was determined first, then the structure of the part with fixed factors. Overparameterisation and unbalanced data was an issue in some models, and complexity was generally reduced by leaving out interactions rather than factors.

2.6. Transition matrix population model

Stage-based transition matrix models in most cases conform better than age-based transition matrix models to the life history of vascular plants (Leslie 1945, Lefkovitch 1965, Caswell 2001). We modelled the population dynamics of *E. latifolium* with a stage-based matrix model of the form $n_{t+1} = \mathbf{A}_{ij} n_t$, in which $\mathbf{A}_{ij}$ is the projection matrix (Caswell 2001). The demographic unit was the clonal fragment, and we defined stage classes based on the number of ramets in clonal fragments. The highest recorded number of ramets in a clonal fragment was ten (Fig. 4), and we considered ten vegetative (V_j) and ten flowering (F_j) stage-classes. A separate class for seedlings was maintained, giving 21 possible stage-classes. A population transition matrix $\mathbf{A}_{ij}$ for *E. latifolium* with 21 classes is shown in Table 5. The transition elements a_{ij} correspond to transitions from the j^{th} stage class in year t to the i^{th} stage class in year $t + 1$. Transitions to vegetative fragments in the i^{th} stage class were entered as V_{ij}, and transitions to flowering fragments in the i^{th} stage class were entered as F_{ij}, and there could potentially be self-loops in, and transitions between, all classes except seedlings. The probability of each transition V_{ij} or F_{ij} depended on the values of the vital rates influencing them. We defined the transitions V_{ij} and F_{ij} as:

$$V_{ij} = \sigma_j(1-\kappa_j)\gamma_j\omega_j(1-\varphi_j) + \sigma_j(1-\kappa_j)(1-\gamma_j)(1-\rho_j)(1-\varphi_j) + \sigma_j(1-\kappa_j)(1-\gamma_j)\rho_j\nu_j(1-\varphi_j) + \sigma_j\kappa_j\pi_j\gamma_{dj}\omega_{dj}(1-\varphi_{dj}) + \sigma_j\kappa_j\pi_j(1-\gamma_{dj})(1-\rho_{dj})(1-\varphi_{dj}) + \sigma_j\kappa_j\pi_j(1-\gamma_{dj})\rho_{dj}\nu_{dj}(1-\varphi_{dj}) \qquad \text{eqn (1)}$$

$$F_{ij} = \sigma_j(1-\kappa_j)\gamma_j\omega_j\varphi_j + \sigma_j(1-\kappa_j)(1-\gamma_j)(1-\rho_j)\varphi_j + \sigma_j(1-\kappa_j)(1-\gamma_j)\rho_j\nu_j\varphi_j + \sigma_j\kappa_j\pi_j\gamma_{dj}\omega_{dj}\varphi_{dj} + \sigma_j\kappa_j\pi_j(1-\gamma_{dj})(1-\rho_{dj})\varphi_{dj} + \sigma_j\kappa_j\pi_j(1-\gamma_{dj})\rho_{dj}\nu_{dj}\varphi_{dj} \qquad \text{eqn (2)}$$

Thus, there were six sets of combinations of probabilities of vital rates defining both V_{ij} (eqn (1)) and F_{ij} (eqn (2)). These were separated in the contribution from intact clonal fragments or split clonal fragments that were growing, staying in the same size class or retrogressing.

At Tågdalen, the population growth rate (λ = largest eigenvalue of $\mathbf{A}_{ij}$ (van Groenendael et al. 1988)) was calculated for 12 combinations of year (three transitions), two vegetation clusters and two mowing regimes, and at Sølendet for 18 combinations of year (three transitions), two vegetation clusters and three mowing regimes, giving a total of 30 transition matrices. Elasticities were calculated for mean matrices (unmowed situations) of vital rates, showing how and how much a change in a vital rate would impact λ on a relative scale (de Kroon et al. 1986, Franco & Silvertown 2004). We conducted nested LTRE's (Elderd & Doak 2006, Endels et al. 2007, Jacquemyn et al. 2010, Jongejans et al. 2010) to study how much vital rate differences between years, study areas, vegetation clusters and mowing regimes contributed to the variation in λ among the transition matrices. Our nested decomposition model was defined as follows:

$$\lambda^{kmnq} \cong \lambda^{\cdots\cdot} + \alpha^{k\cdots} + \theta(\alpha)^{km\cdot\cdot} + \mu(\alpha\theta)^{kmn\cdot} + \beta^{\cdots q} + \alpha\theta\mu\beta^{kmnq} \qquad \text{eqn (5)}$$

study area:

$$\tilde{\alpha}^{k\cdot 0\cdot} \approx \sum_{i,j}\sum_{r}\left(h_r^{k\cdot 0\cdot} - h_r^{\cdot\cdot 0\cdot}\right)\frac{\partial\lambda}{\partial a_{ij}}\frac{\partial a_{ij}}{\partial h_r}\bigg|_{\frac{1}{2}\left(A^{k\cdot 0\cdot}+A^{\cdot\cdot 0\cdot}\right)} \qquad \text{eqn (6)}$$

vegetation cluster within study area:

$$\widetilde{\theta(\alpha)}^{km0\cdot} \approx \sum_{i,j}\sum_{r}\left(h_r^{km0\cdot} - h_r^{k\cdot 0\cdot}\right)\frac{\partial\lambda}{\partial a_{ij}}\frac{\partial a_{ij}}{\partial h_r}\bigg|_{\frac{1}{2}\left(A^{km0\cdot}+A^{k\cdot 0\cdot}\right)} \qquad \text{eqn (7)}$$

mowing regime within vegetation cluster (within study area):

$$\widetilde{\mu(\alpha\theta)}^{kmn\cdot} \approx \sum_{i,j}\sum_{r}\left(h_r^{kmn\cdot} - h_r^{km0\cdot}\right)\frac{\partial\lambda}{\partial a_{ij}}\frac{\partial a_{ij}}{\partial h_r}\bigg|_{\frac{1}{2}\left(A^{kmn\cdot}+A^{km0\cdot}\right)} \qquad \text{eqn (8)}$$

year: $$\tilde{\beta}^{\cdot\cdot 0q} \approx \sum_{i,j}\sum_{r}\left(h_r^{\cdot\cdot 0q} - h_r^{\cdot\cdot 0\cdot}\right)\frac{\partial\lambda}{\partial a_{ij}}\frac{\partial a_{ij}}{\partial h_r}\bigg|_{\frac{1}{2}\left(A^{\cdot\cdot 0q}+A^{\cdot\cdot 0\cdot}\right)} \qquad \text{eqn (9)}$$

residual:

$$\widetilde{\alpha\theta\mu\beta}^{kmnq} \approx \sum_{i,j}\sum_{r}\left(h_r^{kmnq} - h_r^{\cdot\cdot 0\cdot}\right)\frac{\partial\lambda}{\partial a_{ij}}\frac{\partial a_{ij}}{\partial h_r}\bigg|_{\frac{1}{2}\left(A^{kmnq}+A^{\cdot\cdot 0\cdot}\right)}$$

$$-\tilde{\alpha}^{k\cdot 0\cdot} - \widetilde{\theta(\alpha)}^{km0\cdot} - \widetilde{\mu(\theta\alpha)}^{kmn\cdot} - \tilde{\beta}^{\cdot\cdot 0q} \qquad \text{eqn (10)}$$

in which the indices refer to the k^{th} study area, the m^{th} vegetation cluster within study area k, and the n^{th} mowing regime within vegetation cluster θ and to the q^{th} year. The reference matrix was either the overall mean matrix ($A^{\cdot\cdot 0\cdot}$, in eqns (6) and (9)), a study area mean matrix ($A^{k\cdot 0\cdot}$, in eqn 7) or the appropriate vegetation cluster mean matrix ($A^{km0\cdot}$, in eqn 8). Each of these reference matrices was based on averaging vital rates for unmowed situations, hence the ‘0’ index. Vital rates were used as model components in the LTRE’s, and the contribution from a given vital rate x_j was quantified in two steps. The difference between x_j in the matrix of interest and x_j in the appropriate reference matrix was calculated, and the difference multiplied by the sensitivity of x_j computed from the midway matrix between the matrix of interest and the reference matrix (Caswell 2001, Zuidema et al. 2007). Statistical analyses were conducted in the R statistical environment (R Development Core Team 2008), making use of the packages “lattice” (Sarkar 2008), “lme4” (Bates et al. 2008), “Matrix” (Bates & Maechler 2009), “popbio” (Stubben & Milligan 2007) and “VGAM” (Yee 2009).

3. Results

3.1. Vital rates

Here we present the main patterns concerning vital rates, and we refer to the Supplementary material for a more thorough examination of the outcome of the minimal adequate models developed for the vital rates. Whether a clonal fragment was flowering in year t affected the probabilities of survival (σ), retrogression (ρ) and flowering (φ) in year $t + 1$ at Sølendet, and, at Tågdalen, the probabilities of survival (σ), fragmentation (κ), retrogression (ρ) and how much a retrogressing clonal fragment shrinks (v). At Sølendet, mowing affected the probabilities of fragmentation (κ), growth in seedlings (γ_s) and the seedling establishment ratio (ε), and at Tågdalen it affected the probabilities of survival (σ), flowering (φ), growth (γ) and how much a growing clonal fragment grows (ω). Vegetation (cluster) affected at Sølendet only the probabilities of flowering (φ), while at Tågdalen it affected the probabilities of survival (σ), growth (γ) and how much a growing clonal fragment grows (ω). Of the factors included here, the size of a clonal fragment (number of ramets) in year t affected the most vital rates. The probabilities of fragmentation (κ), flowering (φ), growth (γ), how much a growing clonal fragment grows (ω) and how much a fragmented and retrogressing fragment shrinks (v_d) was influenced at both study areas, and, in addition, the probabilities of survival (σ) and the mean number of flowering ramets in a flowering clonal fragment was affected at Sølendet (τ_j). The different years (transitions) affected the probabilities of fragmentation (κ), flowering (φ), growth (γ), retrogression (ρ) and how much an intact and retrogressing fragment shrinks (v) at Sølendet, and, at Tågdalen they affected the probabilities of survival (σ), fragmentation (κ), flowering (φ) and retrogression (ρ). Among the vital rates of split clonal fragments, only the one dealing with how much a retrogressing fragment shrinks (v_d) was influenced by any of the factors. This reflects the low number of fragmented as opposed to intact clonal fragments.

Mortality was not observed in clonal fragments with more than two ramets, and this applied to both vegetative and flowering clonal fragments. Survival (σ) was 90.5 % among those with one ramet, and there was only one example of a clonal fragment of size two that died (σ_2 = 99.7 %). Vegetative and flowering clonal fragments of size one had a 94.3 % and 86.4 % probability of survival respectively. Fragmentation (κ) was registered in 10.3 % of clonal fragments in the transitions 2007-08 and 2008-09, and there was a higher probability of fragmentation in large ($\kappa_{\geq 4}$ = 45.7 %) than in small fragments ($\kappa_{<4}$ = 6.4 %). Four fragments of size class 1 fragmented (κ_1 = 0.8 %), implying that these clonal fragments produced at least one side rosette that got separated from the mother ramet during the same transition. At Tågdalen, the probability of growth (γ) was positively affected by mowing, and the probability of retrogression (ρ) was increased by flowering in year *t* in both study areas. Intact clonal fragments grew larger (γ) in 15.7 % of the cases, while 4.5 % retrogressed (ρ) and 79.8 % stayed in the same class (stasis). Split clonal fragments showed a different pattern, as many as 85.3 % retrogressed (ρ_d), 11.6 % stayed in the same class, and only 3.2 % grew (γ_d). Flowering was observed in 100 clonal fragments (φ = 6.9 %) between 2006 and 2009, mostly with one flowering ramet per clonal fragment. There was a lower probability of flowering among clonal fragments of the two smallest size classes ($\varphi_{\leq 2}$ = 5.5 %) compared to fragments of size class 3 and up ($\varphi_{\geq 3}$ = 15.4 %). There were 44 observations of seedlings, 23 at Tågdalen and 21 at Sølendet, 95.5 % of these survived (σ_s) to year $t + 1$, 38 grew into size class 1, six grew into size class 2, and none became larger than size class 2 (γ_s). The seedling establishment ratio (ε) depended on both flowering density at *t* and seedling density at $t + 1$, and this ratio varied between 1 and 25 (see section 2.5).

The mortality of separate ramets within clonal fragments was higher in unmowed than mowed plots at Tågdalen (14.4 % and 5.5 %), whereas ramets in plots unmowed, extensively mowed and mowed every 3rd year at Sølendet had similar probabilities of mortality (14.9 %, 15.1% and 12.5 %). Clonal reproduction as the production of side rosettes in clonal fragments was little affected by mowing regime both at Tågdalen (14.1 % vs. 16.0 %) and at Sølendet (13.8 %, 10.0 % and 10.4 %).

3.2. Population growth rate

Estimated population growth rate was higher at Tågdalen (λ = 0.80-1.04) than at Sølendet (λ = 0.77-1.00). Mowing every 2nd year lowered λ in both vegetation clusters at Tågdalen compared to unmowed situations, and while the latter had growth rates close to unity, the situations with mowing had λ = 0.80 to 0.95 (Fig. 5). Mowing every

3rd year yielded the overall highest values of λ at Sølendet, while estimated λ was lower in extensively mowed than unmowed plots. The overall growth rate was higher in carpet than in lawn vegetation at Sølendet, but there was considerable variation among mowing regimes and transitions. The estimated population growth rates matched the observed growth rates well at Tågdalen, both in terms of magnitude and relative differences between vegetation communities, mowing regimes and years. The fit was less convincing at Sølendet, where the estimated λ was systematically lower than the observed λ, but where the pattern between communities and mowing regimes fitted well for the transitions 2006-07 and 2007-08 (Fig. 5).

3.3. Elasticities

Survival of adult clonal fragments (σ_j) was the vital rate with the markedly highest elasticity across all vegetation clusters in both study areas (Fig. 6). Vegetation cluster 4 at Tågdalen and both vegetation clusters at Sølendet showed similar patterns concerning value and direction of the elasticities for all vital rates, but vegetation cluster 5 at Tågdalen was set apart from the other three. Elasticities for vital rates concerning fecundity (φ_j, φ_{dj}, τ_j, ε, σ_s, γ_s) were practically zero in this cluster. On the other hand, elasticities were high for ω_j (how much intact clonal fragments grow), a vital rate with very low elasticities in the other three clusters. The probability of growth (γ_j) was the vital rate with second highest (and negative) elasticity for the Sølendet clusters. The Tågdalen clusters had opposing elasticity effects, and an increased probability of growth will increase λ in cluster 5, but decrease λ in cluster 4 (similar to the Sølendet clusters). The retrogression vital rates (ρ_j, v_j) had small elasticity values for all clusters. The probability of fragmentation (κ_j) also had low elasticity, but cluster 5 again stood out with an impact opposite to that of the other clusters. Three vital rates concerned with split clonal fragments had substantial elasticities in cluster 5; how many new clonal fragments (π_j) that arise after fragmentation has taken place, the probability of retrogression (ρ_{dj}), and how large they become when they shrink (v_{dj}). The elasticities for π_j and v_{dj} were positive, while that of ρ_{dj} was negative. The other three clusters had low elasticity values for vital rates concerned with split clonal fragments. Elasticity patterns for different mowing regimes were rather similar (results not shown).

3.4. LTRE analyses

The decomposition analysis showed that the large negative contribution from the seedling establishment ratio (ε) was the main cause of the lower population growth rate at Sølendet compared to Tågdalen (Fig. 7). At Sølendet, a small negative contribution on λ from survival (σ_j) and a positive contribution from growth in intact fragments (γ_j) were evident as well, whereas the other vital rates were of little importance. How much an intact clonal fragment grows conditional on growth (ω_j) and the seedling establishment ratio (ε) were the two elements contributing the most to the difference between the Tågdalen and the mean study area matrix, and they were both positive. Four vital rates associated with fragmentation were also important (ρ_{dj}, ν_{dj}, κ_j, π_j), with the probability of retrogression conditional on fragmentation (ρ_{dj}) as the only vital rate with a negative contribution of some magnitude at Tågdalen.

The difference in λ between vegetation clusters was analysed separately in the study areas, i.e. the reference matrix was the (unmowed) study area matrix. Population growth rate was similar in clusters 4 and 5 at Tågdalen (Fig. 8), but the decomposition into contributions from each vital rate showed there were differences in the effect on λ of elements related to growth in intact clonal fragments. The probability of growth (γ_j) was the main positive contribution in cluster 4, while it played a minor role in cluster 5. How much a fragment grows conditional on growth (ω_j) had a negative contribution in cluster 4 contrasted by a strong positive contribution in cluster 5. The clusters at Sølendet also had similar λ, and the only vital rate with a different contribution in these clusters was the probability of flowering, which was positive in cluster 2 and negative in cluster 6 (Fig. 8). The majority of vital rates did not affect λ differently among the clusters, and this reflects the pattern in the vital rates models, where only four vital rates were affected by differences in vegetation (see section 3.1).

The effect of mowing on λ was analysed for each vegetation cluster with the unmowed matrix for each cluster as the reference matrix. Mowing lowered λ at Tågdalen (Fig. 9), and this was mainly caused by negative contributions from vital rates connected with growth in intact fragments (γ_j, ω_j, both clusters). Lower survival probability (σ_j) had an additional negative impact in cluster 4, while higher flowering probability had a small positive impact. The mowing regimes at Sølendet mostly affected λ through the same vital rates, and the effect of each mowing regime was the same among vegetation clusters. The lowest estimated λ at Sølendet was found with extensive mowing, and the decomposition analyses showed a lower probability of fragmentation (κ_j) and a lower seedling establishment ratio (ε) to be the major contributors to this. Mowing every 3rd year yielded the highest growth rates at Sølendet, and this was mainly brought about by a higher seedling establishment ratio.

Variations in λ between transitions were mainly caused by variation in growth in intact fragments (γ_j) or flowering (φ_j), with survival, retrogression in intact fragments and fragmentation (σ_j, ρ_j, κ_j) playing minor roles (Fig. 10).

4. Discussion

4.1. Two separate elasticity patterns

Population growth rate in perennial vascular plants is often sensitive to changes in survival probability in the adult stages of the life cycle (Silvertown et al. 1993, Franco & Silvertown 2004, Jacquemyn et al. 2010, Sletvold et al. 2010). The elasticity analysis showed that survival was of paramount importance in *E. latifolium* as well, an expected result considering the long-lived nature of both ramets and clonal fragments in this species. The elasticities were calculated for unmowed situations to ensure comparability between the study areas, and the elasticity pattern was similar in both fen carpet and lawn at Sølendet and fen lawn cluster 4 at Tågdalen. Here, survival probability was the vital rate most influential to population growth rate, but fecundity related vital rates were also of some importance. Cluster 5 in fen lawn at Tågdalen represented a different pattern where fecundity had no impact, but where fragmentation and growth were important in addition to survival. Clear signs of a shift in fen vegetation in our study areas due to overgrowing has so far only been detected in unmowed plots in (dry) fen margin (A. Lyngstad, A. Moen & D.-I. Øien unpublished data), and we believe the diverging elasticity pattern was caused by incipient succession in the relatively dry vegetation of this cluster towards a shrub-dominated fen margin/wet grassland community. The included plots had a dense layer of accumulated litter that may impede seedling establishment (cf. Facelli & Pickett 1991), leaving fecundity without influence. Furthermore, the fragments were relatively large (data not shown), and large clonal fragments had a much higher probability of fragmenting, as reflected in the high elasticities involving fragmentation. *E. latifolium* has a narrow range on the wet – dry gradient in fen where it performs well (Moen 1990), and in dry fen lawn it is close to its upper limit along this gradient. The elasticities indicate that the species can persist in an overgrowing fen margin as long as clonal reproduction, fragmentation and survival are high. These vital rates can, however, be negatively affected by competition from surrounding vegetation as succession continues, and the eventual demise of *E. latifolium* in overgrowing fens would likely be caused by a combination of lower probabilities of clonal reproduction, fragmentation and survival. Fragmentation as a demographic process has not been much studied in natural populations (but see e.g. Greig (1993) and Lantz & Antos (2002)), but our results suggest that this may be of importance to maintain populations in unfavourable habitats. However, a model study emphasises that in a habitat where fragmentation is advantageous (in terms of fitness), then only "Splitters" (= clonal fragments that disintegrate completely) can benefit from fragmentation (Oborny & Kun 2001). Fragmentation, as we see it in *E. latifolium*, may therefore be a result of stochastic factors (internal or external) rather than an adaptive trait.

A key assumption in matrix modelling is that vital rate probabilities are the same for all members of a class (e.g. Ehrlén 1997), and a violation of this assumption may affect the outcome of the analyses. Our definition of size classes based on number of ramets did not capture size variation caused by diverging ramet sizes, and this could have affected the elasticity patterns because individual ramets were large in cluster 5 (A. Lyngstad unpublished data). An alternative approach with size classes related to biomass may be appropriate in order to ascertain whether the elasticity analysis was influenced by our definition of classes. As argued by Pedersen (1997), senescence can also cause violation of the assumption of similar vital rate probabilities within size classes. Young clonal fragments entering a size class through growth may not display the same properties as old fragments entering the same size class through retrogression. This could be of relevance to *E. latifolium* in unmowed fen lawn in cluster 5, where survival and fragmentation of existing clonal fragments dominated the dynamics of the population, and there was little recruitment of seedlings.

4.2. Study area and population growth rate

The observed population growth rate was similar between the study areas, but the growth rate estimated from the population transition matrix was lower at Sølendet than at Tågdalen, indicating an underestimation at Sølendet. The decomposition analysis showed that different contributions from the seedling establishment ratio was the most important factor separating the populations, suggesting that the models for this vital rate may have caused the discrepancy between observed and estimated λ. There were several assumptions in our approach to modelling the seedling establishment ratio that may cause inaccuracy in the model output. The seedling establishment ratio was calculated per plot as the ratio seedlings $t + 1$ / flowering ramets t, assuming a relationship between flowering and seedling emergence on a plot level. *E. latifolium* has wind spread seeds that can travel large distances (Soons 2006) and a spatial scale larger than plots would be more realistic. Seedlings were rare (see section 4.3) but tended to be temporally and spatially aggregated. This resulted in many low and a few very high values of the seedling establishment ratio, and made it difficult to develop a model yielding accurate probabilities of this process.

4.3. Mowing and population growth rate

Mowing in boreal rich fens affects plant populations mainly through disturbance (sensu Crawley 1997), not through stress due to removal of macronutrients (Øien & Moen 2001). Our results indicate a different response to mowing (every 2nd or 3rd year) on λ in *E. latifolium* between the study areas, a decrease at Tågdalen, and an increase at Sølendet. Mowing was performed with a scythe every 2nd year at Tågdalen as opposed to every 3rd year with a motorised mower at Sølendet, and the disturbance caused by the mowing treatment was therefore more severe at Tågdalen, which may account for the observed differences in λ. The LTRE analyses showed that lower growth and partly survival caused the decrease in λ at Tågdalen, and this can be a result of high disturbance. There was no sign of lower growth at Sølendet, and an implication of this interpretation is that *E. latifolium* thrives with the levels of disturbance induced by mowing every 3rd year, while mowing every 2nd year with a scythe is severe enough to lower population growth rate.

We defined growth as an increase in the number of ramets in a clonal fragment from year *t* to *t* +1. Hence, the lower growth at Tågdalen could have been caused by either higher mortality of ramets within clonal fragments or decreased clonal reproduction. The mortality among ramets was higher in mowed than unmowed plots at Tågdalen, while the production of clonal offspring was similar between the mowing regimes. This indicated that mowing increased ramet turnover, but that clonal reproduction was unable to make up for the increased ramet mortality. Increased turnover of ramets within clonal fragments is found for *Carex membranacea* and *C. stans* (Tolvanen et al. 2001) and *Agrostis stolonifera* and *Lolium perenne* (Bullock et al. 1994) in disturbed (grazed) areas, and the results from Tågdalen was in accordance with this. While the turnover rate was increased by mowing in *E. latifolium*, it was still low compared to the rates seen in *Carex arenaria* and *C. lasiocarpa* (Noble et al. 1979, Bedford et al. 1988). Tolvanen et al. (2001) found that growth was more important than survival for λ in disturbed areas (vice versa in undisturbed areas), this is in part contrary to our findings. Less growth in clonal fragments was the major impact of mowing on λ at Tågdalen, and lower survival was only important in fen lawn cluster 4.

Accumulation of litter is known to decrease seedling establishment, while removing litter and creating gaps enhances seedling establishment (Facelli & Pickett 1991, Donath & Eckstein 2010). Small seeds are more susceptible to a dense litter cover than large seeds (Stammel et al. 2006, Rasran et al. 2007), and *E. latifolium* has medium sized seeds in this context. Because mowing removes litter, we anticipated a positive contribution from the seedling establishment ratio to λ in moved compared to unmowed plots. This has already been shown for *Dactylorhiza lapponica* in both study areas (Sletvold et al. 2010). A higher seedling establishment ratio caused an increase in λ in plots mowed every 3rd year at Sølendet as expected, but this vital rate did not explain the difference in λ between moved and unmowed plots at Tågdalen. The small seeds in *D. lapponica* compared to *E. latifolium* may explain why the response is more distinct in the orchid, but we see no apparent reason why mowing should have no impact on population growth rate through the seedling establishment ratio at Tågdalen. The seedling establishment ratio was also the main contributor to the differences in λ between the mowing regimes at Sølendet. Extensively mowed areas had a low seedling establishment ratio compared to both areas unmowed and mowed every 3rd year, and this caused the especially low estimated population growth rates found with this mowing regime. The uncertainties attributed to the seedling establishment ratio models may explain the discrepancy between estimated and observed population growth rate.

4.4 Flowering and population growth rate

While long-lived species rarely exhibit high elasticities for fecundity (Silvertown et al. 1993, Franco & Silvertown 2004), elasticities involving flowering can occasionally be substantial (Ehrlén et al. 2005, Sletvold et al. 2010). Fecundity vital rates had overall low elasticities in *E. latifolium*, indicating that even quite large differences in i.e. flowering probability between years would have a limited effect on population growth rate. However, the LTRE analyses showed that the contribution from flowering explained much of the variation in λ among years, and this can come about if there are large temporal differences in flowering density. This is indeed the case in *E. latifolium*, flowering density is up to 70 times higher in years with high compared to low numbers of flowering ramets m^{-2} (A. Lyngstad, A. Moen & B. Pedersen unpublished data). Hence, λ in *E. latifolium* is little affected by perturbations of flowering probability, but, as it turns out, the variation between years is so large that a substantial impact materialises.

5. Conclusions

The perennial nature of *Eriophorum latifolium* was reflected in the high elasticity of survival probability in populations from all the studied rich fen communities. Incipient succession towards shrub-dominated fen margin vegetation was the probable cause of a shift in the elasticity pattern in a dry fen lawn community where clonal reproduction and fragmentation were important in addition to survival. Similar patterns may be found in other stress tolerant but weakly competitive clonal species. Mowing affects plant populations in boreal rich fens for the most part through disturbance (Øien & Moen 2001), and mowing every 2nd year (Tågdalen) was severe enough to cause a decrease in population growth rate through lower growth and survival probabilities. Mowing every 3rd year (Sølendet) yielded an increase in the population growth rate through a higher seedling establishment ratio, and indicated that *E. latifolium* thrives with this level of disturbance. Flowering probability had low elasticity but explained much of the year-to-year variation in population growth rate, emphasising that vital rates with low elasticity can be of importance when they have high variability. As is the case in many studies of long-lived plants, the recruitment phase is the least known also in *E. latifolium*. The seedling establishment ratio was an important factor as it affected the population growth rate differently at the study areas, and further studies should attempt to expand knowledge of this part of the species' life history.

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Tables

Table 1. Characteristics of the two nature reserves used as study areas. Effective temperature sum (*ETS*) after Laaksonen (1979).

	Sølendet	Tågdalen
Latitude (N)	62°40’	63°03’
Longitude (E)	11°50’	9°05’
Mean annual precipitation (mm)	637	1583
Mean annual *ETS* (day degrees)	578	639
Mean July temperature (°C)	10.5	11.2
Mean January temperature (°C)	-9.5	-2.7
Altitude (m a.s.l.)	700-800	380-490
Area (ha)	306	146

Table 2. The represented rich fen plant communities and vegetation clusters at each study area (A. Lyngstad, A. Moen & D.-I. Øien unpublished data) with their relative positioning along a wet – dry gradient (within study area) and number of sample plots.

Study area	Plant community	Vegetation cluster	Relative wet - dry gradient	Number of sample plots
Sølendet	*Eleocharis quinqueflora-Cinclidium* carpet community	Cluster 2	Wet	6
	Equisetum variegatum-Thalictrum-Campylium lawn community	Cluster 6	Dry	9
Tågdalen	*Eriophorum latifolium-Campylium* lawn community	Cluster 4	Wet	10
		Cluster 5	Dry	7

Table 3. Number of ramets (R) and clonal fragments (F) of *E. latifolium* registered in annual censuses (2006-09) in cluster 2 (carpet) and cluster 6 (lawn) and three mowing regimes at Sølendet, and vegetation clusters 4 and 5 (both lawn) and two mowing regimes at Tågdalen.

		Sølendet				Tågdalen			
		Cluster 2		Cluster 6		Cluster 4		Cluster 5	
Mowing regime	Year	R	F	R	F	R	F	R	F
Unmowed	2006	85	59	12	9	79	61	90	47
	2007	88	59	11	8	91	69	110	52
	2008	90	61	13	8	96	73	129	54
	2009	107	60	16	7	113	72	155	54
Mowed extensively	2006	50	27	57	43	-	-	-	-
	2007	47	22	59	44	-	-	-	-
	2008	46	22	61	42	-	-	-	-
	2009	46	23	66	41	-	-	-	-
Mowed every 3rd year	2006	74	46	82	64	-	-	-	-
	2007	78	52	86	61	-	-	-	-
	2008	81	53	88	63	-	-	-	-
	2009	97	53	100	61	-	-	-	-
Mowed every 2nd year	2006	-	-	-	-	90	69	64	48
	2007	-	-	-	-	104	70	74	44
	2008	-	-	-	-	111	64	76	43
	2009	-	-	-	-	114	57	81	42

Table 4. Definitions of 17 vital rates affecting the transition of clonal fragments in *E. latifolium* from year *t* to *t* + 1. The vital rates deal with either the probabilities or the outcomes of demographic processes.

Vital rate	**Demographic process**
σ_j	Survival probability from year *t* to year *t* + 1 of clonal fragments with one or two ramets
κ_j	Fragmentation probability between year *t* and year *t* + 1 of surviving clonal fragments
π_j	Number of new clonal fragments at year *t* + 1 emerging from each fragmenting clonal fragment
γ_j	Growth probability in surviving and intact clonal fragments
γ_{dj}	Growth probability in surviving and fragmented clonal fragments
ρ_j	Retrogression probability in surviving, intact and non-growing clonal fragments
ρ_{dj}	Retrogression probability in surviving, fragmented and non-growing clonal fragments
ω_j	How much a surviving, intact and growing clonal fragment grows
ω_{dj}	How much a surviving, fragmented and growing clonal fragment grows
ν_j	How much a surviving, intact and non-growing clonal fragment shrinks
ν_{dj}	How much a surviving, fragmented and non-growing clonal fragment shrinks
φ_j	Flowering probability at year *t* + 1 of surviving and intact clonal fragments
φ_{dj}	Flowering probability at year *t* + 1 of surviving and fragmented clonal fragments
τ_j	Mean number of flowering ramets at year *t* in flowering clonal fragments
ε	Seedling establishment ratio as seedlings m^{-2} at year *t* + 1 / flowering ramets m^{-2} at year *t*
σ_s	Survival probability from year *t* to year *t* + 1 of seedlings
γ_s	Probability of surviving seedlings to grow to size 2 at year *t* + 1

Table 5. A population transition matrix $\mathbf{A}_{ij}$ with 21 classes for *E. latifolium*. The first row contains transitions from each stage-class to the seedling class, and quantifies the contribution to seedling establishment from each stage-class. The first column contains the transitions from the seedling class to each vegetative and flowering stage-class. All other transitions are between adult vegetative (V_{ij}) or flowering (F_{ij}) clonal fragments of sizes 1-10. σ_s = seedling survival, γ_s = seedling growth, τ = number of flowering ramets, ε = the seedling establishment ratio.

$$A_{ij} = \left(\begin{array}{ccccccccccccccccccccc}
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \tau_{12}\varepsilon & \tau_{13}\varepsilon & \tau_{14}\varepsilon & \tau_{15}\varepsilon & \tau_{16}\varepsilon & \tau_{17}\varepsilon & \tau_{18}\varepsilon & \tau_{19}\varepsilon & \tau_{20}\varepsilon & \tau_{21}\varepsilon \\
\sigma_s(1-\gamma_s) & V_{22} & V_{23} & V_{24} & V_{25} & V_{26} & V_{27} & V_{28} & V_{29} & V_{210} & V_{211} & V_{212} & V_{213} & V_{214} & V_{215} & V_{216} & V_{217} & V_{218} & V_{219} & V_{220} & V_{221} \\
\sigma_s\gamma_s & V_{32} & V_{33} & V_{34} & V_{35} & V_{36} & V_{37} & V_{38} & V_{39} & V_{310} & V_{311} & V_{312} & V_{313} & V_{314} & V_{315} & V_{316} & V_{317} & V_{318} & V_{319} & V_{320} & V_{321} \\
0 & V_{42} & V_{43} & V_{44} & V_{45} & V_{46} & V_{47} & V_{48} & V_{49} & V_{410} & V_{411} & V_{412} & V_{413} & V_{414} & V_{415} & V_{416} & V_{417} & V_{418} & V_{419} & V_{420} & V_{421} \\
0 & V_{52} & V_{53} & V_{54} & V_{55} & V_{56} & V_{57} & V_{58} & V_{59} & V_{510} & V_{511} & V_{512} & V_{513} & V_{514} & V_{515} & V_{516} & V_{517} & V_{518} & V_{519} & V_{520} & V_{521} \\
0 & V_{62} & V_{63} & V_{64} & V_{65} & V_{66} & V_{67} & V_{68} & V_{69} & V_{610} & V_{611} & V_{612} & V_{613} & V_{614} & V_{615} & V_{616} & V_{617} & V_{618} & V_{619} & V_{620} & V_{621} \\
0 & V_{72} & V_{73} & V_{74} & V_{75} & V_{76} & V_{77} & V_{78} & V_{79} & V_{710} & V_{711} & V_{712} & V_{713} & V_{714} & V_{715} & V_{716} & V_{717} & V_{718} & V_{719} & V_{720} & V_{721} \\
0 & V_{82} & V_{83} & V_{84} & V_{85} & V_{86} & V_{87} & V_{88} & V_{89} & V_{810} & V_{811} & V_{812} & V_{813} & V_{814} & V_{815} & V_{816} & V_{817} & V_{818} & V_{819} & V_{820} & V_{821} \\
0 & V_{92} & V_{93} & V_{94} & V_{95} & V_{96} & V_{97} & V_{98} & V_{99} & V_{910} & V_{911} & V_{912} & V_{913} & V_{914} & V_{915} & V_{916} & V_{917} & V_{918} & V_{919} & V_{920} & V_{921} \\
0 & V_{102} & V_{103} & V_{104} & V_{105} & V_{106} & V_{107} & V_{108} & V_{109} & V_{1010} & V_{1011} & V_{1012} & V_{1013} & V_{1014} & V_{1015} & V_{1016} & V_{1017} & V_{1018} & V_{1019} & V_{1020} & V_{1021} \\
0 & V_{112} & V_{113} & V_{114} & V_{115} & V_{116} & V_{117} & V_{118} & V_{119} & V_{1110} & V_{1111} & V_{1112} & V_{1113} & V_{1114} & V_{1115} & V_{1116} & V_{1117} & V_{1118} & V_{1119} & V_{1120} & V_{1121} \\
0 & F_{122} & F_{123} & F_{124} & F_{125} & F_{126} & F_{127} & F_{128} & F_{129} & F_{1210} & F_{1211} & F_{1212} & F_{1213} & F_{1214} & F_{1215} & F_{1216} & F_{1217} & F_{1218} & F_{1219} & F_{1220} & F_{1221} \\
0 & F_{132} & F_{133} & F_{134} & F_{135} & F_{136} & F_{137} & F_{138} & F_{139} & F_{1310} & F_{1311} & F_{1312} & F_{1313} & F_{1314} & F_{1315} & F_{1316} & F_{1317} & F_{1318} & F_{1319} & F_{1320} & F_{1321} \\
0 & F_{142} & F_{143} & F_{144} & F_{145} & F_{146} & F_{147} & F_{148} & F_{149} & F_{1410} & F_{1411} & F_{1412} & F_{1413} & F_{1414} & F_{1415} & F_{1416} & F_{1417} & F_{1418} & F_{1419} & F_{1420} & F_{1421} \\
0 & F_{152} & F_{153} & F_{154} & F_{155} & F_{156} & F_{157} & F_{158} & F_{159} & F_{1510} & F_{1511} & F_{1512} & F_{1513} & F_{1514} & F_{1515} & F_{1516} & F_{1517} & F_{1518} & F_{1519} & F_{1520} & F_{1521} \\
0 & F_{162} & F_{163} & F_{164} & F_{165} & F_{166} & F_{167} & F_{168} & F_{169} & F_{1610} & F_{1611} & F_{1612} & F_{1613} & F_{1614} & F_{1615} & F_{1616} & F_{1617} & F_{1618} & F_{1619} & F_{1620} & F_{1621} \\
0 & F_{172} & F_{173} & F_{174} & F_{175} & F_{176} & F_{177} & F_{178} & F_{179} & F_{1710} & F_{1711} & F_{1712} & F_{1713} & F_{1714} & F_{1715} & F_{1716} & F_{1717} & F_{1718} & F_{1719} & F_{1720} & F_{1721} \\
0 & F_{182} & F_{183} & F_{184} & F_{185} & F_{186} & F_{187} & F_{188} & F_{189} & F_{1810} & F_{1811} & F_{1812} & F_{1813} & F_{1814} & F_{1815} & F_{1816} & F_{1817} & F_{1818} & F_{1819} & F_{1820} & F_{1821} \\
0 & F_{192} & F_{193} & F_{194} & F_{195} & F_{196} & F_{197} & F_{198} & F_{199} & F_{1910} & F_{1911} & F_{1912} & F_{1913} & F_{1914} & F_{1915} & F_{1916} & F_{1917} & F_{1918} & F_{1919} & F_{1920} & F_{1921} \\
0 & F_{202} & F_{203} & F_{204} & F_{205} & F_{206} & F_{207} & F_{208} & F_{209} & F_{2010} & F_{2011} & F_{2012} & F_{2013} & F_{2014} & F_{2015} & F_{2016} & F_{2017} & F_{2018} & F_{2019} & F_{2020} & F_{2021} \\
0 & F_{212} & F_{213} & F_{214} & F_{215} & F_{216} & F_{217} & F_{218} & F_{219} & F_{2110} & F_{2111} & F_{2112} & F_{2113} & F_{2114} & F_{2115} & F_{2116} & F_{2117} & F_{2118} & F_{2119} & F_{2120} & F_{2121}
\end{array}\right)$$

Figures

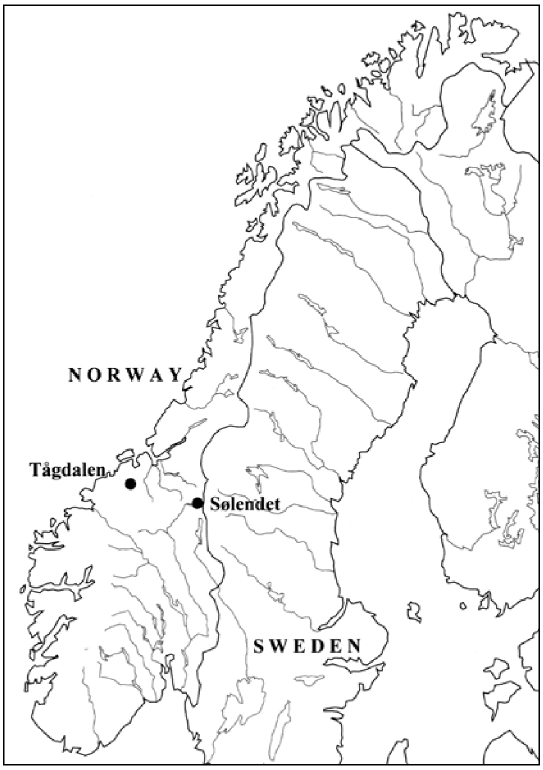

Fig. 1. The location of Sølendet and Tågdalen nature reserves.

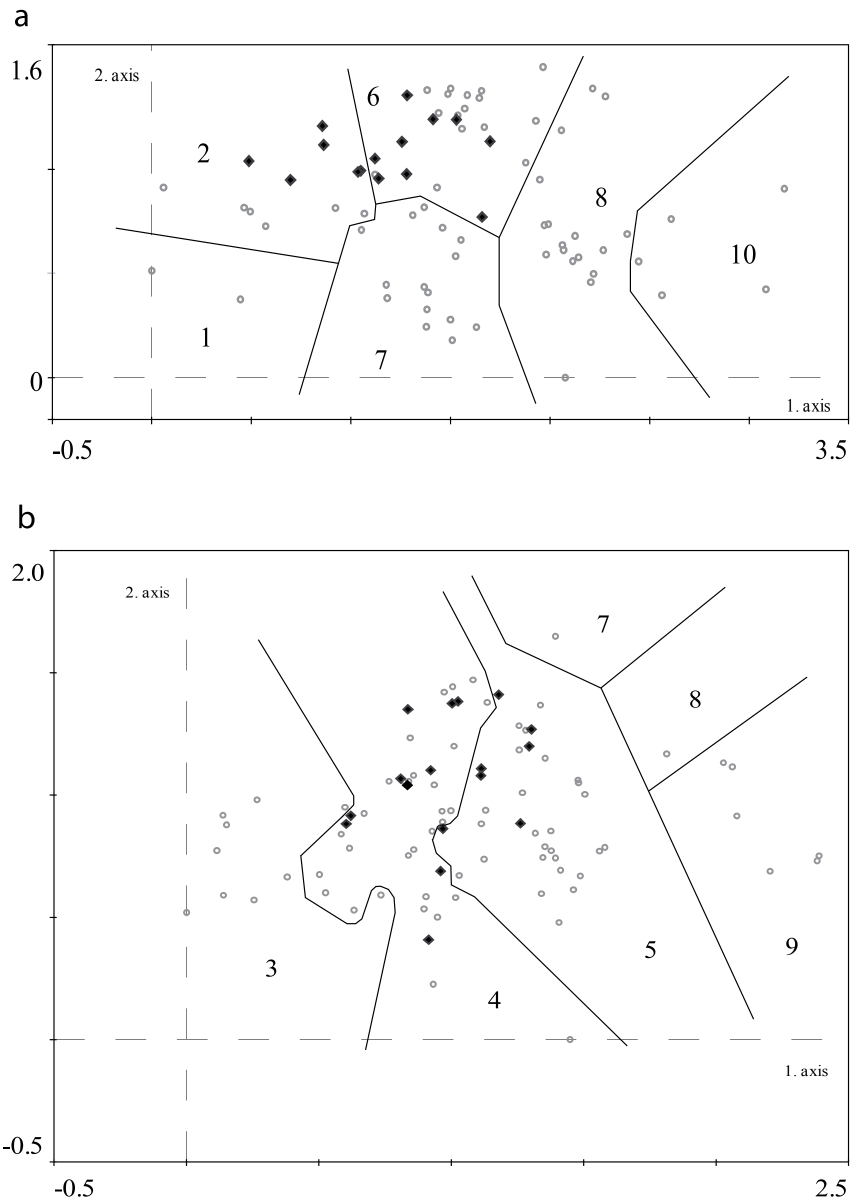

Fig. 2. DCA-ordination (axes 1 and 2) based on (a) 61 vegetation samples from Sølendet, and (b) 73 samples from Tågdalen (open circles) used to describe and classify the rich fen vegetation of the study areas (A. Lyngstad, A. Moen & D.-I. Øien unpublished data). The separation of plant communities and vegetation clusters 1-10 is based on this classification. Axis 1 reflects a wet – dry gradient (left to right) in both (a) and (b). The sample plots utilised in this paper are shown superimposed (black diamonds) and belong to fen carpet (cluster 2) and fen lawn (cluster 6) at Sølendet and fen lawn (clusters 4 and 5) at Tågdalen. Note the differences in scale.

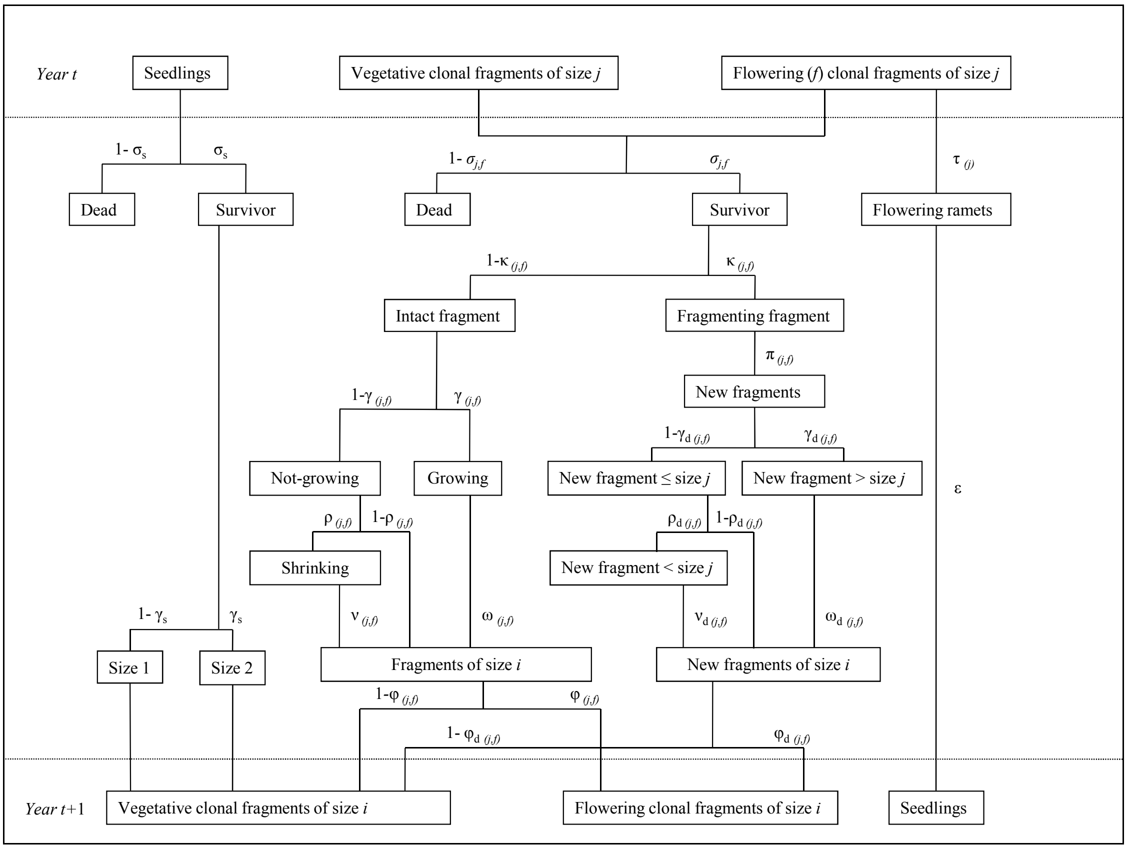

Fig. 3. A model of demographic processes and vital rates (see section 2.5 and Table 4 for details) affecting the transition of clonal fragments of size j in year t to clonal fragments of size i in year $t + 1$. The lines show the relationships between vital rates, with the ones positioned relatively lower conditional on those above. The subscript $_{(j,f)}$ denotes the assumed dependence of probabilities of vital rates on the clonal fragment size j at year t and on whether the fragment is vegetative or flowering *(f)*. Seedlings and intact and split clonal fragments follow separate pathways because they are assumed to have different probabilities of equivalent vital rates.

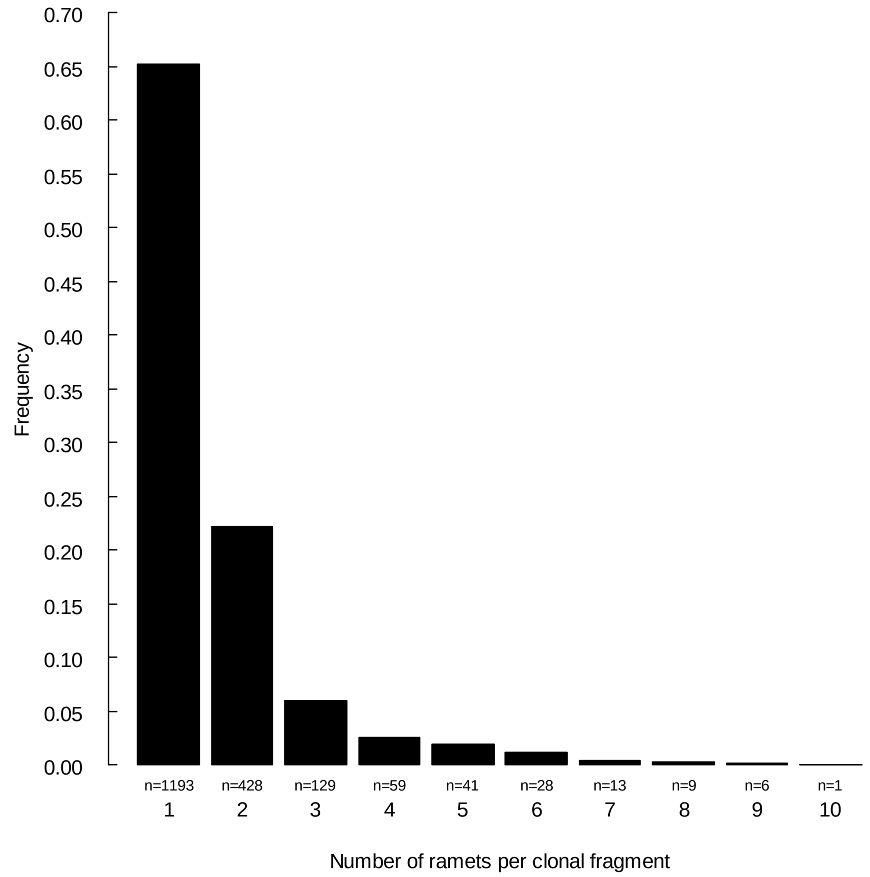

Fig. 4. Frequency of clonal fragments of size classes 1-10 in *E. latifolium* (2006-09), 44 seedlings are included in size class 1.

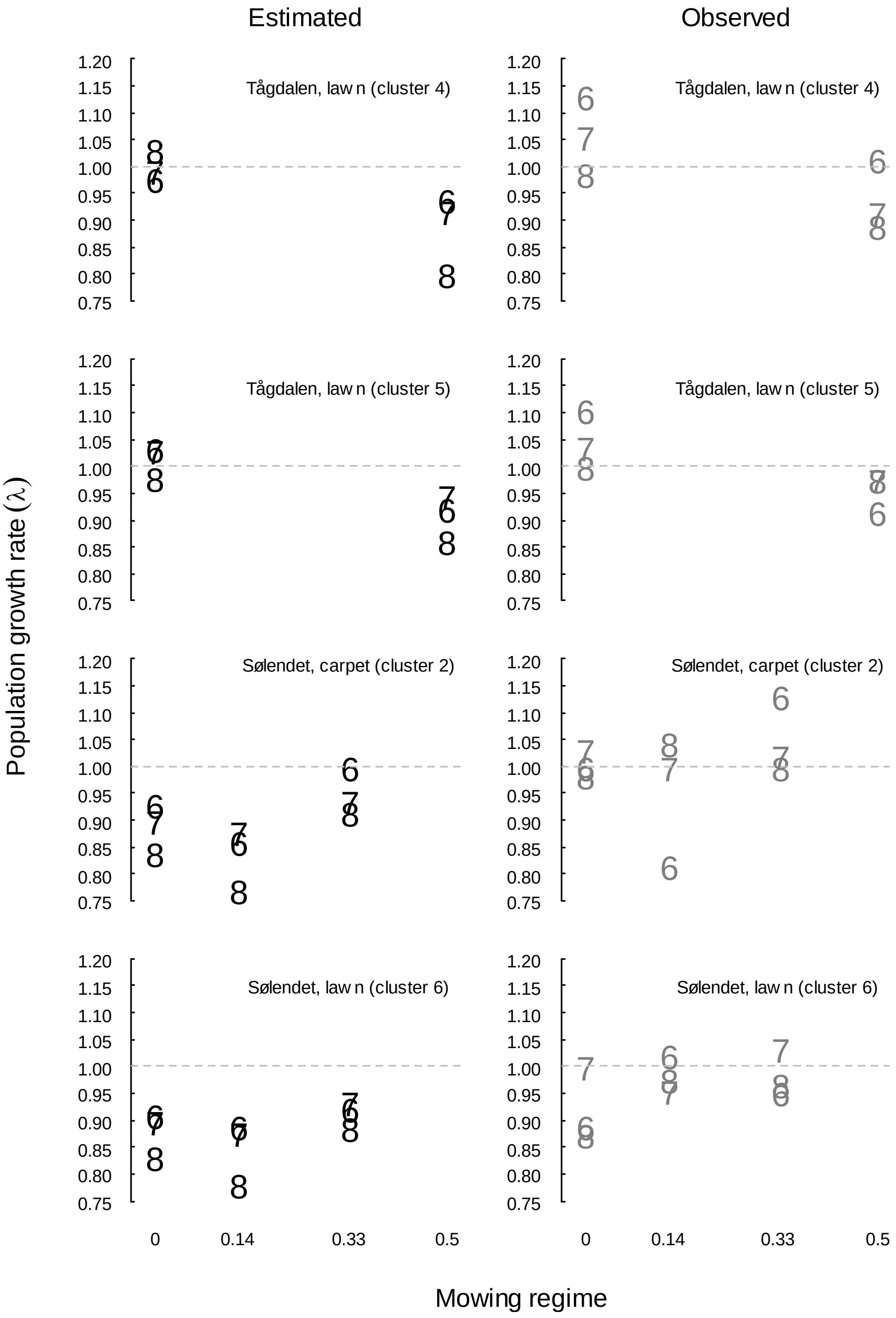

Fig. 5. Population growth rate estimated in transition population matrix models (left) compared with observed growth rate (right) for clonal fragments of *E. latifolium* in fen carpet and lawn vegetation in the study areas Tågdalen and Sølendet. 0 = unmowed, 0.14 = mowed extensively, 0.33 = mowed every 3rd year, 0.5 = mowed every 2nd year, 6 = transition 2006-07, 7 = transition 2007-08, 8 = transition 2008-09.

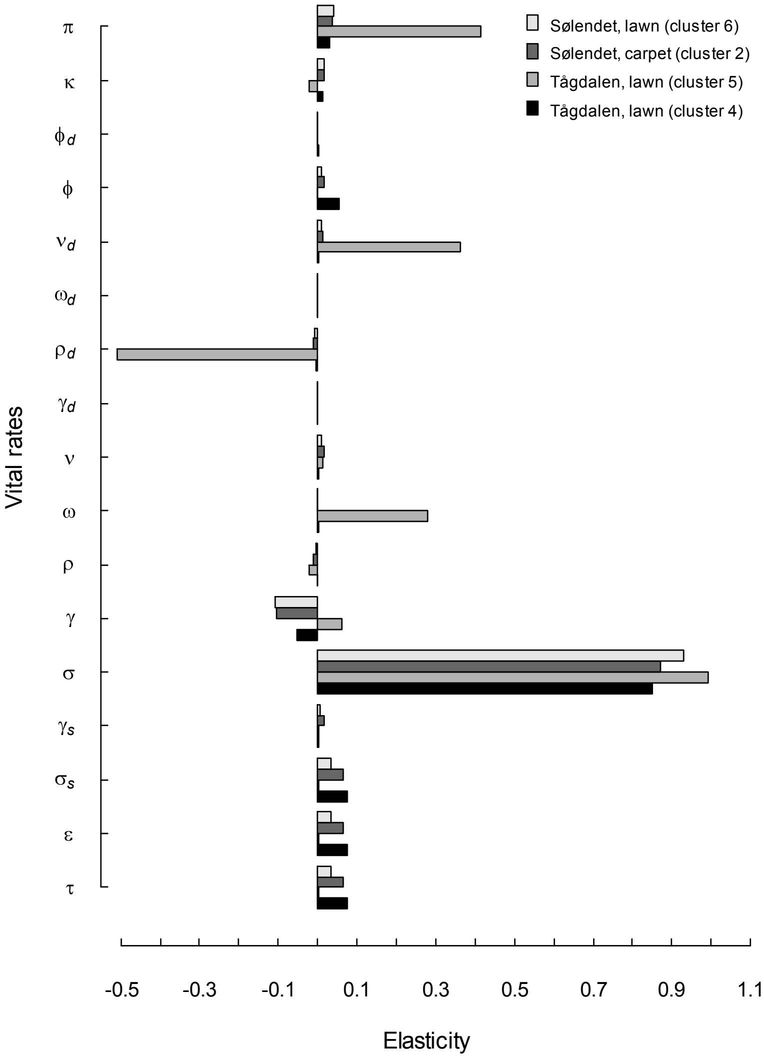

Fig. 6. Elasticities for 17 vital rates in three fen lawn and one fen carpet vegetation cluster. The elasticities were calculated based on matrices of unmowed situations for each vegetation cluster. The subscripts $_d$ and $_s$ denote vital rates related to split clonal fragments and seedlings respectively. The vital rates defining the probabilities of demographic processes were: fragmentation (κ), flowering (φ_d, φ), retrogression (ρ_d, ρ), growth (γ_d, γ, γ_s), survival (σ, σ_s) and the seedling establishment ratio (ε). The vital rates dealing with the outcome of demographic processes (conditional on probabilities) were: how many new fragments arise from fragmentation (π_j), how large retrogressing clonal fragments become (ν_d, ν), how large growing clonal fragments become (ω_d, ω), and how many flowering ramets each flowering fragment contains at year t (τ). See also Fig. 4.

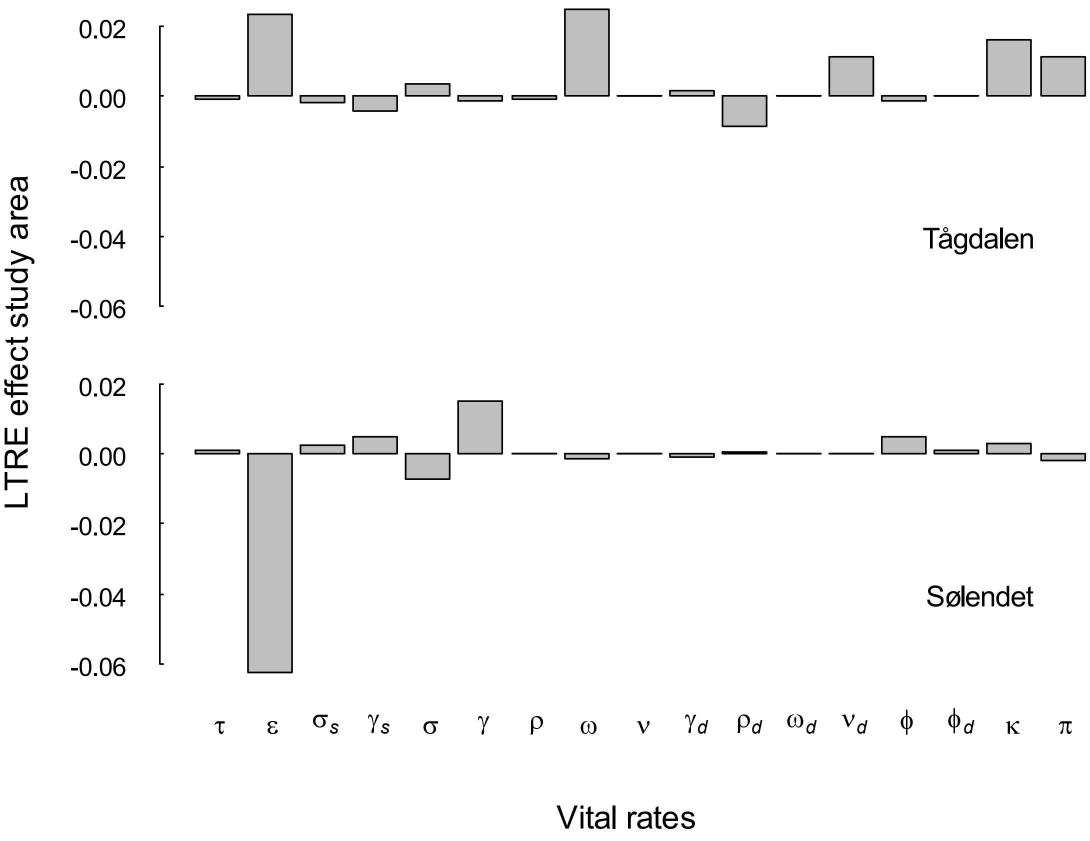

Fig. 7. Decomposition (LTRE) of the differences in population growth rate between the study areas into contributions from each vital rate. The comparisons were made between the unmowed matrix for each study area and the mean unmowed matrix (reference matrix). Vital rate definitions as in Fig. 6.

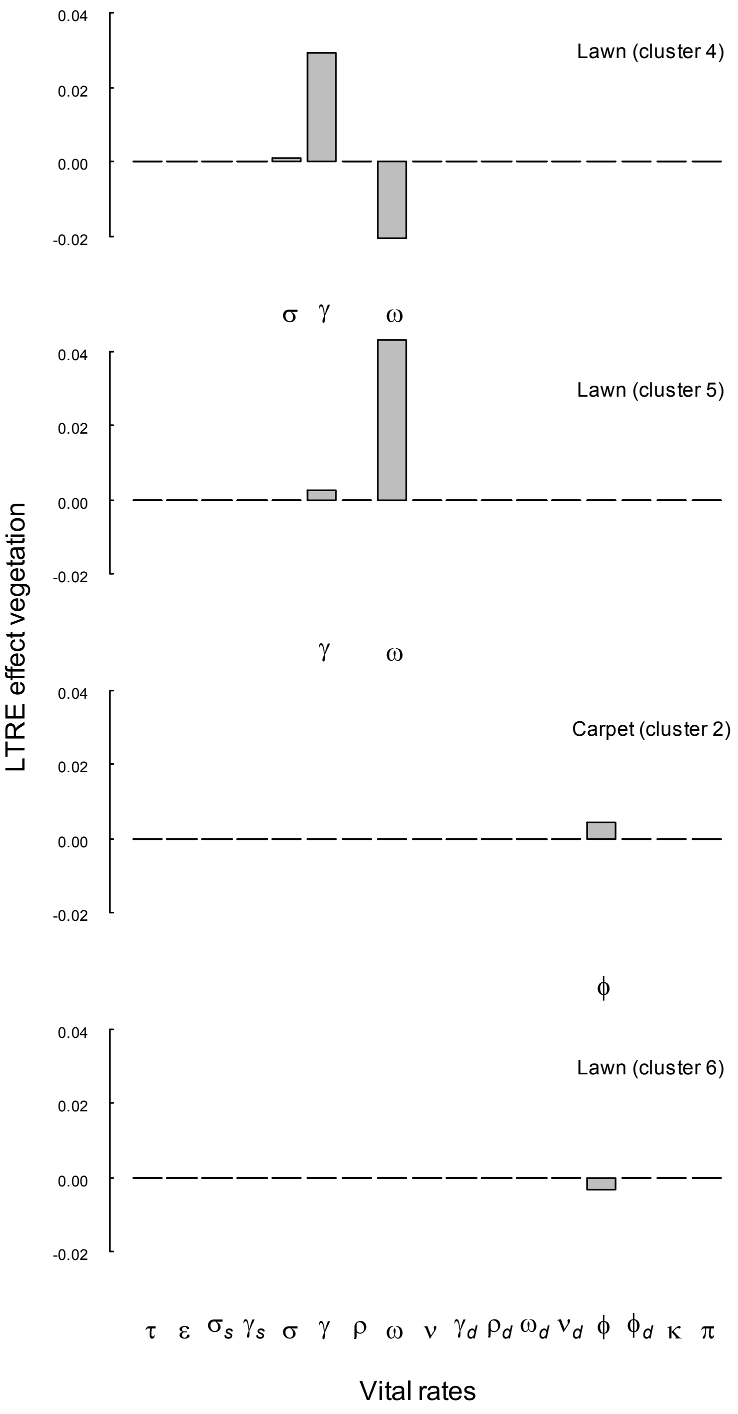

Fig. 8. Decomposition (LTRE) of the differences in population growth rate between fen carpet and lawn vegetation clusters within the study areas into contributions from each vital rate. The comparisons were made between the unmowed matrix for each vegetation cluster and the appropriate mean unmowed matrix for the study areas (reference matrix). Vital rate definitions as in Fig. 6.

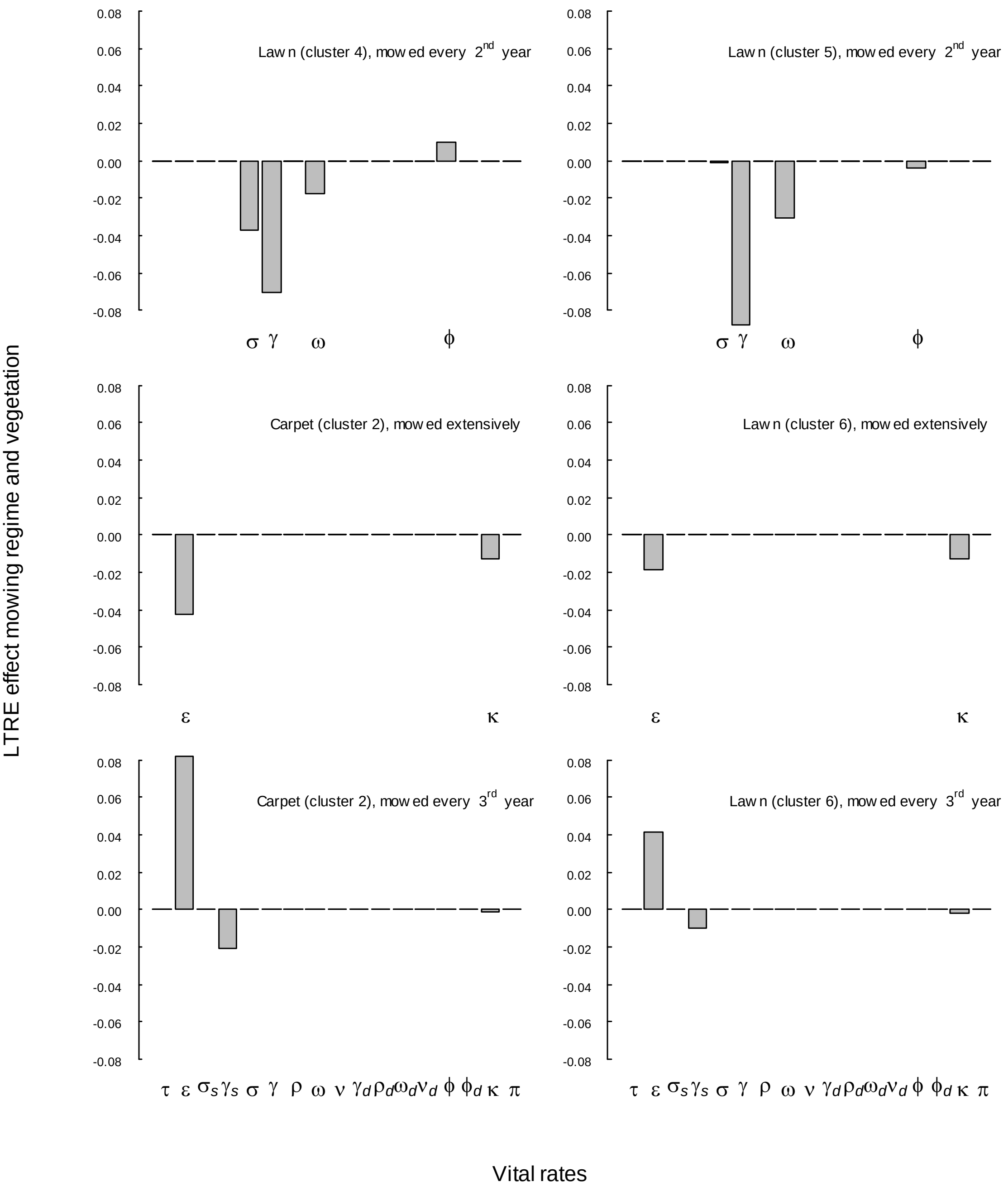

Fig. 9. Decomposition (LTRE) of the differences in population growth rate between unmowed and mowed situations within fen carpet and lawn vegetation clusters into contributions from each vital rate. The comparisons were made between the appropriate mowed matrices and the mean unmowed matrix for each vegetation cluster (reference matrix). Vital rate definitions as in Fig. 6.

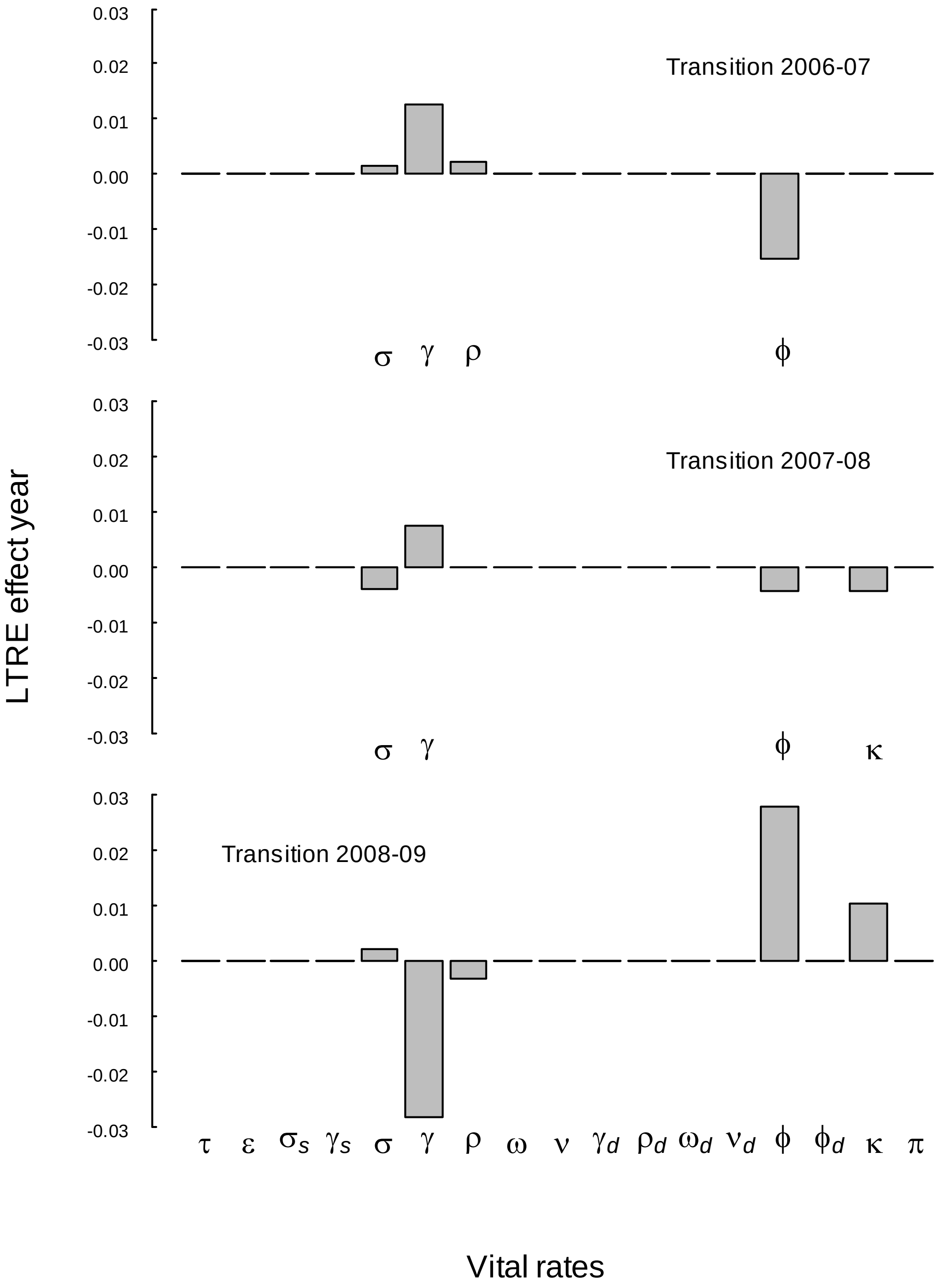

Fig. 10. Decomposition (LTRE) of the differences in population growth rate between transitions into contributions from each vital rate. The comparisons were made between the unmowed matrices for each transition and the mean unmowed matrix (reference matrix). Vital rate definitions as in Fig. 6.

Supplementary material

Summarising minimal adequate models for vital rate elements in two study areas

The minimal adequate models for 17 vital rates with the (quasi-) distribution and link-function applied for each model, dispersion parameter (d.p.), number of observations, which fixed factors and interactions were included, their estimates (+/- se) and p- or t-values. In a model with significant effects of all factors, the intercept (*I*) is based on vegetative clonal fragments in unmowed plots for the transition 2006-07 for both study areas, and vegetation cluster 2 at Sølendet and vegetation cluster 4 in Tågdalen. Effects of factors and interactions are shown with estimates +/- se in $\log_e$ (zero-truncated Poisson and negative binomial distribution) or logit transformed scale (binomial distribution). I = intercept, f_1 = flowering, $m_{0.14}$ = mowed extensively, $m_{0.33}$ = mowed every 3rd year, $m_{0.5}$ = mowed every 2nd year, v_5 = vegetation cluster 5, v_6 = vegetation cluster 6, x = number of ramets, y_{07} = transition 2007-08, y_{08} = transition 2008-09.

Demographic process	**Distribution and link-function**	**d.p.**	**n**	**Study area**	**Factors and interactions**	**Estimates +/- se and p- or t-values**
Survival probability from year t to year $t + 1$ of clonal fragments with one or two ramets (σ_j)	quasibinomial, logit	2.62	660	Sølendet	$I + f + x$	I(-0.88, +/- 1.84, p = 0.633) + f_1(-4.50, +/- 0.83, p < 0.001) + x(4.01, +/- 1.79, p = 0.025)
	binomial, logit	0.82	445	Tågdalen	$I + f + m + v + y + v{:}y$	I(4.41, +/- 0.69, p < 0.001) + f_1(-5.07, +/- 1.14, p < 0.001) + $m_{0.5}$(-1.73, +/- 0.56, p = 0.002) + v_5(-0.91, +/- 0.74, p = 0.221) + y_{07}(-0.44, +/- 0.63, p = 0.488) + y_{08}(-1.12, +/- 0.62, p = 0.069) + $v_5{:}y_{07}$(-0.21, +/- 0.90, p = 0.819) + $v_5{:}y_{08}$(2.38, +/- 1.30, p = 0.066)

Demographic process	**Distribution and link-function**	**d.p.**	**n**	**Study area**	**Factors and interactions**	**Estimates +/- se and p- or t-values**
Fragmentation probability between year t and year $t+1$ of surviving clonal fragments (κ_j)	binomial, logit	0.66	481	Sølendet	$I + m + y + x + m{:}y$	$I(-5.37$, +/- 0.75, $p < 0.001) + m_{0.14}(1.72$, +/- 0.77, $p = 0.025) + m_{0.33}(1.07$, +/- 0.75, $p = 0.153) + y_{08}(0.32$, +/- 0.86, $p = 0.711) + x(1.17$, +/- 0.14, $p < 0.001) + m_{0.14}{:}y_{08}(-3.97$, +/- 1.41, $p = 0.005) + m_{0.33}{:}y_{08}(-0.24$, +/- 0.98, $p = 0.808)$
		0.60	439	Tågdalen	$I + f + y + x$	$I(-6.33$, +/- 0.76, $p < 0.001) + f_1(1.76$, +/- 0.69, $p = 0.011) + y_{08}(2.08$, +/- 0.61, $p = 0.001) + x(0.70$, +/- 0.12, $p < 0.001)$
Number of new clonal fragments at year $t+1$ emerging from each fragmenting clonal fragment (π_j)	zero-truncated Poisson, log	-	60	Sølendet	I	$I(0.66$, +/- 0.10, $t = 6.36)$
		-	29	Tågdalen	I	$I(0.77$, +/- 0.14, $t = 5.53)$
Growth probability in surviving and intact clonal fragments (γ_j)	binomial, logit	1.02	641	Sølendet	$I + x + y$	$I(-2.92$, +/- 0.32, $p < 0.001) + x(0.31$, +/- 0.11, $p = 0.005) + y_{07}(0.17$, +/- 0.35, $p = 0.623) + y_{08}(0.99$, +/- 0.30, $p = 0.001)$
		0.99	612	Tågdalen	$I + m + v + x + m{:}v + m{:}x + v{:}x$	$I(-3.54$, +/- 0.45, $p < 0.001) + m_{0.5}(1.96$, +/- 0.49, $p < 0.001) + v_5(2.15$, +/- 0.52, $p < 0.001) + x(0.77$, +/- 0.22, $p = 0.001) + m_{0.5}{:}v_5(-1.40$, +/- 0.46, $p = 0.002) + m_{0.5}{:}x(-0.63$, +/- 0.23, $p = 0.006) + v_5{:}x(-0.48$, +/- 0.23, $p = 0.033)$
Growth probability in surviving and fragmented clonal fragments (γ_{dj})	binomial, logit	1.04	59	Sølendet	I	$I(-2.93$, +/- 0.59, $p < 0.001)$
		-	36	Tågdalen	-	-
Retrogression probability in surviving, intact and non-growing clonal fragments (ρ_j)	binomial, logit	0.82	173	Sølendet	$I + f + y$	$I(-3.86$, +/- 0.72, $p < 0.001) + f_1(4.38$, +/- 0.71, $p < 0.001) + y_{07}(1.35$, +/- 0.76, $p = 0.073) + y_{08}(2.07$, +/- 0.82, $p = 0.011)$
		0.96	160	Tågdalen	$I + f + y$	$I(-3.32$, +/- 0.80, $p < 0.001) + f_1(3.74$, +/- 0.79, $p < 0.001) + y_{07}(0.54$, +/- 0.93, $p = 0.5627) + y_{08}(1.81$, +/- 0.87, $p = 0.038)$
Retrogression probability in surviving, fragmented and non-growing clonal fragments (ρ_{dj})	binomial, logit	1.04	53	Sølendet	I	$I(2.06$, +/- 0.43, $p < 0.001)$
		1.00	36	Tågdalen	I	$I(2.83$, +/- 0.73, $p < 0.001)$

Demographic process	Distribution and link-function	d.p.	n	Study area	Factors and interactions	Estimates +/- se and p- or t-values
How much a surviving, intact and growing clonal fragment grows (ω_j)	zero-truncated Poisson, log	-	78	Sølendet	$I + x$	I(0.29, +/- 0.14, t = 2.10) + x(0.35, +/- 0.05, t = 7.21)
		-	119	Tågdalen	$I + m + v + x + m{:}x$	I(0.25, +/- 0.21, t = 1.21) + $m_{0.5}$(-0.13, +/- 0.13, t = -1.04) + v_5(0.35, +/- 0.23, t = 1.52) + x(0.42, +/- 0.07, t = 6.32) + $m_{0.5}{:}x$(-0.17, +/- 0.07, t = -2.37)
How much a surviving, fragmented and growing clonal fragment grows (ω_{dj})	zero-truncated Poisson, log	-	3	Sølendet	-	-
		-	0	Tågdalen	-	-
How much a surviving, intact and non-growing clonal fragment shrinks (v_j)	zero-truncated Poisson, log	-	32	Sølendet	$I + y$	I(0.98, +/- 0.23, t = 4.23) + y_{07}(-1.26, +/- 0.45, t = -2.78) + y_{08}(-0.96, +/- 0.45, t = -2.14)
		-	24	Tågdalen	$I + f$	I(0.47, +/- 0.25, t = 1.90) + f_1(-2.11, +/- 1.01, t = -2.08)
How much a surviving, fragmented and non-growing clonal fragment shrinks (v_{dj})	zero-truncated Poisson, log	-	47	Sølendet	$I + x$	I(-1.66, +/- 0.46, t = -3.60) + x(0.35, +/- 0.07, t = 5.28)
		-	34	Tågdalen	$I + x$	I(-1.55, +/- 0.61, t = -2.53) + x(0.33, +/- 0.10, t = 3.26)
Flowering probability at year $t + 1$ of surviving and intact clonal fragments (φ_j)	binomial, logit	1.05	641	Sølendet	$I + f + v + x + y + f{:}x + v{:}y$	I(-2.98, +/- 0.37, p < 0.001) + f_1(1.46, +/- 1.25, p = 0.24) + v_6(-2.19, +/- 0.79, p = 0.006) + x(0.74, +/- 0.14, p < 0.001) + y_{07}(-1.10, +/- 0.51, p = 0.033) + y_{08}(-0.08, +/- 0.40, p = 0.83) + $f_1{:}x$(-0.79, +/- 0.38, p = 0.04) + $v_6{:}y_{07}$(2.22, +/- 1.02, p = 0.029) + $v_6{:}y_{08}$(1.72, +/- 0.91, p = 0.060)
		0.85	612	Tågdalen	$I + m + x + y + m{:}y$	I(-4.42, +/- 0.68, p < 0.001) + $m_{0.5}$(1.77, +/- 0.75, p = 0.018) + x(0.37, +/- 0.11, p = 0.001) + y_{07}(0.74, +/- 0.73, p = 0.312) + y_{08}(1.26, +/- 0.70, p = 0.072) + $m_{0.5}{:}y_{07}$(-1.90, +/- 0.92, p = 0.040) + $m_{0.5}{:}y_{08}$(-2.20, +/- 0.88, p = 0.013)
Flowering probability at year $t + 1$ of surviving and fragmented clonal fragments (φ_{dj})	binomial, logit	1.03	60	Sølendet	I	I(-2.40, +/- 0.47, p < 0.001)
		0.54	37	Tågdalen	I	I(-3.86, +/- 1.13, p = 0.001)

Demographic process	Distribution and link-function	d.p.	n	Study area	Factors and interactions	Estimates +/- se and p- or t-values
Mean number of flowering ramets at year t in flowering clonal fragments (τ_j)	zero-truncated Poisson, log	-	65	Sølendet	$I + x$	$I(-4.47, +/- 1.26, t = -3.55) + x(0.56, +/- 0.18, t = 3.11)$
		-	35	Tågdalen	-	-
Seedling establishment probability as seedlings m^{-2} at year $t + 1$ / flowering ramets m^{-2} at year t (ε)	negative binomial, log	-	42	Sølendet	$I + m$	$I(-0.54, +/- 0.47, p = 0.25) + m_{0.14}(-1.25, +/- 0.77, p = 0.106) + m_{0.33}(1.05, +/- 0.58, p = 0.073)$
		-	63	Tågdalen	I	$I(1.09, +/- 0.38, p = 0.004)$
Survival probability of seedlings (σ_s)	binomial, logit	-	21	Sølendet	-	-
		1.00	23	Tågdalen	I	$I(2.35, +/- 0.74, p = 0.002)$
Probability of surviving seedlings to grow to size 2 at year $t + 1$ (γ_s)	binomial, logit	1.12	19	Sølendet	$I + m$	$I(4.53 \times 10^{-18}, +/- 0.82, p = 1.000) + m_{0.33}(-2.49, +/- 1.32, p = 0.060)$
		1.00	21	Tågdalen	I	$I(-2.25, +/- 0.74, p = 0.003)$

Paper IV

Effects of mowing and climate on flowering in *Eriophorum latifolium* in boreal rich fens, results from long-term monitoring

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Summary

The relationship between flowering density in *Eriophorum latifolium*, mowing and climatic variables in boreal rich fens in central Norway was investigated. Time series (1982-2008) of flowering density (number of flowering ramets m^{-2}) in 126 plots in the study areas Tågdalen (oceanic climate) and Sølendet (continental climate) nature reserves were analysed using an autoregressive model. This modelling approach allowed a simultaneous assessment of the relative impact of mowing and flowering at year t - 1 and direct (year t) and indirect (year t - 1) climatic effects on flowering density. The short-term effect of mowing was a reduction in flowering density due to reduced resource storage. This was contrasted by a positive long-term effect of mowing on both mean and trend in flowering density, highlighting the need for long-term monitoring to assess long-term phenomena. Cost of reproduction was the most influential of the factors affecting flowering density, and it impacted flowering negatively in all flowering time series. The population in the oceanic study area was more sensitive to climatic variables than that in the continental study area. This was likely because of larger year-on-year variations in precipitation in the oceanic area, and partly because of local topographical and hydrological differences that rendered the population at Tågdalen more susceptible to climatic variation. Warm conditions in spring were optimal for plant development, and were positively correlated with flowering density in both study areas. Drought in summer year t - 1 affected flowering density in south-facing, steeply sloping fens at Tågdalen negatively, while inundation in spring year *t* - 1 was adverse at Sølendet. A long growing season in year *t* - 1 at Tågdalen enabled increased resource acquisition and subsequent increased flowering density.

Key words: flowering density, cost of reproduction, management, effective temperature sum, precipitation, time series, autocorrelation, oceanic, continental

Introduction

Traditional hay production by mowing has ceased in outlying lands in Europe over the last century (Emanuelsson 2009). This has led to successional changes in several meadow (Losvik 1988, Hansson & Fogelfors 2000) and fen vegetation types (Moen 1990, Diemer et al. 2001), where low-growing species are encroached upon by shrubs, tall herbs and grasses. Flowering is a fundamental aspect of the life history in vascular plants, contributing to the long-term survival of plant populations through genetic recombination and recruitment of genets (Crawley 1997b). Many grassland and fen species are well adapted to the disturbance caused by traditional mowing, and show a decrease in flowering when mowing ceases, and an increase when mowing is reintroduced. Conversely, species that are less adapted to disturbance benefit when mowing ceases, but their flowering density (number of flowering ramets m^{-2}) declines when they are subject to mowing again (Moen et al. 1999). Woody plants and tall-growing herbs with their elevated positioning of meristems and large proportion of biomass above the stubble are vulnerable to mowing, also in terms of flowering. Less apparent is the decline in flowering in the relatively low-growing boreal grassland and fen orchids *Gymnadenia conopsea* and *Dactylorhiza lapponica* in mowed compared to unmowed areas (Øien & Moen 2002), or the increase in flowering in the rosette plant *Succisa pratensis* after abandonment in fens in Scandinavia and central Europe (Moen et al. 1999, Billeter et al. 2003). Increased flowering due to mowing can be exemplified by *Primula veris* and *P. vulgaris* in grassland vegetation in Belgium (Brys et al. 2004, Endels et al. 2007), and *Nigritella nigra*, a rare orchid in boreal grasslands and fens where abandonment affects flowering negatively and recommencement of mowing increases flowering density (Moen & Øien 2003).

Clearly, the outcome of mowing on flowering depends on the species, but it also depends on the productivity of the vegetation, and both the frequency and timing of mowing. Plants compensate faster in more productive habitats, and higher productivity requires shorter mowing intervals to achieve the same effects from mowing (Buttler 1992, Wilson & Clark 2001, Oostermeijer et al. 2002, Øien & Moen 2002, Jantunen et al. 2007). Studies of above- and below-ground biomass in boreal rich fen has shown that biomass values are lower with mowing every year than every 2nd year (Aune et al. 1994, 1996). There is, however, no indication of depletion of soil nitrogen or phosphorus as a result of mowing in boreal rich fen, and the reduced biomass in regularly mowed areas is regarded as mainly a result of disturbance by mowing rather than stress by nutrient limitation (Øien & Moen 2001). The majority of boreal grassland and fen species flower between May and August, and early mowing (before August) has been shown to generally reduce flowering compared to mowing late in the season (Losvik 1991, Jantunen et al. 2007). The short- and long-term effects of mowing may differ. In the present context, we define short-term mowing effects to be those affecting flowering the same year or the year after mowing through disturbance (Crawley 1997a). Mowing may affect flowering density adversely in the short run through damage or removal of biomass (stored resources), but the long-term effects may be positive for stress-tolerant species when competition is reduced (Grime 2001).

Evidence as to whether plants generally have to grow larger than a certain size to be able to flower (as shown by e.g. Werner (1975) and Worley & Harder (1996)) or if no such size threshold exists (e.g. Ohlson 1988) has been conflicting. A recent review concludes that both strategies are common, and also that a linear relationship between plant size and investment in sexual reproduction is common in perennial herbs and graminoids (Weiner et al. 2009). A size threshold implies that plants invest all available resources in growth and survival up to a certain point, and this can be viewed as a sign of cost of reproduction. A trade-off between current sexual reproduction on one hand, and survival, growth and/or future reproduction on the other hand is commonly believed to exist in vascular plants (Crawley 1997a), and this cost of reproduction can be considerable (Calvo & Horvitz 1990, Ashman 1994, Ehrlén & Eriksson 1995). The negative impact of flowering in year *t* - 1 on flowering in year *t* in *Sanicula europaea* (Inghe & Tamm 1985, 1988) and *Dactylorhiza lapponica* (Øien & Moen 2002) can be interpreted as a result of cost of reproduction. Thus, the cost of reproduction may obscure the short-term effects of mowing on flowering density through the effects on flowering in year *t* - 1.

Varying climatic conditions may also counteract or enhance the short-term effects of mowing. The climatic variables assumed to be most important for flowering are the length of the growing season, temperature and precipitation. The length of the growing season increases biomass production in arctic vegetation zones (Hudson & Henry 2009), higher temperature affects the flowering density of orchids in the northern boreal vegetation zone (Blinova 2008) and of *Primula scotica* in Scotland (Bullard et al. 1987). The effective temperature sum correlates well with the growth of plants in boreal zones (Bronson et al. 2009) and flowering density in *Dactylorhiza lapponica* in boreal rich fens (Øien & Moen 2002). Both the length of the growing season and the effective temperature sum can be expected to correlate positively with resource acquisition and, ultimately, flowering density. Summer drought has been shown to be detrimental to flowering the next year in three species in meadow vegetation (Inghe & Tamm 1985, 1988). Drought is probably negative in dry fen vegetation like hummock, but may be positive or have no effect in wet fen vegetation like carpet. Waterlogging is the contrast to drought, and can be assumed to have opposite effects on flowering. Flowering in *Betula nana* in bog vegetation is negatively affected by waterlogging (Ejankowski 2008). Waterlogging can occur because of heavy rainfall or snowmelt, and elevated rain and snowfall levels may be negatively correlated with flowering. It may also be more important in an oceanic climate with plentiful precipitation (Crawford 2000). Winter snowfall determines snow depth, and Blinova (2008) reported negative (four species) and positive (two species) effects of snow depth on flowering in orchids on the Kola Peninsula. Flowering in *Primula scotica* in Scotland was negatively correlated with snow cover and number of days with snowfall (Bullard et al. 1987). However, snow depth has also been shown to correlate positively with flowering in two species of

Delphinium in the Rocky Mountains due to protection from cold spells in spring (Inouye et al. 2002, Saavedra et al. 2003).The reported effects of snow cover shows there is no conclusive pattern; it may result in waterlogged conditions during snowmelt, which can impact flowering negatively, but may also protect sprouting plants from cold spells in spring.

Flowering density is likely to depend on the climatic conditions and the amount of stored resources available to the plant. These resources are, in turn, dependent on the vegetation, mowing regime, climatic conditions and flowering in earlier years. This implies that climate may affect flowering through two separate pathways, either directly through its impact on flower development, or indirectly through its effect on biomass production in the previous growing season. Our aim is to quantify the short- and long-term effects of different mowing regimes on flowering in *Eriophorum latifolium* Hoppe, a common species in boreal rich fen, and whether these effects vary along a wet – dry gradient in two study areas with continental and oceanic climate respectively. We further aim to find the relative importance of cost of reproduction, identify the climatic variables affecting flowering density directly and indirectly, quantify the contribution of the most important climatic variables, and assess how short- and long-term effects of mowing, climate and cost of reproduction combined explain the variation in flowering density between years.

Both drought and waterlogging can impact flowering density negatively, and we hypothesise an intermediate state to be optimal for flowering density. The groundwater level depends on topography and climate, and we propose that wet and dry summers affect flowering in *E. latifolium* differently along the wet – dry gradient. Furthermore, the impact of climatic variables can be assumed to change along the oceanity gradient represented by our study areas. Evapotranspiration may mitigate or counteract the effects of high precipitation, or lead to drought when precipitation is low. The cool climate of our study areas makes these scenarios less probable, and we assume that the effects of precipitation will balance those of evapotranspiration during the growing season. We further hypothesise a positive relationship between winter precipitation and flowering in a continental climate with limited snowfall, and a negative relationship in an oceanic climate with copious snowfall. A comprehensive assessment of climatic trends in the Baltic Sea Basin (including Norway) in the period 1871-2004 documented an increase in the annual and seasonal mean temperatures from 1970 to the present (The BACC Author Team 2008). Long-term studies of the phenology of flowering have shown that rising global temperatures have advanced the onset of flowering in spring in several plant species over the last decades (e.g. Hughes 2000, Menzel et al. 2006, Bertin 2008). The effect of warming is species dependent (Sandvik et al. 2004), and may also vary between populations (Blinova 2008), but we expect an analogous positive relationship between the effective temperature sum and flowering density in our study areas over this period.

The effects of mowing and climate on flowering in *E. latifolium* were investigated in two study areas in central Norway where flowering density has been recorded annually in permanent plots for up to 27 years (1982-2008). We analyse these flowering time series using an autoregressive model with standardised climatic variables and mowing included as covariables. These analyses are based on, and the results interpreted in terms of, a conceptual model relating flowering density to the amount of stored resources in the local populations of *E. latifolium*. Long-term effects of mowing and differences in flowering density among community groups and study areas are evaluated by comparing time series characteristics as well as parameter estimates from the autoregressive analyses using generalised linear models.

Materials and methods

STUDY SPECIES

Eriophorum latifolium is a rich fen and spring species growing in areas with base-rich peat with pH most often in the range 5.5-7.5 and electrical conductivity in surface water mostly above 100 µS (Kutschera et al. 1982, Moen 1990, Petraglia & Tomaselli 2003). It is widely distributed throughout Europe (Hultén & Fries 1986), reaching 2100 m a.s.l. in the Alps (Jäger et al. 1965) and 1120 m a.s.l. in Norway (Elven 2005), where it is rather common in boreal areas up to the climatic forest limit. In Norway, *E. latifolium* may be locally abundant or dominant in open lawn communities of sloping fens formerly used for production of hay.

E. latifolium has perennial clonal fragments typically consisting of one to three (occasionally up to ten) ramets connected with rhizomes (A. Lyngstad, unpublished data). Each mother ramet can produce 1-4 daughter ramets, and the species forms loose tufts. New rhizomes emerge from below-ground leaf axils (Raunkiær 1895), the rhizome is short, and the new ramet typically remains within 5 cm of its mother ramet. Roots are mostly 10-20 cm long, and in rich fen in Fennoscandia they normally extend down to 10 cm, occasionally to 20 cm (Metsävainio 1931). Flowering ramets lack a basal rosette and are on average 40 cm tall with four spikelets in the inflorescence (A. Lyngstad, unpublished data). The ramets die after flowering because the apical meristems are consumed when the ramets flower (Jónsdóttir & Watson 1997). Induction of flower primordia has been shown to depend on either low temperatures or short day length in four boreal or alpine species of *Carex* (Heide 2002). We assume similar requirements in *E. latifolium*, i.e. that apical meristems transform into floral meristems some time during late autumn or winter. The seeds are about 1.5 mm long with a 100-seed weight of 0.04 g (Kutschera et al. 1982), and have attached numerous, up to 25 mm long, cotton-like bristles that facilitate wind dispersal (Tutin et al. 1980, Elven 2005, Vrijdaghs et al. 2005). This trait is shared with the closely related *E. angustifolium*, which is among the wetland plants best adapted to wind dispersal, and whose seeds can travel several kilometres (Grime 2001, Soons 2006). Similar dispersal distances can be expected in *E. latifolium*. The species flowers in early to mid summer (June or early July in our study areas), and seeds ripen and spread in late summer (late July and August). The density of *E. latifolium* ramets is higher in mowed than unmowed fen areas (92 m^{-2} and 35 m^{-2}, respectively), and this pattern is also seen for above-ground biomass (21.3 and 14.7 g/m^2) and below-ground biomass (29.1 and 24.4 g/m^2) (Aune et al. 1996). Thus, the total biomass and root/shoot (biomass) ratio is higher in mowed than unmowed areas, but the weight of individual ramets is lower in mowed areas.

STUDY AREAS

The study was conducted at Sølendet and Tågdalen (with surroundings), two nature reserves situated 145 km apart in central Norway (Table 1, Fig. 1). Extremely rich fen vegetation (sensu Sjörs 1948, 1952) formerly used for haymaking covers substantial areas in both nature reserves, a type of vegetation considered near threatened (NT) in Norway due to overgrowing (Fremstad & Moen 2001). Mowing is currently implemented as a management tool in both areas to prevent encroachment. The study areas hold large populations of *E. latifolium*, and the annual flowering density in *E. latifolium* has been recorded to assess the effects of the management (Moen 1990, 2000). The study areas are situated at the transition between the middle boreal and northern boreal vegetation zones (Moen 1999). Tågdalen has an oceanic climate, while Sølendet has a more continental climate, and precipitation is markedly higher at Tågdalen than at Sølendet (Table 1). The variation in precipitation among years (1973-2008) is much higher at Tågdalen (968-2254 mm per year) than at Sølendet (471-862 mm per year). The growing season is from May to September in both study areas, and the effective temperature sums in May-July are similar, but August and September are warmer at Tågdalen than at Sølendet. There has been a significant increase in the annual effective temperature sum at Tågdalen (1973-2008), and Tågdalen now has a higher annual effective temperature sum than Sølendet. The mean length of the growing season (1980-2008) is 122 days at Sølendet and 127 days at Tågdalen. See Appendix S1 for further details concerning climatic conditions.

FLOWERING DENSITY, MOWING AND VEGETATION

Uninterrupted time series with annual counts of flowering ramets of *E. latifolium* in permanent plots stretch back to 1982 at Sølendet and 1983 at Tågdalen, with the majority commencing between 1982 and 1986 (Fig. 2). 126 flowering time series from Sølendet (67) and Tågdalen (59) with a total of 2879 observations of flowering density were included (Fig. 3). The standard area of a permanent plot was 12.5 m^2, but this varied between 4 m^2 and 25 m^2, and the count data were standardised to the number of flowering ramets per m^2. Counting was performed in July or early August, depending on the phenology in the study areas in different years. All flowering ramets were counted if the flowering density was below approximately 15 m^{-2}, or the distribution of ramets was markedly heterogeneous within plots. When the density exceeded 15 m^{-2}, the flowering density was estimated based on the density in the SW and NE corners of the plots. The plots were nested within localities with homogeneous vegetation (Moen 1990), and a typical locality had one mowed and one unmowed plot (but varied between one and nine). The annual flowering density from 1982 to 2008 is shown separately for each study area, and also as the overall mean in Fig. 4.

The mowing regimes were mowed every year, every 2nd year, every 4th year or unmowed (Fig. 2). Mowing was performed with a scythe in early August, after flowering in *E. latifolium*. Mowing every 2nd year and no mowing were common regimes in both study areas, whereas mowing every year was only applied at Sølendet, and mowing every 4th year was common only at Tågdalen. Mowing time series were constructed for each plot with mowing as a binomial factor for each year. The first years of observations after mowing recommenced were likely to be biased, and measurements of flowering density were included only after the third cycle of the assigned treatment was completed. All the time series included had 15 years or more of uninterrupted observations with the same mowing regime.

Three local vegetation gradients in mire vegetation are recognised and used in the Fennoscandian tradition of mire studies (e.g Tuomikoski 1942, Sjörs 1948, Du Rietz 1949, Ruuhijärvi 1960, Persson 1961, Eurola 1962, Malmer 1962, Moen 1990, Rydin & Jeglum 2006). The poor – rich gradient reflects the pH and mineral concentration, the mire expanse – mire margin gradient (often) reflects peat depth, and the hummock – mud bottom gradient reflects the groundwater level. In this study, the poor – rich fen gradient is only represented by rich (including extremely rich) fen vegetation, and the mire expanse – mire margin and hummock – mud bottom gradients are combined in a wet – dry gradient. The rich fen vegetation of Sølendet and Tågdalen was described and classified by A. Lyngstad, A. Moen & D.-I. Øien (unpublished data), and the vegetation resembles that of sloping rich fens described from northern Sweden (Persson 1961, 1962) and eastern Finland (Havas 1961). The 126 plots with flowering time series of *E. latifolium* belong to nine vegetation clusters that are part of six plant communities: *Eleocharis quinqueflora-Cinclidium* carpet, *Drosera anglica-Scorpidium scorpioides* carpet, *Eriophorum latifolium-Campylium* lawn, *Equisetum variegatum-Thalictrum-Campylium* lawn, *Gymnadenia-Succisa-Campylium* margin and *Galium boreale-Molinia-Hylocomiastrum pyrenaicum* margin. These plant communities were aggregated in three community groups, fen carpet, fen lawn (both fen expanse) and fen margin, for the purpose of this study (Table 2). The three community groups were separated along the wet – dry gradient, with carpet occurring in rather flat areas with deep peat, lawn mainly in sloping fens with a thinner peat layer, and margin most often with a very thin peat layer.

AN AUTOREGRESSIVE MODEL FOR FLOWERING

We propose a conceptual model where flowering density in *E. latifolium* in year t (f_t) depends on the amount of stored resources in the population when apical meristems transform into floral meristems ($r_{t\text{-}1}$) and a set of climatic factors affecting the development from flower initiation to mature inflorescences ($c1$) (Fig. 5). We further propose that r_t depends on $r_{t\text{-}1}$, f_t, allowing the possibility for a cost of reproduction, another set of climatic factors affecting the growth conditions during the growing season of year t ($c2_t$), and whether the plot is mowed or not in year t (m_t). According to this model, climate may affect flowering in two ways, either directly through its impact on flower development, or indirectly through its effect on production of biomass during the growing season, and thus the amount of stored resources when the flower meristems develop. Stored resources were not monitored in the permanent plots, so we attempt to eliminate r_t and $r_{t\text{-}1}$, and express flowering density through $c1_t$, m_t, $c2_t$ and f_t. The interactions between stored resources, mowing, two sets of climatic factors and flowering can thus be summarised in the following set of equations:

$$r_t = r_{t\text{-}1}\, g_1\,(m_t\,,\, c2_t\,, f_t) \qquad \text{eqn 1a}$$

$$f_t = r_{t\text{-}1}\, g_2\,(c1_t), \qquad \text{eqn 1b}$$

where the function g_1 describes the contribution to r_t from each unit of stored resources at t - 1, and the function g_2 describes the contribution to f_t from each unit of stored resources at t - 1. For simplicity we assume that both g_1 and g_2 are independent of $r_{t\text{-}1}$, which means that the fraction of resources allocated to flowering and the fraction allocated to vegetative growth are independent of $r_{t\text{-}1}$. Both equations (1a) and (1b) are multiplicative, so by transforming them to $\log_e$ scale and using Taylor expansion, they can be approximated by the following linear equations:

$$R_t = \alpha_0 + R_{t\text{-}1} + \alpha_1 M_t + \alpha_2 C2_t + \alpha_3 F_t \qquad \text{eqn 2a}$$

$$F_t = \beta_0 + R_{t\text{-}1} + \beta_1 C1_t \qquad \text{eqn 2b}$$

where $R_t = \log_e(r_t)$ and $F_t = \log_e(f_t)$, $M_t = \log_e(m_t + 1)$, $C1_t$ and $C2_t$ are linear combinations of $\log_e$-transformed climatic variables that affect flowering directly and indirectly respectively. Parameters $\alpha_0 - \alpha_3$ are associated with the factors affecting R_t, and parameters β_0 and β_1 are associated with the factors affecting F_t.

R_t and $R_{t\text{-}1}$ are still included in eqns 2a and 2b, so they are not useful for analysing the flowering density time series. However, R may be eliminated through substitutions and rearrangements of eqns 2a and 2b (see Appendix S2 for details), which as a result gives the following autoregressive model:

$$F_t = \alpha_0 + \beta_1 \Delta C1_t + \alpha_1 M_{t\text{-}1} + \alpha_2 C2_{t\text{-}1} + \omega F_{t\text{-}1} + \varepsilon_t, \qquad \text{eqn 3}$$

where $\Delta C1_t = C1_t - C1_{t\text{-}1}$, $\omega = (\alpha_3+1)$, and ε_t incorporates stochasticity and the remaining variance in flowering density not accounted for by the deterministic components of the model (assuming additive stochasticity on a $\log_e$ scale). Two implications of eqn 3 for the analysis of the flowering time series and its interpretation are as follows. First, $\log_e$-transformed climatic factors with direct effect on flowering should be entered with their Δ values. Second, autoregressive coefficients (ω) less than 1 (i.e. $\alpha_3 < 0$) indicate a cost of reproduction in *E. latifolium*.

CLIMATIC DATA

Spatially interpolated estimates of temperature and precipitation was provided by the Norwegian Meteorological Institute for both study areas. The method applied to estimate temperature was residual kriging, and for precipitation it was triangulation with terrain adjustment (Tveito et al. 2005). The target elevations used in these estimations were 460 m a.s.l. for Tågdalen and 725 m a.s.l. for Sølendet. The weather station closest to Tågdalen is Rindal, some 5 km east of the nature reserve. Brekken weather station 3-4 km southeast of Sølendet is the closest with precipitation measurements, and Røros 25 km southwest of Sølendet is the closest with temperature measurements (Øien & Moen 2003). Time series with temperature and precipitation data were defined from 1973 to 2008 at Tågdalen, and from 1974 to 2008 at Sølendet (Appendix S1). A model for the effective temperature sum (*ETS*) developed by Laaksonen (1979) for the boreal vegetation zone was used:

$$ETS = \sum_{n=a}^{b} T_m - 5^\circ, \qquad \text{eqn 4}$$

where T_m is the mean daily temperature, *a* is the third day in the first five-day period in spring with mean $T_m > 5$ °C and no snow cover, and *b* is the third day in the last five-day period in autumn with mean $T_m > 5$ °C and no snow cover. Thus, *ETS* incorporates both the duration and warmth of the growing season. The length of the growing season was defined as the period between *a* and *b* in this model, and was calculated for both study areas from 1980 to 2008 (Appendix S1).

We initially used one month time spans (Janečková et al. 2006) when constructing 24 candidate, climatic variables to be included in the autoregressive model. They were monthly precipitation May to December year *t* - 1 and January to June year *t*, monthly *ETS* May to September year *t* - 1 and May to June year *t*, aggregated *ETS* year *t* - 1, the length of the growing season year *t* - 1 and the start of the growing season year *t*, where *t* refers to the year the flowering density was measured. Correlations between each candidate climatic variable and each flowering time series were performed to identify the variables correlating with the highest number of time series (Table 3). Subsequent monthly precipitation or *ETS* variables with the same effect (positive or negative) on flowering were merged, and the seven most important climatic variables (four of which were merged) were used to construct the covariables *C*1 and *C*2 in the autoregressive model. The climatic variables included in *C*1 were *ETS* May - June$_t$ and precipitation

December - January$_t$. In *C*2 they were the length of the growing season *t* - 1, precipitation May - June$_{t\text{-}1}$, *ETS* July - September $_{t\text{-}1}$, precipitation in July$_{t\text{-}1}$ and precipitation in October$_{t\text{-}1}$ (Table 3). Note that *C*1 and *C*2 were separated on the turn of the month between November and December.

STATISTICAL ANALYSIS

The autoregressive model (eqn 3) was fitted to each of the 126 time series of flowering density from Sølendet and Tågdalen. The time series were log$_e$-transformed and detrended before analysis. The covariables were standardised to zero mean and unit variance, which enables a direct comparison of their relative effect on flowering density. The trend in flowering density for each time series was analysed with linear regression. In order to evaluate differences between study areas, community groups and mowing regimes (fixed factors) in the characteristics of the flowering time series, we used mean flowering density, trend (i.e. slope) in flowering density, and the estimated parameters obtained from fitting of the autoregressive model (eqn 3) as response variables in generalised linear models (GLM, McCulloch & Searle 2001). The minimal adequate models (i.e. most parsimonious) for all response variables were identified through stepwise exclusion of factors and interactions between factors (starting with full models) based on deviance tests (e.g. Jongman et al. 1995). The permanent plots were, however, nested in localities, so we also applied generalised linear mixed models (GLMM, Zuur et al. 2009) with locality as an additional, random factor to evaluate possible random effects in the design. For most response variables, the variance explained by locality was of the same magnitude as the variance among plots within localities (results not shown), and we concluded that locality could be removed from the models for all response variables except mean flowering density. All statistical analyses were conducted in the R statistical environment (R Development Core Team 2008), making use of the packages “gplots” (Warnes), “lattice” (Sarkar 2008), “lme4” (Bates et al. 2008), “MASS” (Venables & Ripley 2002) and “tseries” (Trapletti & Hornik 2009).

Results

FLOWERING DENSITY

The overall mean flowering density in *E. latifolium* (1982-2008) was 1.17 m^{-2} (126 time series, n = 2879). The density was higher in fen lawn than in the other community groups ($t > 2$ in both cases, Fig. 6), and also higher in plots mowed every 2nd and 4th year compared to unmowed plots and plots mowed every year ($t > 2$ in all cases, Fig. 6). There were no differences ($t < 2$) in the mean flowering density between Sølendet and Tågdalen. We refer to Appendix S3 for detailed comparisons of levels of factors or interactions of factors for the mean flowering density, the trend in flowering density, the short-term effect of mowing and the effect of climatic variables on flowering.

TRENDS IN FLOWERING DENSITY AND LONG-TERM EFFECTS OF MOWING

The overall trend in the flowering density was weakly positive at Sølendet and weakly negative at Tågdalen (Figs. 4 and 7), and the difference between the study areas was significant ($p = 0.009$). The trend was more positive in plots that were mowed every 2nd or 4th year compared to unmowed plots ($p = 0.045$ and $p = 0.016$). The trend was negative in unmowed plots and positive under all other mowing regimes, but there was considerable variation within the treatments, especially among plots mowed every 2nd or 4th year (Fig. 7).

SHORT-TERM EFFECT OF MOWING

The flowering density was negatively affected by mowing in the previous year in 47 out of 55 time series mowed every 2nd or 4th year (Fig. 8). This effect was similar for both study areas and all community groups ($p > 0.05$ in all comparisons), and was not demonstrated to differ between plots mowed every 4th compared to every 2nd year either ($p = 0.074$).

COST OF REPRODUCTION

Flowering was estimated to have a negative effect on the amount of stored resources at the end of the growing season (i.e. $\omega < 1$ implying that $\alpha_3 < 0$) in all time series (Fig. 9), indicating that there is a cost of reproduction in *E. latifolium*. The effect was present for all combinations of study area, mowing regime and community group, with no differences between the levels of these factors ($p > 0.05$).

DIRECT CLIMATIC IMPACT ON FLOWERING DENSITY

ETS in May - June$_t$ affected the flowering density positively for all combinations of study area and community group (Fig. 10). The positive influence was more pronounced in fen lawn and margin than in fen carpet at Tågdalen ($p < 0.001$, $p = 0.038$), whereas the community groups at Sølendet did not differ from any combination of study area and community group. The mowing regime did not affect the influence of *ETS* in May - June$_t$ on the flowering density ($p > 0.05$).

There was little correlation between precipitation in February - June year t and the flowering density, whereas precipitation in December - January$_t$ was among the climatic variables identified as possibly important for the flowering density (Table 3). The outcome of the autoregressive analysis showed that this climatic variable had minor influence on the flowering density, and the GLM analysis showed no differences between study areas, mowing regimes or community groups in terms of response to precipitation in December - January$_t$ (results not shown).

INDIRECT CLIMATIC IMPACT ON FLOWERING DENSITY

The *ETS* in July - September$_{t-1}$ affected the flowering density negatively at Tågdalen, and this differed from Sølendet ($p < 0.001$) where there was no overall effect (Fig. 11). The effect was more negative in fen lawn than fen carpet ($p < 0.001$), and probably also more negative in fen margin than fen carpet ($p = 0.051$). The length of the growing season t - 1, had a positive effect on the flowering density at Tågdalen (Fig. 12), but significantly more so in fen lawn than in fen carpet ($p < 0.001$), whereas a difference could not be demonstrated between fen carpet and fen margin ($p = 0.069$). The impact at Sølendet was weakly negative, and differed significantly from that in fen lawn and margin at Tågdalen ($p < 0.05$). The mowing regime did not affect the influence of either *ETS* in July - September$_{t-1}$ or the length of the growing season t - 1 on the flowering density ($p > 0.05$).

The flowering density at Sølendet was negatively affected by precipitation in May - June$_{t\text{-}1}$, whereas there was little effect at Tågdalen (Fig. 13). The difference between the study areas was significant ($p < 0.001$). The effect was also more negative in fen lawn than fen margin ($p = 0.034$) and in plots mowed every 2nd year than in unmowed plots ($p = 0.003$). There was a markedly positive effect of precipitation in July$_{t\text{-}1}$ on flowering in fen lawn at Tågdalen (Fig. 14), in contrast to its negative effect in fen lawn at Sølendet ($p = 0.006$). Fen lawn at Tågdalen also differed from fen carpet in both study areas ($p = 0.001$, $p < 0.001$), whereas no difference could be demonstrated in fen margin at Sølendet ($p = 0.089$). The effect of precipitation in July$_{t\text{-}1}$ was also influenced by the mowing regime (Fig. 14). A larger positive effect was found in plots that were unmowed and mowed every 4th year compared to plots mowed every 2nd year ($p = 0.008$, $p = 0.022$). There was a significant correlation between precipitation in October$_{t\text{-}1}$ and flowering density in more time series at Tågdalen than at Sølendet (Table 3). However, the autoregressive analyses showed there was no consistent effect separating the study areas, some time series being influenced negatively, others positively. Fen lawn and carpet at Tågdalen were the only combinations of study area and community group that differed ($p = 0.039$).

RELATIVE CONTRIBUTION OF FACTORS AFFECTING FLOWERING DENSITY

Cost of reproduction was the factor affecting flowering density the most (Fig. 9). The impact on current flowering from flowering the previous year was up to twice that of the second most important factor at Tågdalen, and several times higher at Sølendet. The length of the growing season t - 1 was the climatic variable contributing most to flowering density at Tågdalen (positive), followed by precipitation in July$_{t\text{-}1}$ (positive), *ETS* July - September$_{t\text{-}1}$ (negative) and *ETS* May - June$_{t}$ (positive) (Figs 10-12 and 14). The relationships between climatic variables and flowering density were less pronounced at Sølendet, but *ETS* May - June$_{t}$ (positive) contributed most, followed by the length of the growing season t - 1 (negative) and precipitation in July$_{t\text{-}1}$ (negative) (Figs 10, 12 and 14). Precipitation in October$_{t\text{-}1}$ considerably affected many flowering time series and in relative terms just as much as the other climatic variables, but the effects (negative or positive) varied significantly within both single study areas and community groups. The short-term effect of mowing was about as important to the flowering density as *ETS* May - June$_t$ (Figs 8 and 10). Because climatic variables influenced flowering density more at Tågdalen than at Sølendet, the relative importance of cost of reproduction and the short-term effect of mowing was greater at Sølendet than at Tågdalen.

Discussion

SHORT- AND LONG-TERM EFFECTS OF MOWING

The short-term effect of mowing was quantified by comparing years with mowing to years without mowing in the same time series, and a decrease in flowering density the next year was found in most cases (Fig. 8). This confirmed that the short-term disturbance (Crawley 1997a) caused by mowing had a negative impact on flowering density, and we believe this is best explained by the loss of biomass and damage from the cutting, i.e. a reduction in the resource storage of the plants. The above-ground biomass is larger in plots mowed every 4th than every 2nd year (Aune et al. 1996, A. Lyngstad, A. Moen & D.-I. Øien, unpublished data), and each mowing incident can therefore be expected to have a larger proportional impact during the longer mowing interval. This may cause a larger, negative short-term effect of mowing on flowering the next year in plots mowed every 4th year. We were unable to demonstrate such an effect, but attribute this to lack of power in the test due to few sample plots mowed every 4th year.

While the short-term disturbance caused by mowing was negative, the long-term effects of mowing every 2nd or 4th year on the mean flowering density were clearly positive (Fig. 6), highlighting the importance of long-term monitoring to assess long-term phenomena. The overall trend in flowering density was also positive in mowed plots compared to unmowed plots, and the majority of the time series in unmowed plots showed a decline (Fig. 7). Boreal rich fens often have low nutrient availability (e.g. Øien & Moen 2001), and stress-tolerant species (Grime 2001) are at an advantage if the disturbance is moderate. The mean flowering density was lower with mowing every year compared to mowing every 2nd or 4th year, but the trend in flowering was similar. So, even if mowing every year resulted in a lower flowering density than longer mowing intervals, there was no reduction with time. This suggests that the disturbance caused by mowing every 2nd or 4th year is ideal for the long-term performance of *E. latifolium* in boreal rich fen, and also that mowing every year is tolerable but not optimal. *E. latifolium* is at its ecological optimum in rich fen lawn vegetation (Sjörs 1948, Persson 1961, Moen 1990), as shown also by the high density of ramets in open lawn communities (Aune et al. 1996). Thus, the higher flowering density in fen lawn than fen carpet and margin was expected (Fig. 6). The negative trend in flowering density at Tågdalen (Fig. 7) may partly be caused by the collapse in flowering in 1995.

COST OF REPRODUCTION

Flowering occurs in 5.2 % of ramets and 7.0 % of clonal fragments in *E. latifolium* (A. Lyngstad, unpublished data). This investment in sexual reproduction had a real cost, as the flowering density was negatively correlated with the flowering density the previous year in all time series irrespective of study area, mowing regime or community group (Fig. 9). A cost of reproduction has been found in several other vascular plants (e.g. Syrjänen & Lehtilä 1993, Primack & Stacy 1998), but the effects may only be detectable after several years (Ehrlén & van Groenendael 2001). The relative impact was higher at Sølendet because climatic variables were more strongly correlated with flowering density at Tågdalen, which means that the course of the flowering density was more dependent on the flowering density the previous year at Sølendet than at Tågdalen. The cost of reproduction was interpreted in the light of the autoregressive model, and the validity of the conclusions rests on the validity of the model. The main assumption of our model is that flowering depends on the resource storage the previous year, but if this does not hold, ω (eqn 3) would become zero (i.e. $\alpha_3 = 1$). We argue, however, that the indirect, negative short-term effect of mowing strongly suggests that this is a relevant assumption.

DIRECT CLIMATIC EFFECTS

The only climatic variable of some importance and having a direct effect on flowering density was *ETS* May - June$_t$ (Fig. 10). A warm spring enables a high reproductive effort through optimal conditions for plant development, but is also likely to be correlated with fewer cold spells. Cold spells lower the flowering density (Inouye et al.

2002), and there are fewer cold spells when temperatures increase (The BACC Author Team 2008, Matthes et al. 2009). The effect of *ETS* May - June$_t$ was more pronounced in fen lawn than fen carpet vegetation at Tågdalen, suggesting less benefit from a warm spring at the wet end of the wet – dry gradient. This may be due to lower irradiance in the wettest plots because they are also the most level ones. In addition, the more sloping fen lawn plots at Tågdalen mostly face south, and the energy m^{-2} received is substantially higher than in most fen carpet plots. The fen lawn vegetation may also dry to optimal peat moisture levels in a warm spring, whereas the wetter fen carpet never dries up enough for such an effect to set in. *E. latifolium* has a narrow range on the wet – dry gradient in fen where it performs well (Moen 1990), and in fen carpet it is close to its upper tolerance limit along this gradient, as witnessed by the low flowering density in this vegetation.

Precipitation in spring year *t* was a variable we believed was important for flowering density, but we found no such correlation. Furthermore, snowfall (winter precipitation) also had little influence on flowering density, suggesting that peat moisture in spring is generally not important for flowering density the same year. The length of the snow cover may still be a relevant factor because it affects the length of the growing season (Laaksonen 1979), but snow cover may depend more on the weather in spring than the snow depth.

INDIRECT CLIMATIC EFFECTS

Five of six climatic variables that substantially affected the flowering density were indirect ones, i.e. their contribution affected the resource storage of plants which, in turn, affected the flowering density. Contrary to our expectations, the flowering density at Tågdalen was negatively correlated with *ETS* July - September$_{t\text{-}1}$, while flowering at Sølendet was neither positively nor adversely affected by this variable (Fig. 11). The negative effect was only seen in fen lawn vegetation, which suggests that this was due to drought in warm summers. Drought stress may result in diminished resource acquisition and, through that, lower flowering density the next year (Grace 1997, Grime 2001, Peñuelas et al. 2004). The impact of precipitation in July$_{t\text{-}1}$ was strongly positive in fen lawns at Tågdalen, a response diametrically opposed to that at Sølendet (Fig. 14).

This lends further support to the interpretation of summer drought as a negative factor for flowering in the south-facing and steep fen lawns at Tågdalen. If July is wet, evapotranspiration and run-off maintain beneficial groundwater levels, drought stress is avoided and the resources stored allow high levels of flowering next year. In want of ample July rain, the fen lawns dry up, affecting resource storage negatively. We expected evapotranspiration to be of little importance due to the cool climate of the study areas, but this was refuted. This is an important factor influencing *E. latifolium* in south-facing fens with high inclination. We had also expected the increase in *ETS* (Appendix S1) to yield increasing flowering densities over time. The trend was, however, negative in many (especially unmowed) plots (Fig. 7), so the increasing *ETS* at least did not result in a uniform increase in flowering density. The negative impact of *ETS* July - September$_{t\text{-}1}$ and positive impact of precipitation in July$_{t\text{-}1}$ at Tågdalen show that the water budget of the fens is essential for resource storage and later flowering in *E. latifolium*. A continued increase in *ETS* can therefore be a disadvantage for mire species, which are adapted to wet conditions.

The length of the growing season *t* - 1 was positively correlated with flowering at Tågdalen, especially in fen lawn (Fig. 12). This was in accordance with our hypothesis that a long growing season enables clonal fragments to store resources (Hudson & Henry 2009) and, through that, has a positive impact on flowering the next year. However, the correlation at Sølendet was somewhat negative (applied to about 75 % of the time series, Fig. 12), and this was in contradiction to our expectations. We believe it is unlikely that the length of the growing season affects the build-up of biomass differently in the two study areas, but if a long growing season is correlated with a high *ETS* May - June$_t$, it may well affect flowering the next year negatively through cost of reproduction. Because both the cost of reproduction and *ETS* May - June$_t$ were relatively more important at Sølendet than at Tågdalen, this may explain the negative relationship between the length of the growing season *t* - 1 and the flowering density at Sølendet.

Precipitation in May - June$_{t\text{-}1}$ had a clear, negative impact at Sølendet, and was also negatively correlated with flowering in mowed plots, but had no particular effect in unmowed plots (Fig. 13). Diminished resource storage as a consequence of waterlogging can explain these patterns. Water is nearly always abundant at Sølendet (see below), and the fens will become waterlogged more easily here than at Tågdalen. There was a similar negative effect of precipitation in July$_{t\text{-}1}$ in many of the time series in fen lawn at Sølendet that can be attributed to inundation (Fig. 14). Among the effects of long-term mowing are a lowering of the fen surface through removal of litter and biomass. This manifests as a shorter distance to the water table in mowed plots (A. Moen, unpublished data), and precipitation can result in waterlogged conditions in mowed plots while unmowed plots remain aerated. In addition, ramets tend to be larger in unmowed than mowed plots (Aune et al. 1996, A. Lyngstad, unpublished data), and may thus be better able to withstand wet conditions. The relatively more negative effect of precipitation in mowed plots was also seen for precipitation in July$_{t\text{-}1}$ (Fig. 14).

The mean flowering density in the oceanic study area was about 70 times higher in 1994 when the density was highest (18.5 ramets m^{-2}) compared to 1995 when it was lowest (0.26 ramets m^{-2}). The collapse in Tågdalen in 1995 (Fig. 4) seems to have been caused by a chain of events starting in 1993. The summer and autumn of 1993 were positive for resource storage with a relatively cool summer and a wet July. This primed *E. latifolium* for an unprecedented surge in flowering in 1994, a year that had a warm summer with a dry July (negative factors for flowering the next year). The high flowering density (equals high cost of reproduction) and a simultaneous negative impact from various climatic variables left clonal fragments vulnerable and with depleted resources. Spring 1995 was the fourth coldest in 1973-2008, with a long-lasting snow cover and high precipitation, giving an extremely high water table in spring and early summer. These factors combined to give the backlash in 1995 when the flowering density was only 1.4 % of 1994.

REGIONAL AND LOCAL DIFFERENCES

Our study areas mainly differ along the oceanic – continental gradient, with Tågdalen being markedly more oceanic than Sølendet, with more precipitation, more snow and far greater temporal variation in precipitation (Appendix S1). This gradient is steep in Norway due to the westerly winds that are halted by the mountains along the coast. The

Tågdalen - Sølendet transect covers a distance along this gradient corresponding roughly to the difference in oceanity between parts of Britain (e.g. northern England) and central Europe (e.g. southern Germany and northern Switzerland) (Grünig 1994, Moen 1999, Crawford 2000). We have shown that the flowering density was influenced more by climatic variables in the oceanic area, which leaves cost of reproduction and short-term effects of mowing as more important in explaining temporal flowering patterns in the continental area. Similar regional patterns can be expected to be found elsewhere.

On a local scale, the study areas differ in topography and hydrological conditions. The gently sloping fens (inclination 0-6^g) at Sølendet are fed calcareous, mineral-rich water evenly throughout the year through a system of more than 50 springs (Moen 1990). The sloping fens at Tågdalen are steeper (up to 20^g), and although numerous springs are found, their influence is less conspicuous than at Sølendet. The topography at Tågdalen is quite different from that at Sølendet, with many low ridges traversing the area in an east-west direction, interrupting waterflow and creating abrupt shifts in ecological conditions over short distances. The fen lawns at Tågdalen are mostly found on the south-facing slopes of these low ridges, while fen carpet is found in level areas, often at the foot of the same slopes. The combination of topographical features and a less reliable influx of water from springs contribute to the larger impact of climatic variables on flowering density at Tågdalen than at Sølendet.

CONCLUDING REMARKS

Our autoregressive modelling approach allowed us to simultaneously assess the relative impact of mowing and flowering at year *t* - 1 and direct (year *t*) and indirect (year *t* - 1) climatic effects on flowering density in *E. latifolium*. The short-term effect of mowing is a disturbance (Crawley 1997a) that reduces the resource storage in the plants making up the population, and was found to have a negative effect on flowering the next year. The negative short-term effect of mowing was balanced by the positive long-term effect of mowing on both the mean and the trend in the flowering density, highlighting the need for long-term monitoring to assess long-term phenomena. A negative autocorrelation in flowering between years was interpreted as a cost of reproduction

(Calvo & Horvitz 1990, Ehrlén & Eriksson 1995), and this was demonstrated in all the flowering time series. Cost of reproduction had the highest impact on the flowering density among the factors considered here. The flowering density in the *E. latifolium* population in the oceanic study area (Tågdalen) was more sensitive to climatic factors than the population in the continental study area (Sølendet). This was partly because of larger year-on-year variations in precipitation on a regional scale at Tågdalen, and partly due to local topographical and hydrological differences that render the population at Tågdalen more susceptible to climatic variation. The more stable course of flowering density through time in the population at Sølendet may be a consequence of stronger internal control through cost of reproduction, whereas the more fluctuating progress in flowering density at Tågdalen may be a result of climate temporarily overriding this controlling mechanism. Whether large fluctuations in flowering density is a general consequence of a varying oceanic climate is a topic suitable for further studies.

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Tables

Table 1. Characteristics of Sølendet and Tågdalen nature reserves.

	Sølendet	Tågdalen
Latitude (N)	62°40’	63°03’
Longitude (E)	11°50’	9°05’
Mean annual precipitation (mm)	637	1583
Mean annual *ETS* (day degrees)	578	639
Mean July temperature (°C)	10.5	11.2
Mean January temperature (°C)	-9.5	-2.7
Altitude (m a.s.l.)	700-800	380-490
Area (ha)	306	146

Table 2. The number of flowering time series in two study areas, four mowing regimes and nine vegetation clusters (1-9). The nine clusters are based on a classification of rich fen vegetation in permanent plots (A. Lyngstad, A. Moen & D.-I. Øien, unpublished data). The clusters belong to the plant communities *Eleocharis quinqueflora-Cinclidium* carpet (I), *Drosera anglica-Scorpidium scorpioides* carpet (II), *Eriophorum latifolium-Campylium* lawn (III), *Equisetum variegatum-Thalictrum-Campylium* lawn (IV), *Gymnadenia-Succisa-Campylium* margin (V) and *Galium boreale-Molinia-Hylocomiastrum pyrenaicum* margin (VI), and the plant communities are grouped in the community groups fen carpet, fen lawn and fen margin.

Community group		Fen carpet			Fen lawn				Fen margin	
Plant community		I		II	III		IV		V	VI
Vegetation cluster		1	2	3	4	5	6	7	8	9
Study area	Mowing regime									
Tågdalen	Unmowed	-	-	6	17	9	-	2	-	2
	Mowed every 4th year	-	-	2	4	3	-	-	-	-
	Mowed every 2nd year	-	-	1	6	6	-	-	-	1
	Mowed every year	-	-	-	-	-	-	-	-	-
Sølendet	Unmowed	1	4	-	-	-	12	8	3	-
	Mowed every 4th year	-	-	-	-	-	-	2	-	-
	Mowed every 2nd year	2	3	-	-	-	10	11	4	-
	Mowed every year	1	-	-	-	-	2	2	2	-

Table 3. The number of flowering time series at Sølendet and Tågdalen correlated ($p < 0.05$ and $p < 0.1$) with each of 24 candidate climatic variables (left). The seven climatic variables included in *C*1 and *C*2 (four of which are merged) on the right.

Candidate climatic variables	Sølendet (n=67) p < 0.05	Sølendet (n=67) p < 0.1	Tågdalen (n=59) p < 0.05	Tågdalen (n=59) p < 0.1	Included climatic variables	Pathway
Precipitation May	5	6	2	5	Precipitation May - June$_{t-1}$	*C*2
Precipitation June	6	12	1	2		
Precipitation July	1	2	13	22	Precipitation July$_{t-1}$	*C*2
Precipitation August	2	5	0	1	-	
Precipitation September	3	4	0	1	-	
Precipitation October	6	9	14	24	Precipitation October$_{t-1}$	*C*2
Precipitation November	1	2	4	5	-	
Precipitation December	5	9	5	12	Precipitation December - January$_{t}$	*C*1
Precipitation January	3	4	6	14		
Precipitation February	0	1	0	2	-	
Precipitation March	0	2	1	3	-	
Precipitation April	1	1	0	1	-	
Precipitation May	0	2	0	1	-	
Precipitation June	2	5	0	1	-	
ETS May	4	12	0	0	-	
ETS June	5	9	1	1	-	
ETS July	15	23	2	13	*ETS* July - September$_{t-1}$	*C*2
ETS August	7	12	2	13		
ETS September	4	7	4	11		
ETS May	4	4	0	0	*ETS* May - June$_{t}$	*C*1
ETS June	18	30	2	6		
Aggregated *ETS*	7	13	8	23	-	
Length growing season	8	12	22	27	Length growing season *t* - 1	*C*2
Start growing season	2	4	2	5	-	

Figures

Fig. 1. The location of Sølendet and Tågdalen nature reserves.

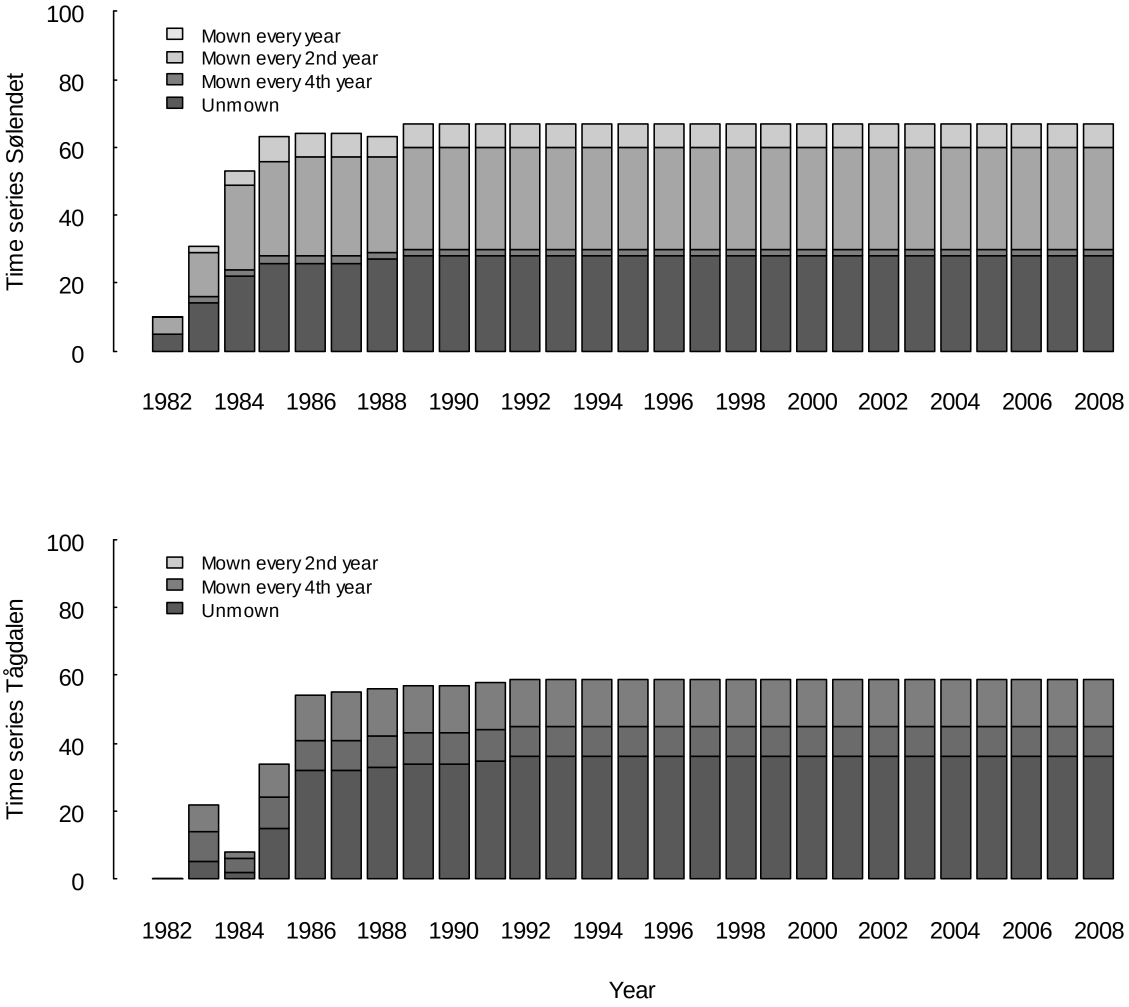

Fig. 2. The number of time series with counting of flowering ramets of *E. latifolium* (1982-2008) in four mowing regimes at Sølendet (above) and Tågdalen (below).

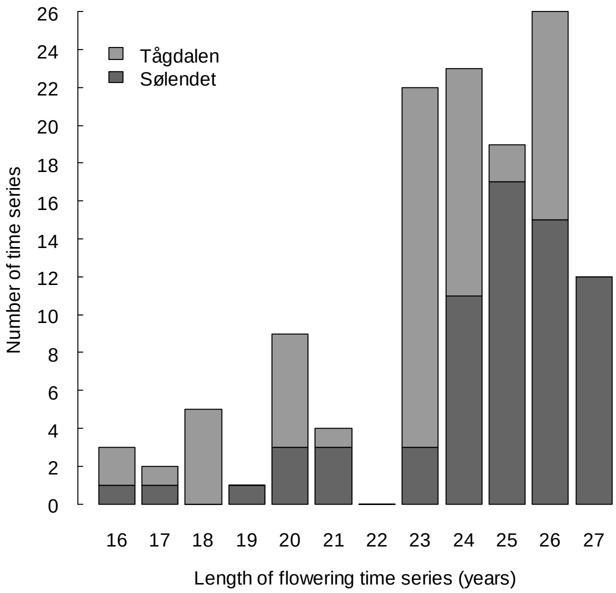

Fig. 3. The number of flowering time series included from each study area of length 16-27 years (n = 126).

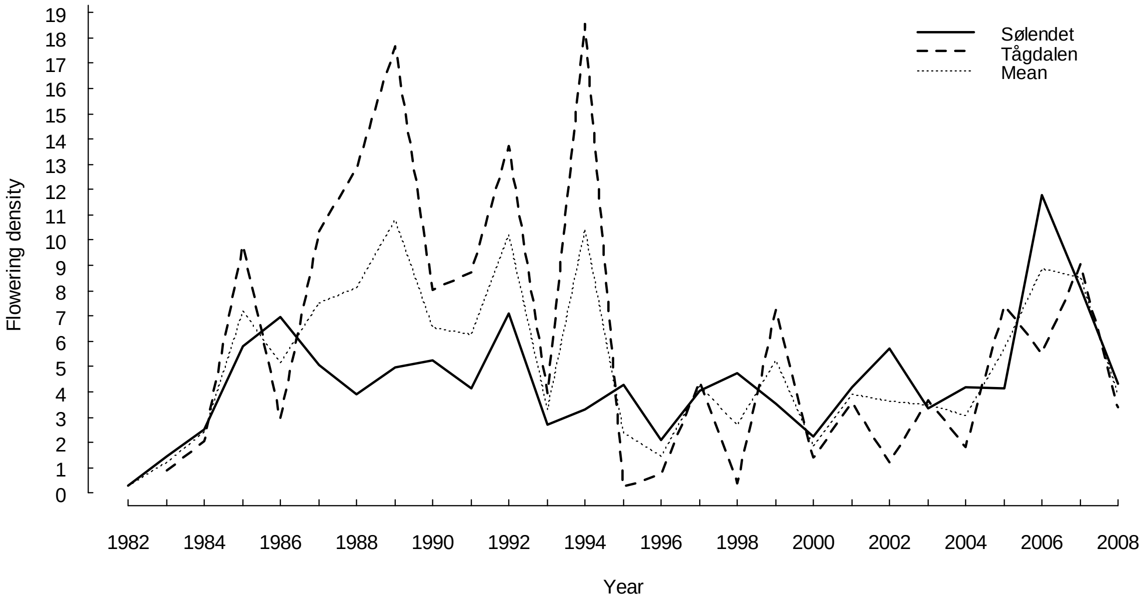

Fig. 4. Annual flowering density in *E. latifolium* (1982-2008) at Sølendet and Tågdalen.

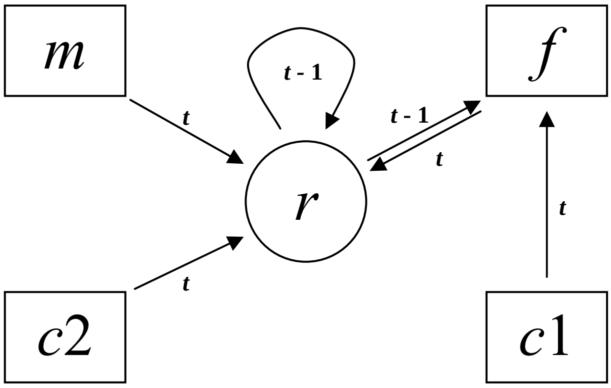

Fig. 5. A conceptual model describing the relationship between stored resources (*r*), flowering *(f)*, climate (*c*1 and *c*2) and whether the plot is mowed or not (*m*). Arrows marked with t indicate effects operating within the same growing season, while effects operating between years are marked with *t* - 1. The model explains the development in the state variables *r* and *f* over years by identifying the factors affecting them and the pathways through which they work. f_t possibly consumes resources through a cost of reproduction, consequently reducing *r*. Mowing reduces *r* through disturbance, so mowing potentially reduces flowering the following year through a reduction of *r*. The climatic factors *c*1 and *c*2 were considered separately because they contribute through different mechanisms. *c*1 is the direct climatic impact on flower development. *c*2 relates to the effect climate has on production of biomass, and thus the amount of stored resources, *r*, that may be allocated to flowering in the next growing season. Measured variables are enclosed in squares, while the unmeasured variable *r* is in a circle.

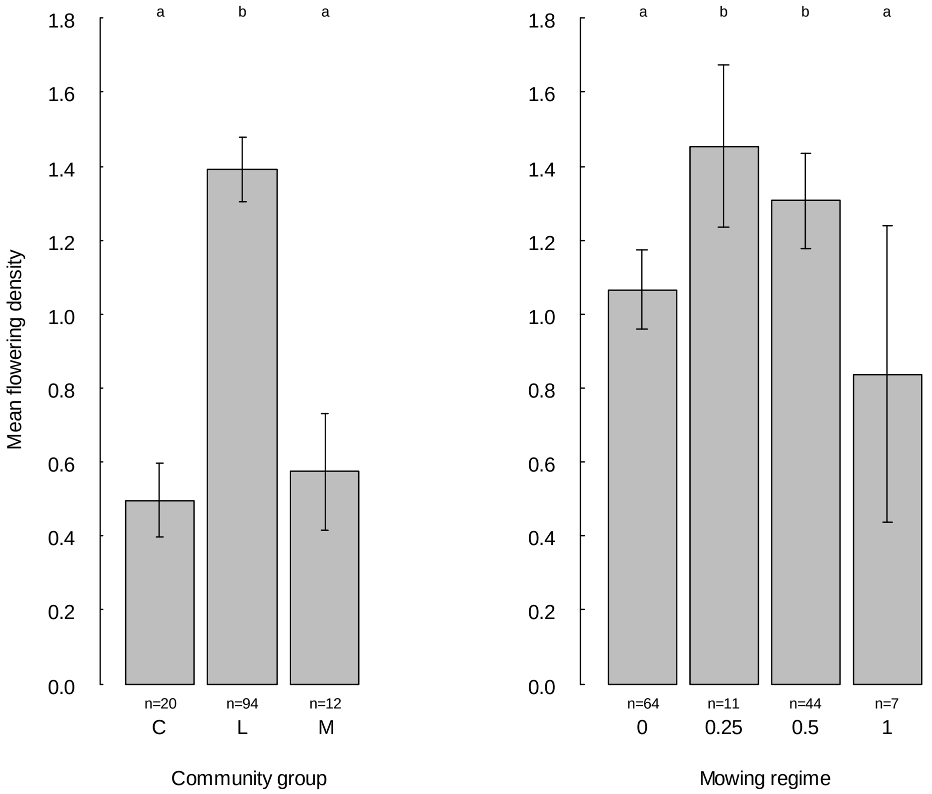

Fig. 6. Mean flowering density +/- se in *E. latifolium* (1982-2008) in three community groups (left) and under four mowing regimes (right). Differences (|t| > 2) between levels of the factors are indicated by the letters a and b at the top, and the number of time series is indicated on the x axis. C = fen carpet, L = fen lawn, M = fen margin, 0 = unmowed, 0.25 = mowed every 4th year, 0.5 = mowed every 2nd year, 1 = mowed every year.

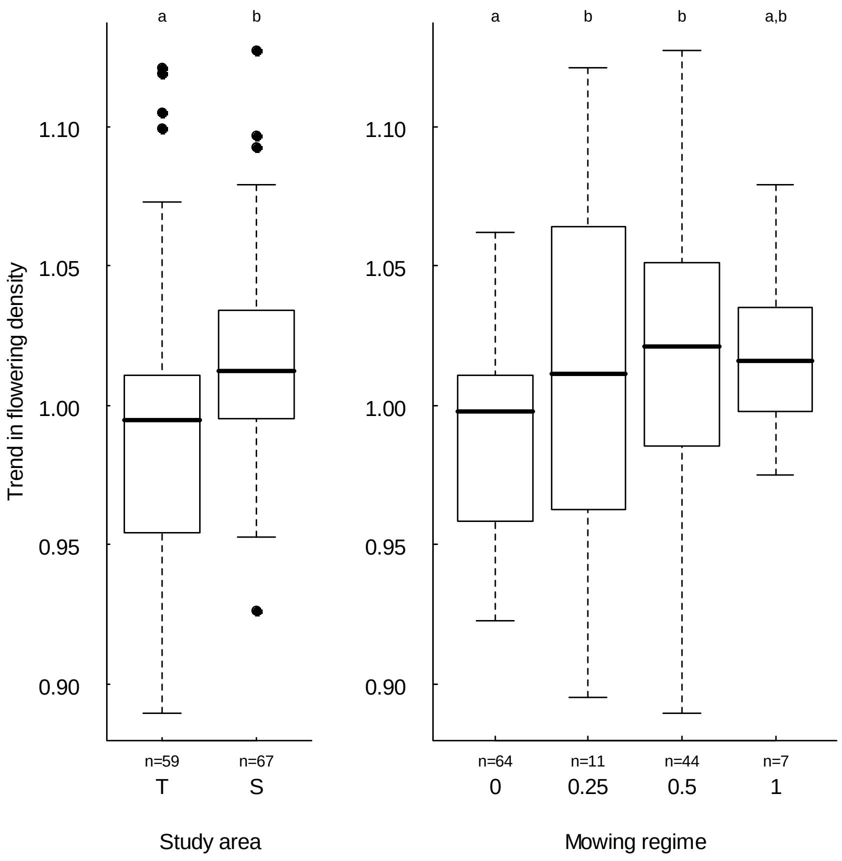

Fig. 7. The impact of study areas (left) and mowing regimes (right) on the trend in flowering density in *E. latifolium* (1982-2008). Differences ($p < 0.05$) are indicated by the letters a and b at the top, and the number of time series is indicated on the x axis. Abbreviations: T = Tågdalen, S = Sølendet and as in Fig. 6.

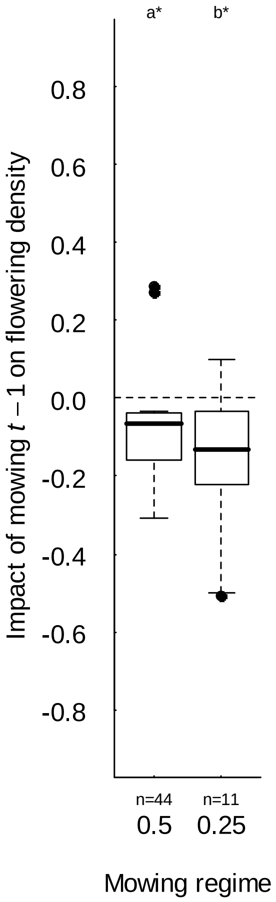

Fig. 8. The impact of mowing on flowering density the following year (expressed through α_1, eqn 3). Differences between mowing regimes ($0.1 > p > 0.05$) are indicated by a* and b* at the top, and the number of time series is indicated on the x axis. Abbreviations as in Fig. 6.

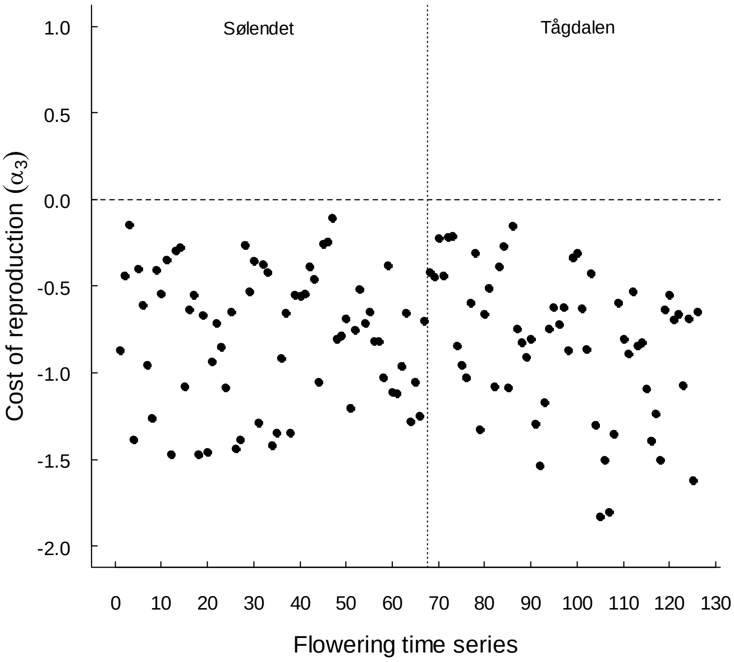

Fig. 9. The cost of reproduction (expressed through α_3) in 126 flowering time series of *E. latifolium* at Sølendet (1-67) and Tågdalen (68-126). An autoregressive coefficient $\omega = (\alpha_3+1)$ (eqn 3) less than 1, i.e. $\alpha_3 < 0$, signifies a cost of reproduction.

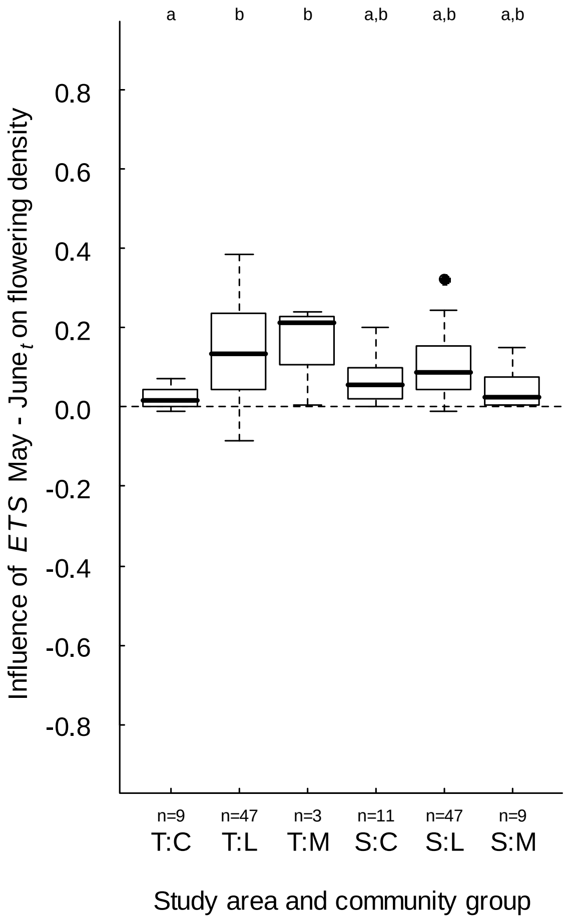

Fig. 10. The influence of *ETS* May - June$_t$ (expressed through β_1, eqn 3) on flowering density in study areas and community groups. Differences ($p < 0.05$) between groups of time series are indicated by the letters a and b at the top, and the number of time series is indicated on the x axis. Abbreviations as in Figs. 6 and 7.

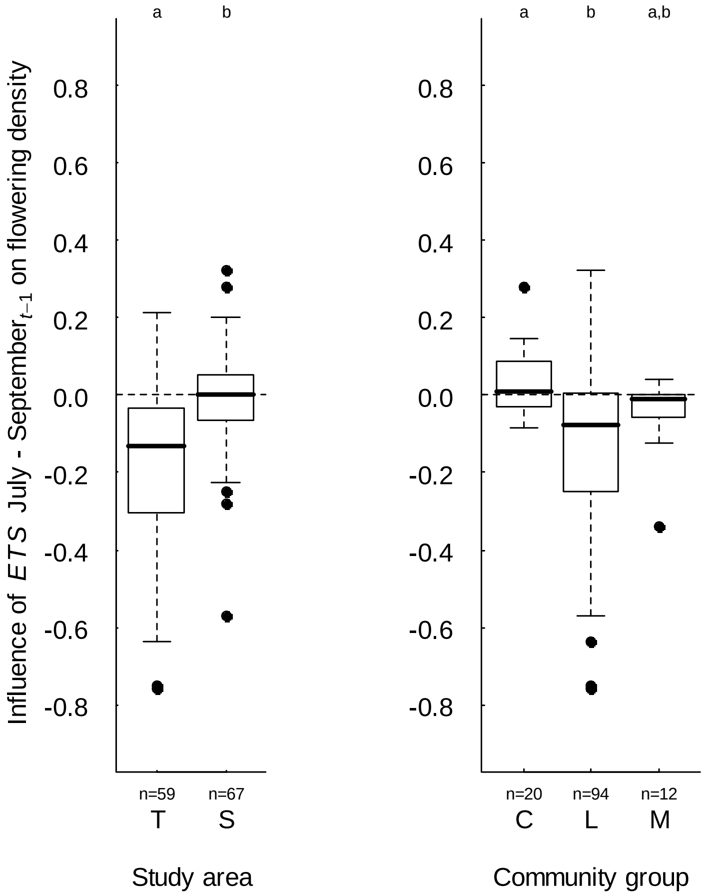

Fig. 11. The influence of *ETS* July - September$_{t\text{-}1}$ (expressed through α_2, eqn 3) on the flowering density in study areas (left) and community groups (right). Differences ($p < 0.05$) between groups of time series are indicated by the letters a and b at the top, and the number of time series is indicated on the x axis. Abbreviations as in Figs. 6 and 7.

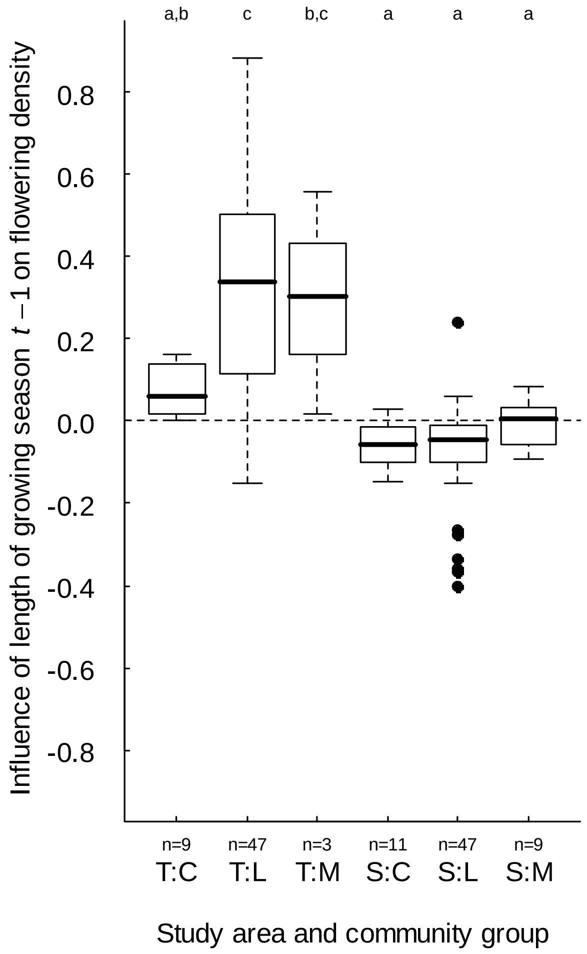

Fig. 12. The influence of the length of the growing season at year *t* - 1 (expressed through α_2, eqn 3) on the flowering density in study areas and community groups. Differences ($p < 0.05$) between groups of time series are indicated by the letters a, b and c at the top, and the number of time series is indicated on the x axis. Abbreviations as in Figs. 6 and 7.

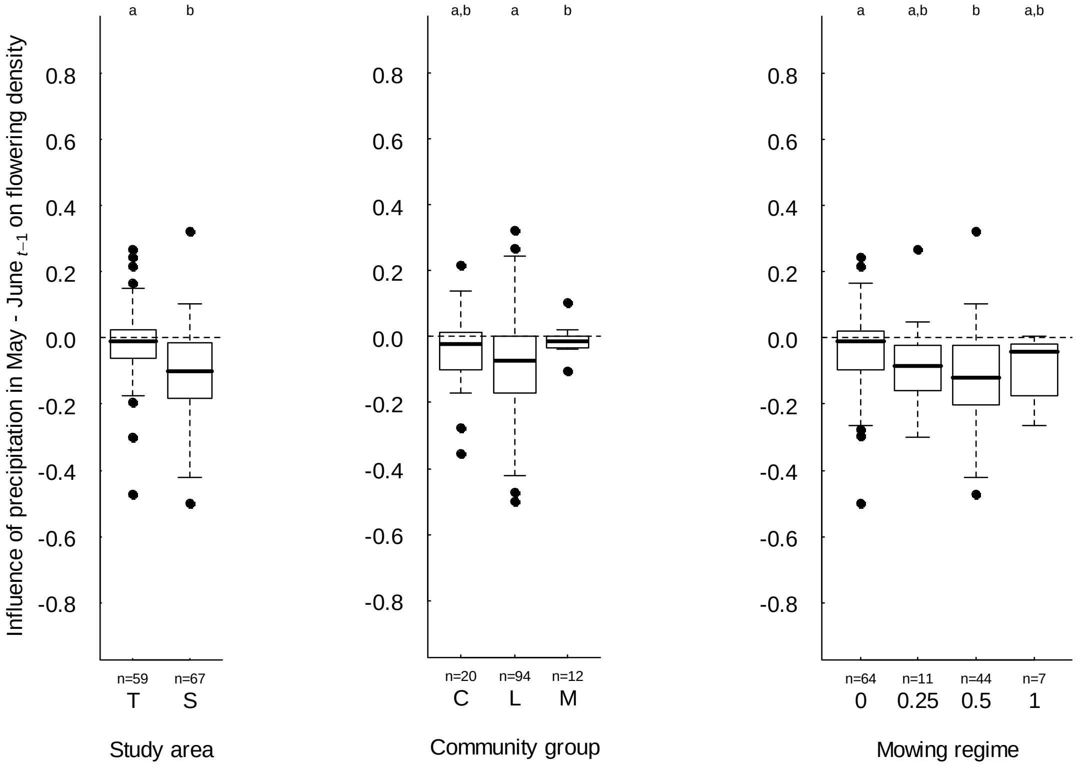

Fig. 13. The influence of precipitation May - June$_{t-1}$ (expressed through α_2, eqn 3) on flowering density in study areas (left), community groups (middle) and mowing regimes (right). Differences ($p < 0.05$) between groups of time series are indicated by the letters a and b at the top, and the number of time series is indicated on the x axis. Abbreviations as in Figs. 6 and 7.

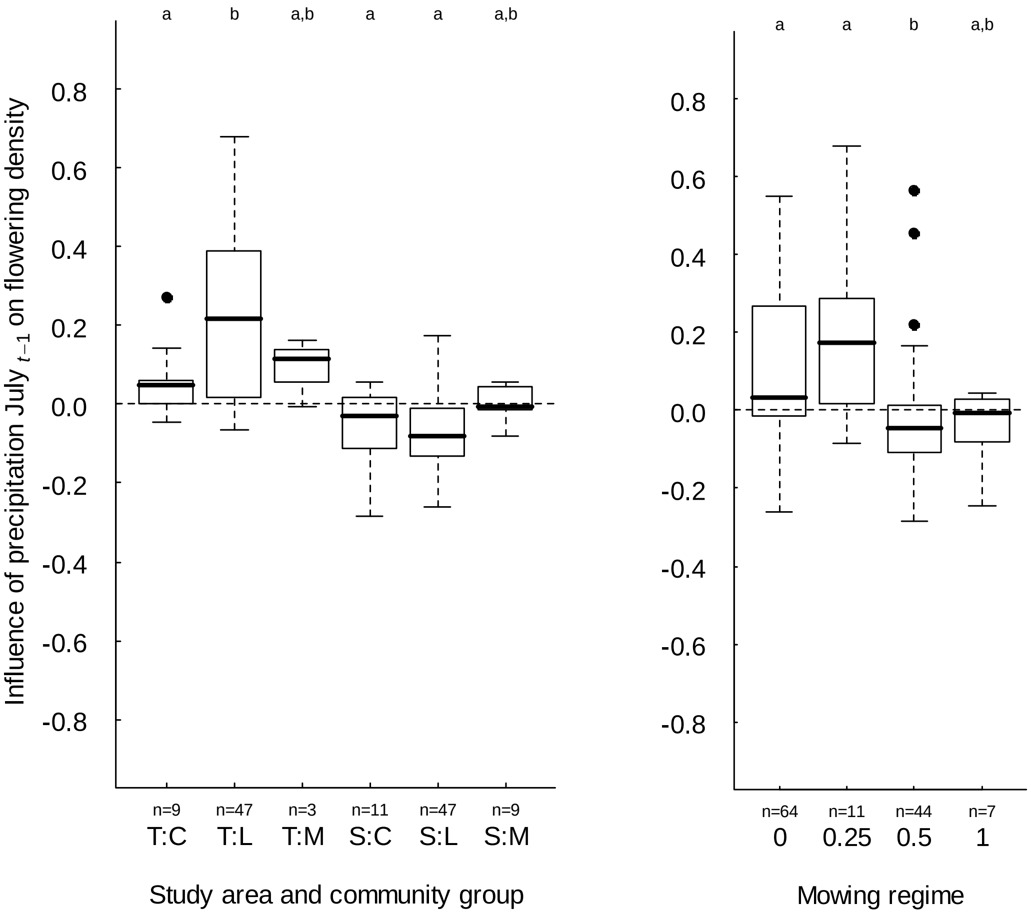

Fig. 14. The influence of precipitation in July$_{t\text{-}1}$ (expressed through α_2, eqn 3) on flowering density in study areas and community groups (left) and mowing regimes (right). Differences ($p < 0.05$) between groups of time series are indicated by the letters a and b at the top, and the number of time series is indicated on the x axis. Abbreviations as in Figs. 6 and 7.

Appendix S1. The climate at Sølendet and Tågdalen nature reserves

Precipitation

Mean monthly precipitation (+/- se) at Sølendet (1974-2008) and Tågdalen (1973-2008) is shown in Fig. S1. Annual precipitation is shown for both study areas in Fig. S2. Monthly precipitation has increased in February and possibly also August at both study areas during this period (Table S1).

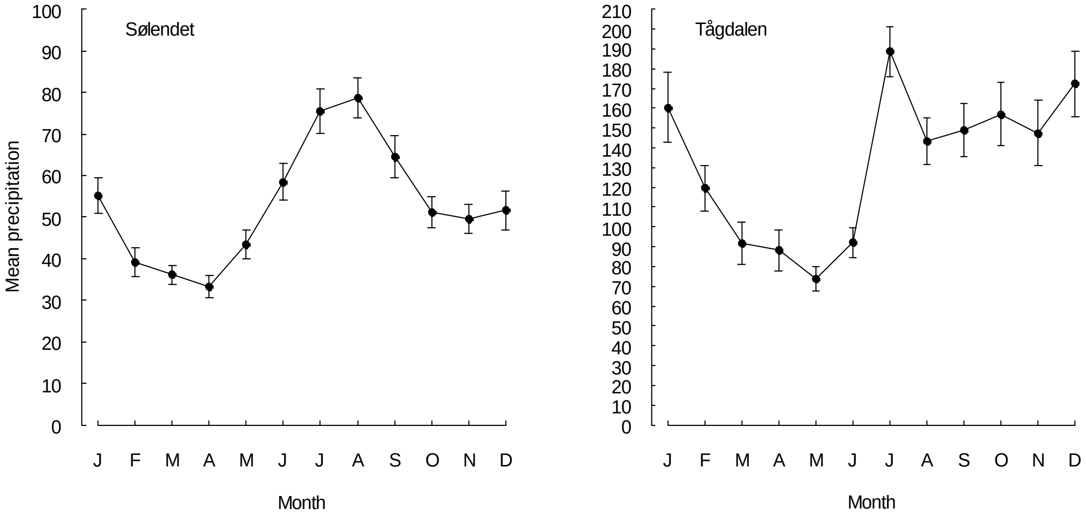

Fig. S1. Mean monthly precipitation (+/- se) at Sølendet (1974-2008) to the left and Tågdalen (1973-2008) to the right. Note the differences in scale.

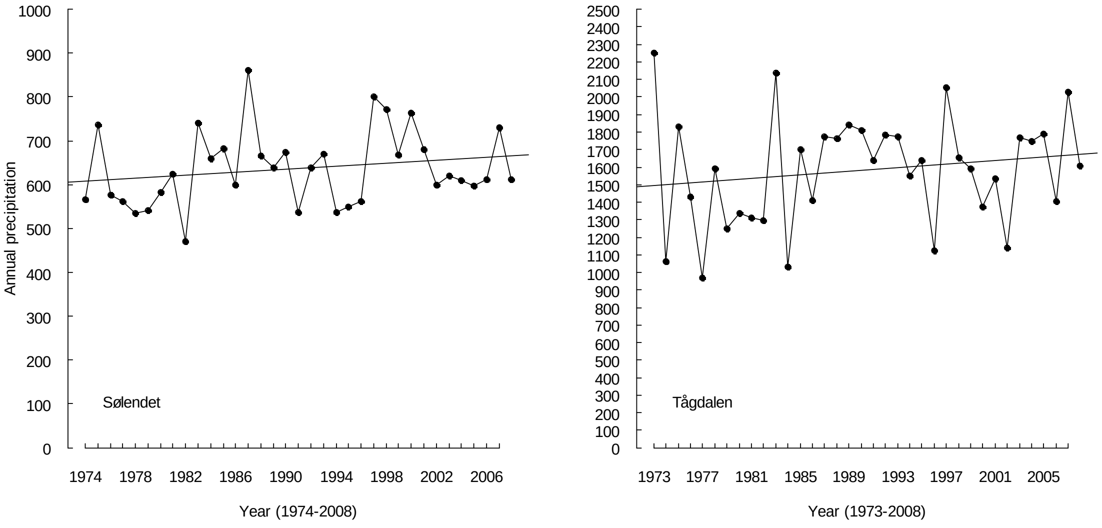

Fig. S2. Annual precipitation in the period 1973/74-2008 with trendlines added for Sølendet (left) and Tågdalen (right). Note the differences in scale.

Effective temperature sum

Mean monthly effective temperature sum (*ETS*) at Sølendet (1974-2008) and Tågdalen (1973-2008) is shown in Fig. S3. There is an increase in annual *ETS* at Tågdalen and probably at Sølendet during the period (Table S1, Fig. S4). The difference in annual *ETS* between the study areas has increased from 1974 to 2008 ($p < 0.001$, $r^2 = 0.34$, linear regression), and Tågdalen now has higher annual *ETS* than Sølendet (Fig. S5).

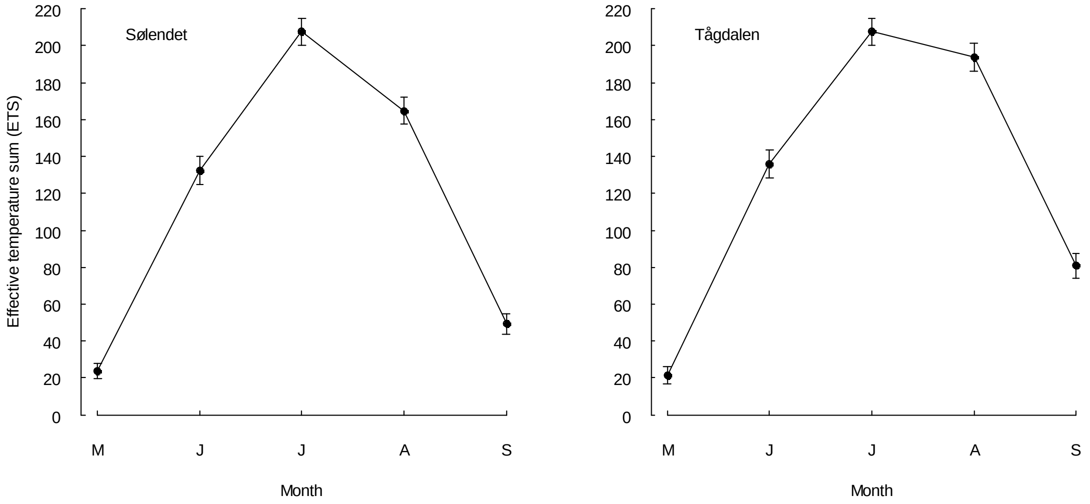

Fig. S3. Mean monthly *ETS* (+/- se) May – September at Sølendet (1974-2008) to the left, and at Tågdalen (1973-2008) to the right.

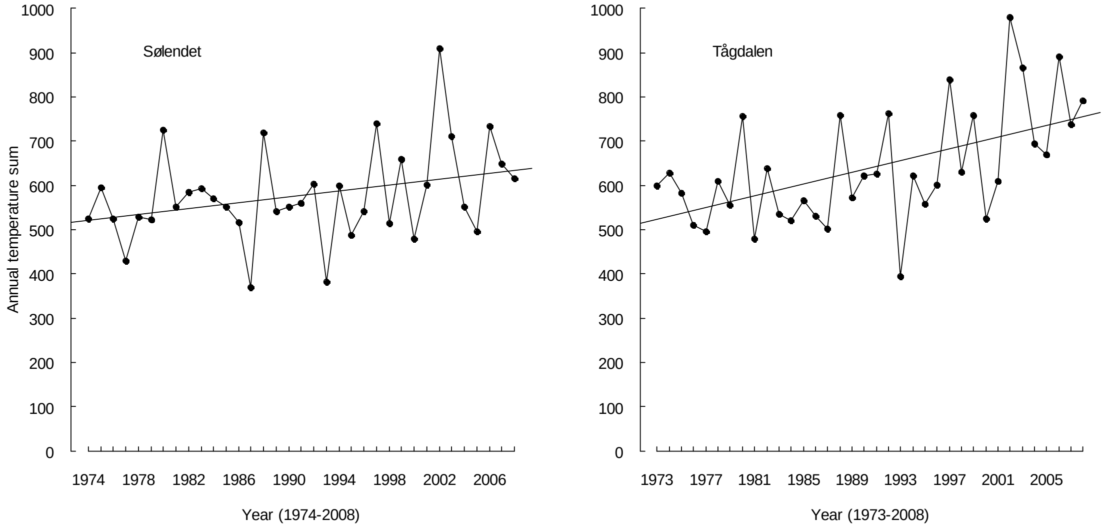

Fig. S4. Annual *ETS* in the period 1973/74-2008 with trendlines added for Sølendet (left) and Tågdalen (right).

Table S1. Trend in monthly *ETS* (May-September), annual *ETS*, monthly precipitation (January-December), and annual precipitation at Sølendet (1974-2008) and Tågdalen (1973-2008). All tests are linear regressions with r^2, estimated yearly change in day degrees or mm precipitation +/- se, and p-values ($p < 0.05$ in bold, $0.05 \leq p < 0.10$ in italics).

	Sølendet				Tågdalen			
	r^2	estimate	se	p-value	r^2	estimate	se	p-value
Trend in *ETS*								
May	0.01	-0.28	0.40	0.491	0.07	0.71	0.45	0.122
June	0.01	0.35	0.77	0.652	0.03	0.73	0.74	0.329
July	0.12	1.50	0.70	**0.039**	0.22	1.90	0.62	**0.004**
August	0.05	1.01	0.74	0.180	0.16	1.74	0.69	**0.017**
September	0.05	0.74	0.54	0.183	0.18	1.58	0.58	**0.010**
Annual	0.10	3.32	1.72	*0.062*	0.29	6.65	1.78	**0.001**
Trend in precipitation								
January	0.00	0.02	0.42	0.957	0.01	0.95	1.71	0.584
February	0.11	0.66	0.32	**0.049**	0.14	2.45	1.04	**0.024**
March	0.00	0.09	0.23	0.694	0.02	0.85	1.04	0.422
April	0.01	-0.16	0.26	0.558	0.01	-0.68	0.99	0.495
May	0.04	0.39	0.35	0.267	0.04	0.67	0.60	0.273
June	0.00	0.03	0.45	0.944	0.06	1.06	0.71	0.142
July	0.00	0.16	0.53	0.767	0.03	-1.21	1.21	0.325
August	0.10	0.90	0.46	*0.059*	0.09	1.97	1.09	*0.079*
September	0.01	-0.33	0.49	0.505	0.00	-0.51	1.34	0.705
October	0.00	-0.07	0.38	0.853	0.03	-1.56	1.55	0.319
November	0.08	0.56	0.34	0.104	0.02	1.45	1.58	0.367
December	0.04	-0.55	0.46	0.244	0.00	-0.28	1.61	0.862
Annual	0.04	1.72	1.44	0.241	0.03	5.13	5.04	0.316

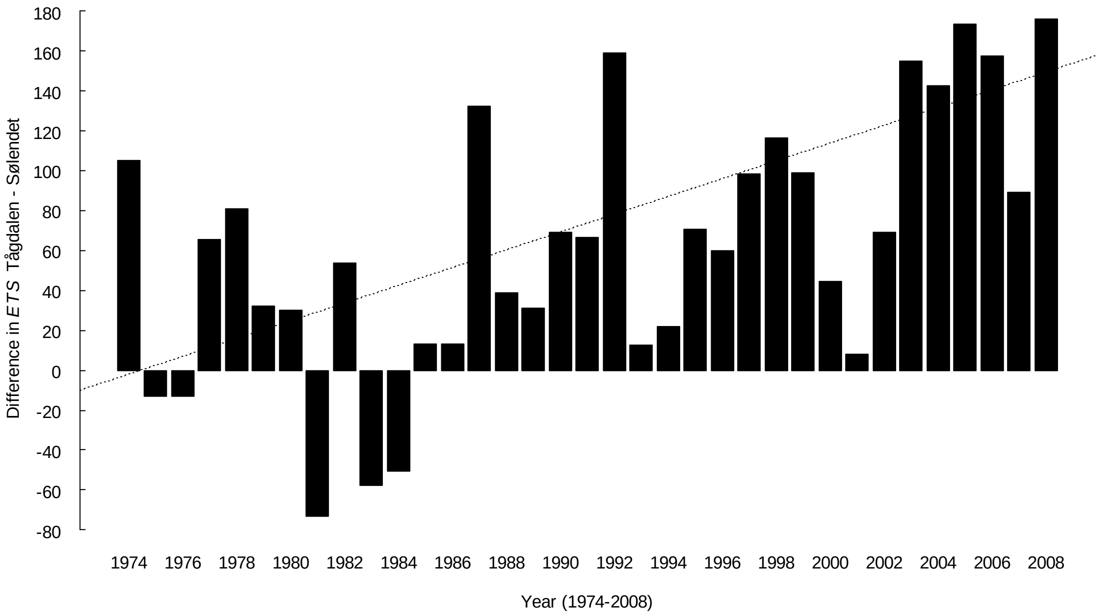

Fig. S5. The difference in annual *ETS* calculated as $ETS_{\text{Tågdalen}}$ - $ETS_{\text{Sølendet}}$ over the period 1974-2008. The difference between the study areas increases with time ($p < 0.001$, $r^2 = 0.34$, linear regression, dotted line).

Length of the growing season

The length of the growing season (1980-2008) is shown for both study areas in Fig. S6. There is no trend in the length of the growing season at Sølendet ($p = 0.728$, $r^2 = 0.005$, linear regression), but a possible positive trend at Tågdalen ($p = 0.080$, $r^2 = 0.110$, linear regression).

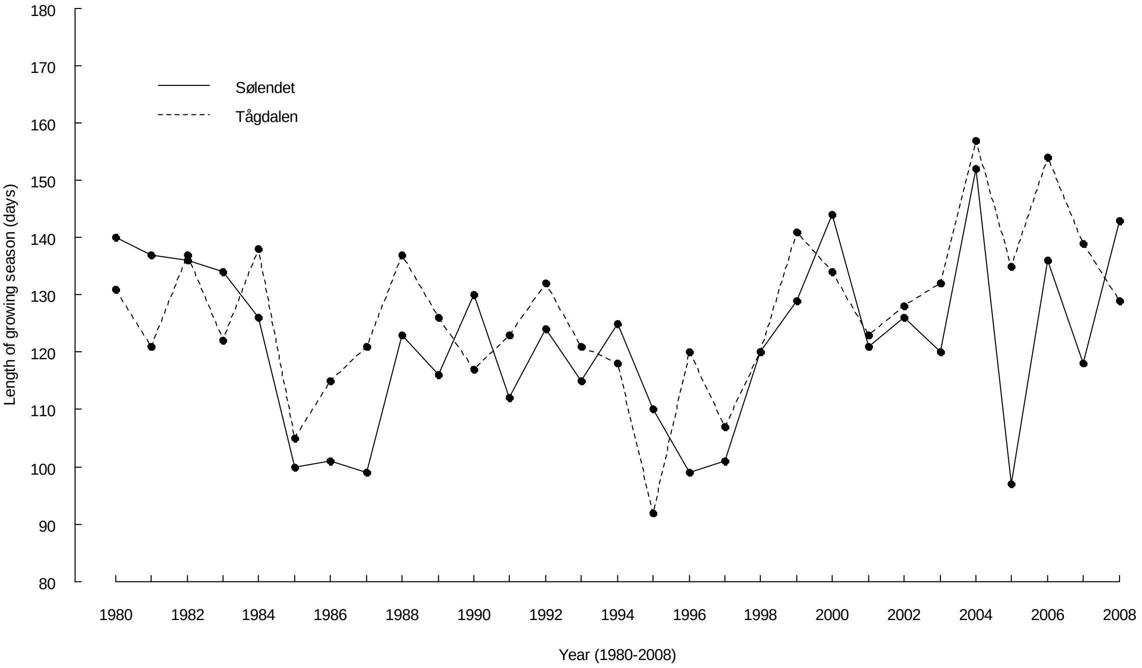

Fig. S6. The length of the growing season at Sølendet and Tågdalen (1980-2008).

Appendix S2. An autoregressive model for flowering density in mowed populations of *Eriophorum latifolium*

The interactions between stored resources, mowing, two sets of climatic variables and flowering density can be summarised in the following set of equations (see the main text):

$$r_t = r_{t-1}\, g_1\,(m_t\,,\, c2_t\,,\, f_t) \tag{A1a}$$

$$f_t = r_{t-1}\, g_2\,(c1_t), \tag{A1b}$$

where r_t is the amount of stored resources in year t, m_t is mowing in year t, f_t is flowering density in year t, $c1_t$ is the set of climatic factors affecting flowering directly, and $c2_t$ the set of climatic factors affecting resource storage. The function g_1 describes the contribution to r_t from each unit of stored resources at t - 1, and the function g_2 describes the contribution to f_t from each unit of stored resources at t - 1. Transforming the equations (A1a) and (A1b) to $\log_e$ scale and using Taylor expansion, they can be approximated by the linear equations:

$$R_t = \alpha_0 + R_{t-1} + \alpha_1 M_t + \alpha_2 C2_t + \alpha_3 F_t \tag{A2a}$$

$$F_t = \beta_0 + R_{t-1} + \beta_1 C1_t \tag{A2b}$$

where $R_t = \log_e(r_t\,)$, $F_t = \log_e(f_t)$, $M_t = \log_e(m_t + 1)$, $C1_t$ and $C2_t$ are linear combinations of $\log_e$-transformed climatic variables that affect flowering directly and indirectly respectively. The parameters α_0 - α_3 are associated with factors affecting R_t, and the parameters β_0 and β_1 are associated with factors affecting F_t.

Rearranging (A2b) leads to

$$R_{t-1} = -\beta_0 - \beta_1 C1_t + F_t\,,$$

which after substitution into (A2a) gives

Appendix S2. An autoregressive model for flowering

$$R_t = \alpha_0 + F_t - \beta_0 - \beta_1 C1_t + \alpha_1 M_t + \alpha_2 C2_t + \alpha_3 F_t.$$

Writing this formula for year t - 1 instead of t and further rearrangements leads to

$$R_{t\text{-}1} = \alpha_0 - \beta_0 - \beta_1 C1_{t\text{-}1} + \alpha_1 M_{t\text{-}1} + \alpha_2 C2_{t\text{-}1} + (\alpha_3+1)F_{t\text{-}1}.$$

Substituting into (A2b) and solving for F_t gives the following equation

$$F_t = \beta_0 + \alpha_0 - \beta_0 - \beta_1 C1_{t\text{-}1} + \alpha_1 M_{t\text{-}1} + \alpha_2 C2_{t\text{-}1} + (\alpha_3+1)F_{t\text{-}1} + \beta_1 C1_t.$$

An autoregressive model for flowering density can thus be written

$$F_t = \alpha_0 + \beta_1(C1_t - C1_{t\text{-}1}) + \alpha_1 M_{t\text{-}1} + \alpha_2 C2_{t\text{-}1} + (\alpha_3+1)F_{t\text{-}1}. \qquad \text{(A3)}$$

Equation (3) in the main text follows from (A3).

Appendix S3. Summarising statistical analyses of mean and trend in flowering density, and the effects of mowing and climatic variables on flowering density

Statistical analyses were performed to determine which factors affect mean flowering density (number of flowering ramets m^{-2}) (Table S1), trend in flowering density (Table S2), the short-term effect of mowing on flowering density (Table S3) and the effects of six separate climatic variables on flowering density in *Eriophorum latifolium* (Tables S4-S9). Generalised linear mixed models (GLMM) was used to analyse mean flowering density, generalised linear models (GLM) were used in the other analyses. The fixed factors considered in all models were study area, mowing regime and community group, but only factors or interactions remaining in the minimal adequate models (most parsimonious models) are shown. The tables summarise the differences (pairwise comparisons) between levels of fixed factors (Δ levels) when no interactions are present, and between groups of levels of fixed factors when interactions are present. The differences between the levels compared are shown with accompanying t- or p-values, and $|t| > 2$ and $p < 0.05$ are indicated in bold, $0.1 > p > 0.05$ in italics. The following abbreviations are used in all tables: C = fen carpet, L = fen lawn, M = fen margin, 0 = unmowed, 0.25 = mowed every 4th year, 0.5 = mowed every 2nd year, 1 = mowed every year, T = Tågdalen, S = Sølendet.

Table S1. Mean flowering density in *E. latifolium* affected by community group and mowing regime, no interactions are demonstrated. The differences between estimated mean flowering densities for the compared levels of factors (Δ levels) are shown with accompanying |t|-values.

Fixed factor	Levels	Δ levels	|t|
Community group	C:L	0.98	**3.67**
	C:M	0.18	0.45
	L:M	0.80	**2.00**
Mowing regime	0:0.25	0.43	**3.42**
	0:0.5	0.39	**5.24**
	0:1	0.09	0.35
	0.25:0.5	0.05	0.37
	0.25:1	0.38	**2.59**
	0.5:1	0.34	**2.27**

Appendix S3. Summarising statistical analyses

Table S2. Trend in flowering density in *E. latifolium* affected by study area and mowing regime, no interactions are demonstrated. The differences between estimated trend in flowering densities for the compared levels of factors (Δ levels) are shown with accompanying p-values.

Fixed factor	Levels	Δ levels	p
Study area	T:S	0.022	**0.009**
Mowing regime	0:0.25	0.029	**0.045**
	0:0.5	0.021	**0.016**
	0:1	0.016	0.371
	0.25:0.5	0.008	0.590
	0.25:1	0.013	0.471
	0.5:1	0.005	0.772

Table S3. The short-term effect of mowing on flowering density in *E. latifolium* affected by community group and mowing regime, no interactions are demonstrated. The differences between estimated short-term effect of mowing for the compared levels of factors (Δ levels) are shown with accompanying p-values.

Fixed factor	Levels	Δ levels	p
Community group	C:L	0.084	0.145
	C:M	0.024	0.776
	L:M	0.108	0.207
Mowing regime	0.25:0.5	0.092	*0.074*

Table S4. The effect of effective temperature sum (*ETS*) May - June$_t$ on flowering density in *E. latifolium* affected by study area and community group. There is an interaction between the factors. The differences between estimated effect of *ETS* in spring$_t$ for the compared groups of levels of factors (Δ levels) are shown with accompanying p-values.

Fixed factor	Levels	Δ levels	p
Study area : community group	TC:TL	0.120	**<0.001**
	TC:TM	0.128	**0.038**
	TC:SC	0.046	0.268
	TC:SL	0.075	0.101
	TC:SM	0.021	0.772
	TL:TM	0.008	0.892
	TL:SC	0.074	*0.074*
	TL:SL	0.045	0.321
	TL:SM	0.099	0.184
	TM:SC	0.082	0.180
	TM:SL	0.053	0.383
	TM:SM	0.107	0.150
	SC:SL	0.029	0.524
	SC:SM	0.025	0.741
	SL:SM	0.054	0.719

Table S5. The effect of *ETS* July - September$_{t-1}$ on flowering density in *E. latifolium* affected by study area and community group, no interactions are demonstrated. The differences between estimated effect of *ETS* in summer$_{t-1}$ for the compared levels of factors (Δ levels) are shown with accompanying p-values.

Fixed factor	Levels	Δ levels	p
Study area	T:S	0.189	**<0.001**
Community group	C:L	0.145	**<0.001**
	C:M	0.117	*0.051*
	L:M	0.028	0.653

Table S6. The effect of the length of the growing season *t* - 1 on flowering density in *E. latifolium* affected by study area and community group. There is an interaction between the factors. The differences between estimated effect of the length of the growing season *t* - 1 for the compared groups of levels of factors (Δ levels) are shown with accompanying p-values.

Fixed factor	Levels	Δ levels	p
Study area : community group	TC:TL	0.244	**<0.001**
	TC:TM	0.217	*0.069*
	TC:SC	0.131	0.103
	TC:SL	0.147	0.933
	TC:SM	0.084	0.626
	TL:TM	0.027	0.815
	TL:SC	0.375	**<0.001**
	TL:SL	0.391	**<0.001**
	TL:SM	0.328	**0.023**
	TM:SC	0.348	**0.004**
	TM:SL	0.364	**0.003**
	TM:SM	0.301	**0.037**
	SC:SL	0.016	0.858
	SC:SM	0.047	0.744
	SL:SM	0.063	0.663

Appendix S3. Summarising statistical analyses

Table S7. The effect of precipitation May - June$_{t-1}$ on flowering density in *E. latifolium* affected by study area, community group and mowing regime, no interactions are demonstrated. The differences between estimated effect of precipitation in spring$_{t-1}$ for the compared levels of factors (Δ levels) are shown with accompanying p-values.

Fixed factor	Levels	Δ levels	p
Study area	T:S	0.090	**<0.001**
Community group	C:L	0.044	0.163
	C:M	0.057	0.232
	L:M	0.101	**0.034**
Mowing regime	0:0.25	0.054	0.201
	0:0.5	0.077	**0.003**
	0:1	0.035	0.502
	0.25:0.5	0.023	0.587
	0.25:1	0.019	0.727
	0.5:1	0.042	0.436

Table S8. The effect of precipitation in July$_{t-1}$ on flowering density in *E. latifolium* affected by mowing regime and the interacting factors study area and community group. The differences between estimated effect of precipitation in July$_{t-1}$ for the compared groups of levels of factors (Δ levels) are shown with accompanying p-values.

Fixed factor	Levels	Δ levels	p
Mowing regime	0:0.25	0.031	0.508
	0:0.5	0.078	**0.008**
	0:1	0.031	0.604
	0.25:0.5	0.109	**0.022**
	0.25:1	0.062	0.297
	0.5:1	0.047	0.428
Study area : community group	TC:TL	0.176	**0.001**
	TC:TM	0.054	0.574
	TC:SC	0.084	0.204
	TC:SL	0.103	0.147
	TC:SM	0.022	0.851
	TL:TM	0.122	0.204
	TL:SC	0.260	**<0.001**
	TL:SL	0.279	**0.006**
	TL:SM	0.198	*0.089*
	TM:SC	0.138	0.152
	TM:SL	0.157	0.424
	TM:SM	0.076	0.513
	SC:SL	0.019	0.525
	SC:SM	0.062	0.591
	SL:SM	0.081	0.481

Table S9. The effect of precipitation in October$_{t\text{-}1}$ on flowering density in *E. latifolium* affected by study area and community group. There is an interaction between the factors. The differences between estimated effect of precipitation in October$_{t\text{-}1}$ for the compared groups of levels of factors (Δ levels) are shown with accompanying p-values.

Fixed factor	Levels	Δ levels	p
Study area : community group	TC:TL	0.136	**0.039**
	TC:TM	0.070	0.557
	TC:SC	0.083	0.307
	TC:SL	0.004	0.968
	TC:SM	0.076	0.528
	TL:TM	0.066	0.585
	TL:SC	0.053	0.510
	TL:SL	0.132	0.138
	TL:SM	0.060	0.482
	TM:SC	0.013	0.919
	TM:SL	0.066	0.577
	TM:SM	0.006	0.971
	SC:SL	0.079	0.374
	SC:SM	0.007	0.962
	SL:SM	0.072	0.832

Doctoral theses in Biology
Norwegian University of Science and Technology
Department of Biology

Year	Name	Degree	Title
1974	Tor-Henning Iversen	Dr. philos Botany	The roles of statholiths, auxin transport, and auxin metabolism in root gravitropism
1978	Tore Slagsvold	Dr. philos. Zoology	Breeding events of birds in relation to spring temperature and environmental phenology.
1978	Egil Sakshaug	Dr.philos Botany	"The influence of environmental factors on the chemical composition of cultivated and natural populations of marine phytoplankton"
1980	Arnfinn Langeland	Dr. philos. Zoology	Interaction between fish and zooplankton populations and their effects on the material utilization in a freshwater lake.
1980	Helge Reinertsen	Dr. philos Botany	The effect of lake fertilization on the dynamics and stability of a limnetic ecosystem with special reference to the phytoplankton
1982	Gunn Mari Olsen	Dr. scient Botany	Gravitropism in roots of *Pisum sativum* and *Arabidopsis thaliana*
1982	Dag Dolmen	Dr. philos. Zoology	Life aspects of two sympartic species of newts (*Triturus, Amphibia*) in Norway, with special emphasis on their ecological niche segregation.
1984	Eivin Røskaft	Dr. philos. Zoology	Sociobiological studies of the rook *Corvus frugilegus.*
1984	Anne Margrethe Cameron	Dr. scient Botany	Effects of alcohol inhalation on levels of circulating testosterone, follicle stimulating hormone and luteinzing hormone in male mature rats
1984	Asbjørn Magne Nilsen	Dr. scient Botany	Alveolar macrophages from expectorates – Biological monitoring of workers exosed to occupational air pollution. An evaluation of the AM-test
1985	Jarle Mork	Dr. philos. Zoology	Biochemical genetic studies in fish.
1985	John Solem	Dr. philos. Zoology	Taxonomy, distribution and ecology of caddisflies (*Trichoptera*) in the Dovrefjell mountains.
1985	Randi E. Reinertsen	Dr. philos. Zoology	Energy strategies in the cold: Metabolic and thermoregulatory adaptations in small northern birds.
1986	Bernt-Erik Sæther	Dr. philos. Zoology	Ecological and evolutionary basis for variation in reproductive traits of some vertebrates: A comparative approach.
1986	Torleif Holthe	Dr. philos. Zoology	Evolution, systematics, nomenclature, and zoogeography in the polychaete orders *Oweniimorpha* and *Terebellomorpha*, with special reference to the Arctic and Scandinavian fauna.
1987	Helene Lampe	Dr. scient. Zoology	The function of bird song in mate attraction and territorial defence, and the importance of song repertoires.

1987	Olav Hogstad	Dr. philos. Zoology	Winter survival strategies of the Willow tit *Parus montanus*.
1987	Jarle Inge Holten	Dr. philos Botany	Autecological investigations along a coust-inland transect at Nord-Møre, Central Norway
1987	Rita Kumar	Dr. scient Botany	Somaclonal variation in plants regenerated from cell cultures of *Nicotiana sanderae* and *Chrysanthemum morifolium*
1987	Bjørn Åge Tømmerås	Dr. scient. Zoology	Olfaction in bark beetle communities: Interspecific interactions in regulation of colonization density, predator - prey relationship and host attraction.
1988	Hans Christian Pedersen	Dr. philos. Zoology	Reproductive behaviour in willow ptarmigan with special emphasis on territoriality and parental care.
1988	Tor G. Heggberget	Dr. philos. Zoology	Reproduction in Atlantic Salmon (*Salmo salar*): Aspects of spawning, incubation, early life history and population structure.
1988	Marianne V. Nielsen	Dr. scient. Zoology	The effects of selected environmental factors on carbon allocation/growth of larval and juvenile mussels (*Mytilus edulis*).
1988	Ole Kristian Berg	Dr. scient. Zoology	The formation of landlocked Atlantic salmon (*Salmo salar* L.).
1989	John W. Jensen	Dr. philos. Zoology	Crustacean plankton and fish during the first decade of the manmade Nesjø reservoir, with special emphasis on the effects of gill nets and salmonid growth.
1989	Helga J. Vivås	Dr. scient. Zoology	Theoretical models of activity pattern and optimal foraging: Predictions for the Moose *Alces alces*.
1989	Reidar Andersen	Dr. scient. Zoology	Interactions between a generalist herbivore, the moose *Alces alces*, and its winter food resources: a study of behavioural variation.
1989	Kurt Ingar Draget	Dr. scient Botany	Alginate gel media for plant tissue culture,
1990	Bengt Finstad	Dr. scient. Zoology	Osmotic and ionic regulation in Atlantic salmon, rainbow trout and Arctic charr: Effect of temperature, salinity and season.
1990	Hege Johannesen	Dr. scient. Zoology	Respiration and temperature regulation in birds with special emphasis on the oxygen extraction by the lung.
1990	Åse Krøkje	Dr. scient Botany	The mutagenic load from air pollution at two work-places with PAH-exposure measured with Ames Salmonella/microsome test
1990	Arne Johan Jensen	Dr. philos. Zoology	Effects of water temperature on early life history, juvenile growth and prespawning migrations of Atlantic salmion (*Salmo salar*) and brown trout (*Salmo trutta*): A summary of studies in Norwegian streams.
1990	Tor Jørgen Almaas	Dr. scient. Zoology	Pheromone reception in moths: Response characteristics of olfactory receptor neurons to intra- and interspecific chemical cues.
1990	Magne Husby	Dr. scient. Zoology	Breeding strategies in birds: Experiments with the Magpie *Pica pica*.
1991	Tor Kvam	Dr. scient. Zoology	Population biology of the European lynx (*Lynx lynx*) in Norway.
1991	Jan Henning L'Abêe Lund	Dr. philos. Zoology	Reproductive biology in freshwater fish, brown trout *Salmo trutta* and roach *Rutilus rutilus* in particular.

1991	Asbjørn Moen	Dr. philos Botany	The plant cover of the boreal uplands of Central Norway. I. Vegetation ecology of Sølendet nature reserve; haymaking fens and birch woodlands
1991	Else Marie Løbersli	Dr. scient Botany	Soil acidification and metal uptake in plants
1991	Trond Nordtug	Dr. scient. Zoology	Reflctometric studies of photomechanical adaptation in superposition eyes of arthropods.
1991	Thyra Solem	Dr. scient Botany	Age, origin and development of blanket mires in Central Norway
1991	Odd Terje Sandlund	Dr. philos. Zoology	The dynamics of habitat use in the salmonid genera *Coregonus* and *Salvelinus*: Ontogenic niche shifts and polymorphism.
1991	Nina Jonsson	Dr. philos.	Aspects of migration and spawning in salmonids.
1991	Atle Bones	Dr. scient Botany	Compartmentation and molecular properties of thioglucoside glucohydrolase (myrosinase)
1992	Torgrim Breiehagen	Dr. scient. Zoology	Mating behaviour and evolutionary aspects of the breeding system of two bird species: the Temminck's stint and the Pied flycatcher.
1992	Anne Kjersti Bakken	Dr. scient Botany	The influence of photoperiod on nitrate assimilation and nitrogen status in timothy (*Phleum pratense* L.)
1992	Tycho Anker-Nilssen	Dr. scient. Zoology	Food supply as a determinant of reproduction and population development in Norwegian Puffins *Fratercula arctica*
1992	Bjørn Munro Jenssen	Dr. philos. Zoology	Thermoregulation in aquatic birds in air and water: With special emphasis on the effects of crude oil, chemically treated oil and cleaning on the thermal balance of ducks.
1992	Arne Vollan Aarset	Dr. philos. Zoology	The ecophysiology of under-ice fauna: Osmotic regulation, low temperature tolerance and metabolism in polar crustaceans.
1993	Geir Slupphaug	Dr. scient Botany	Regulation and expression of uracil-DNA glycosylase and O^6-methylguanine-DNA methyltransferase in mammalian cells
1993	Tor Fredrik Næsje	Dr. scient. Zoology	Habitat shifts in coregonids.
1993	Yngvar Asbjørn Olsen	Dr. scient. Zoology	Cortisol dynamics in Atlantic salmon, *Salmo salar* L.: Basal and stressor-induced variations in plasma levels ans some secondary effects.
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1993	Thrine L. M. Heggberget	Dr. scient. Zoology	Reproductive strategy and feeding ecology of the Eurasian otter *Lutra lutra*.
1993	Kjetil Bevanger	Dr. scient. Zoology	Avian interactions with utility structures, a biological approach.
1993	Kåre Haugan	Dr. scient Bothany	Mutations in the replication control gene trfA of the broad host-range plasmid RK2
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1994	Kjell Inge Reitan	Dr. scient Botany	Nutritional effects of algae in first-feeding of marine fish larvae
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1996	Christina M. S. Pereira	Dr. scient. Zoology	Glucose metabolism in salmonids: Dietary effects and hormonal regulation.
1996	Jan Fredrik Børseth	Dr. scient. Zoology	The sodium energy gradients in muscle cells of *Mytilus edulis* and the effects of organic xenobiotics.

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1997	Jon Arne Grøttum	Dr. scient. Zoology	Physiological effects of reduced water quality on fish in aquaculture.
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1997	Torgeir Nygård	Dr. scient. Zoology	Temporal and spatial trends of pollutants in birds in Norway: Birds of prey and Willow Grouse used as Biomonitors.
1997	Signe Nybø	Dr. scient. Zoology	Impacts of long-range transported air pollution on birds with particular reference to the dipper *Cinclus cinclus* in southern Norway.
1997	Atle Wibe	Dr. scient. Zoology	Identification of conifer volatiles detected by receptor neurons in the pine weevil (*Hylobius abietis*), analysed by gas chromatography linked to electrophysiology and to mass spectrometry.
1997	Rolv Lundheim	Dr. scient. Zoology	Adaptive and incidental biological ice nucleators.
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1997	Jarle Tufto	Dr. scient. Zoology	Gene flow and genetic drift in geographically structured populations: Ecological, population genetic, and statistical models
1997	Trygve Hesthagen	Dr. philos. Zoology	Population responces of Arctic charr (*Salvelinus alpinus* (L.)) and brown trout (*Salmo trutta* L.) to acidification in Norwegian inland waters
1997	Trygve Sigholt	Dr. philos. Zoology	Control of Parr-smolt transformation and seawater tolerance in farmed Atlantic Salmon (*Salmo salar*) Effects of photoperiod, temperature, gradual seawater acclimation, NaCl and betaine in the diet
1997	Jan Østnes	Dr. scient. Zoology	Cold sensation in adult and neonate birds
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1998	Thor Harald Ringsby	Dr. scient. Zoology	Variation in space and time: The biology of a House sparrow metapopulation
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1998	Gunnar Austrheim	Dr. scient Botany	Plant biodiversity and land use in subalpine grasslands. – A conservtaion biological approach.
1998	Bente Gunnveig Berg	Dr. scient. Zoology	Encoding of pheromone information in two related moth species
1999	Kristian Overskaug	Dr. scient. Zoology	Behavioural and morphological characteristics in Northern Tawny Owls *Strix aluco*: An intra- and interspecific comparative approach
1999	Hans Kristen Stenøien	Dr. scient Bothany	Genetic studies of evolutionary processes in various populations of nonvascular plants (mosses, liverworts and hornworts)
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1999	Ingvar Stenberg	Dr. scient. Zoology	Habitat selection, reproduction and survival in the White-backed Woodpecker *Dendrocopos leucotos*
1999	Stein Olle Johansen	Dr. scient Botany	A study of driftwood dispersal to the Nordic Seas by dendrochronology and wood anatomical analysis.
1999	Trina Falck Galloway	Dr. scient. Zoology	Muscle development and growth in early life stages of the Atlantic cod (*Gadus morhua* L.) and Halibut (*Hippoglossus hippoglossus* L.)
1999	Marianne Giæver	Dr. scient. Zoology	Population genetic studies in three gadoid species: blue whiting (*Micromisistius poutassou*), haddock (*Melanogrammus aeglefinus*) and cod (*Gradus morhua*) in the North-East Atlantic
1999	Hans Martin Hanslin	Dr. scient Botany	The impact of environmental conditions of density dependent performance in the boreal forest bryophytes *Dicranum majus*, *Hylocomium splendens*, *Plagiochila asplenigides*, *Ptilium crista-castrensis* and *Rhytidiadelphus lokeus*.
1999	Ingrid Bysveen Mjølnerød	Dr. scient. Zoology	Aspects of population genetics, behaviour and performance of wild and farmed Atlantic salmon (*Salmo salar*) revealed by molecular genetic techniques
1999	Else Berit Skagen	Dr. scient Botany	The early regeneration process in protoplasts from *Brassica napus* hypocotyls cultivated under various g-forces
1999	Stein-Are Sæther	Dr. philos. Zoology	Mate choice, competition for mates, and conflicts of interest in the Lekking Great Snipe
1999	Katrine Wangen Rustad	Dr. scient. Zoology	Modulation of glutamatergic neurotransmission related to cognitive dysfunctions and Alzheimer's disease
1999	Per Terje Smiseth	Dr. scient. Zoology	Social evolution in monogamous families: mate choice and conflicts over parental care in the Bluethroat (*Luscinia s. svecica*)
1999	Gunnbjørn Bremset	Dr. scient. Zoology	Young Atlantic salmon (*Salmo salar* L.) and Brown trout (*Salmo trutta* L.) inhabiting the deep pool habitat, with special reference to their habitat use, habitat preferences and competitive interactions

1999 Frode Ødegaard	Dr. scient. Zoology	Host spesificity as parameter in estimates of arhrophod species richness
1999 Sonja Andersen	Dr. scient Bothany	Expressional and functional analyses of human, secretory phospholipase A2
2000 Ingrid Salvesen, I	Dr. scient Botany	Microbial ecology in early stages of marine fish: Development and evaluation of methods for microbial management in intensive larviculture
2000 Ingar Jostein Øien	Dr. scient. Zoology	The Cuckoo (*Cuculus canorus*) and its host: adaptions and counteradaptions in a coevolutionary arms race
2000 Pavlos Makridis	Dr. scient Botany	Methods for the microbial econtrol of live food used for the rearing of marine fish larvae
2000 Sigbjørn Stokke	Dr. scient. Zoology	Sexual segregation in the African elephant (*Loxodonta africana*)
2000 Odd A. Gulseth	Dr. philos. Zoology	Seawater tolerance, migratory behaviour and growth of Charr, (*Salvelinus alpinus*), with emphasis on the high Arctic Dieset charr on Spitsbergen, Svalbard
2000 Pål A. Olsvik	Dr. scient. Zoology	Biochemical impacts of Cd, Cu and Zn on brown trout (*Salmo trutta*) in two mining-contaminated rivers in Central Norway
2000 Sigurd Einum	Dr. scient. Zoology	Maternal effects in fish: Implications for the evolution of breeding time and egg size
2001 Jan Ove Evjemo	Dr. scient. Zoology	Production and nutritional adaptation of the brine shrimp *Artemia* sp. as live food organism for larvae of marine cold water fish species
2001 Olga Hilmo	Dr. scient Botany	Lichen response to environmental changes in the managed boreal forset systems
2001 Ingebrigt Uglem	Dr. scient. Zoology	Male dimorphism and reproductive biology in corkwing wrasse (*Symphodus melops* L.)
2001 Bård Gunnar Stokke	Dr. scient. Zoology	Coevolutionary adaptations in avian brood parasites and their hosts
2002 Ronny Aanes	Dr. scient	Spatio-temporal dynamics in Svalbard reindeer (*Rangifer tarandus platyrhynchus*)
2002 Mariann Sandsund	Dr. scient. Zoology	Exercise- and cold-induced asthma. Respiratory and thermoregulatory responses
2002 Dag-Inge Øien	Dr. scient Botany	Dynamics of plant communities and populations in boreal vegetation influenced by scything at Sølendet, Central Norway
2002 Frank Rosell	Dr. scient. Zoology	The function of scent marking in beaver (*Castor fiber*)
2002 Janne Østvang	Dr. scient Botany	The Role and Regulation of Phospholipase A_2 in Monocytes During Atherosclerosis Development
2002 Terje Thun	Dr.philos Biology	Dendrochronological constructions of Norwegian conifer chronologies providing dating of historical material
2002 Birgit Hafjeld Borgen	Dr. scient Biology	Functional analysis of plant idioblasts (Myrosin cells) and their role in defense, development and growth
2002 Bård Øyvind Solberg	Dr. scient Biology	Effects of climatic change on the growth of dominating tree species along major environmental gradients
2002 Per Winge	Dr. scient Biology	The evolution of small GTP binding proteins in cellular organisms. Studies of RAC GTPases in *Arabidopsis thaliana* and

2002	Henrik Jensen	Dr. scient Biology	Causes and consequenses of individual variation in fitness-related traits in house sparrows
2003	Jens Rohloff	Dr. philos Biology	Cultivation of herbs and medicinal plants in Norway – Essential oil production and quality control
2003	Åsa Maria O. Espmark Wibe	Dr. scient Biology	Behavioural effects of environmental pollution in threespine stickleback *Gasterosteus aculeatur* L.
2003	Dagmar Hagen	Dr. scient Biology	Assisted recovery of disturbed arctic and alpine vegetation – an integrated approach
2003	Bjørn Dahle	Dr. scient Biology	Reproductive strategies in Scandinavian brown bears
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2003	Kristian Hassel	Dr.scient Biology	Life history characteristics and genetic variation in an expanding species, *Pogonatum dentatum*
2003	David Alexander Rae	Dr.scient Biology	Plant- and invertebrate-community responses to species interaction and microclimatic gradients in alpine and Artic environments
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2004	Torkild Bakken	Dr.scient Biology	A revision of Nereidinae (Polychaeta, Nereididae)
2004	Ingar Pareliussen	Dr.scient Biology	Natural and Experimental Tree Establishment in a Fragmented Forest, Ambohitantely Forest Reserve, Madagascar
2004	Tore Brembu	Dr.scient Biology	Genetic, molecular and functional studies of RAC GTPases and the WAVE-like regulatory protein complex in *Arabidopsis thaliana*
2004	Liv S. Nilsen	Dr.scient Biology	Coastal heath vegetation on central Norway; recent past, present state and future possibilities
2004	Hanne T. Skiri	Dr.scient Biology	Olfactory coding and olfactory learning of plant odours in heliothine moths. An anatomical, physiological and behavioural study of three related species (*Heliothis virescens, Helicoverpa armigera* and *Helicoverpa assulta*).
2004	Lene Østby	Dr.scient Biology	Cytochrome P4501A (CYP1A) induction and DNA adducts as biomarkers for organic pollution in the natural environment
2004	Emmanuel J. Gerreta	Dr. philos Biology	The Importance of Water Quality and Quantity in the Tropical Ecosystems, Tanzania
2004	Linda Dalen	Dr.scient Biology	Dynamics of Mountain Birch Treelines in the Scandes Mountain Chain, and Effects of Climate Warming

2004	Lisbeth Mehli	Dr.scient Biology	Polygalacturonase-inhibiting protein (PGIP) in cultivated strawberry (*Fragaria* x *ananassa*): characterisation and induction of the gene following fruit infection by *Botrytis cinerea*
2004	Børge Moe	Dr.scient Biology	Energy-Allocation in Avian Nestlings Facing Short-Term Food Shortage
2005	Matilde Skogen Chauton	Dr.scient Biology	Metabolic profiling and species discrimination from High-Resolution Magic Angle Spinning NMR analysis of whole-cell samples
2005	Sten Karlsson	Dr.scient Biology	Dynamics of Genetic Polymorphisms
2005	Terje Bongard	Dr.scient Biology	Life History strategies, mate choice, and parental investment among Norwegians over a 300-year period
2005	Tonette Røstelien	ph.d Biology	Functional characterisation of olfactory receptor neurone types in heliothine moths
2005	Erlend Kristiansen	Dr.scient Biology	Studies on antifreeze proteins
2005	Eugen G. Sørmo	Dr.scient Biology	Organochlorine pollutants in grey seal (*Halichoerus grypus*) pups and their impact on plasma thyrid hormone and vitamin A concentrations.
2005	Christian Westad	Dr.scient Biology	Motor control of the upper trapezius
2005	Lasse Mork Olsen	ph.d Biology	Interactions between marine osmo- and phagotrophs in different physicochemical environments
2005	Åslaug Viken	PhD Biology	Implications of mate choice for the management of small populations
2005	Ariaya Hymete Sahle Dingle	PhD Biology	Investigation of the biological activities and chemical constituents of selected *Echinops* spp. growing in Ethiopia
2005	Anders Gravbrøt Finstad	ph.d Biology	Salmonid fishes in a changing climate: The winter challenge
2005	Shimane Washington Makabu	ph.d Biology	Interactions between woody plants, elephants and other browsers in the Chobe Riverfront, Botswana
2005	Kjartan Østbye	Dr.scient Biology	The European whitefish *Coregonus lavaretus* (L.) species complex: historical contingency and adaptive radiation
2006	Kari Mette Murvoll	ph.d Biology	Levels and effects of persistent organic pollutans (POPs) in seabirds Retinoids and α-tocopherol – potential biomakers of POPs in birds?
2006	Ivar Herfindal	Dr.scient Biology	Life history consequences of environmental variation along ecological gradients in northern ungulates
2006	Nils Egil Tokle	ph.d Biology	Are the ubiquitous marine copepods limited by food or predation? Experimental and field-based studies with main focus on *Calanus finmarchicus*
2006	Jan Ove Gjershaug	Dr.philos Biology	Taxonomy and conservation status of some booted eagles in south-east Asia
2006	Jon Kristian Skei	Dr.scient Biology	Conservation biology and acidification problems in the breeding habitat of amphibians in Norway
2006	Johanna Järnegren	ph.d Biology	Acesta Oophaga and Acesta Excavata – a study of hidden biodiversity

2006	Bjørn Henrik Hansen	ph.d Biology	Metal-mediated oxidative stress responses in brown trout (*Salmo trutta*) from mining contaminated rivers in Central Norway
2006	Vidar Grøtan	ph.d Biology	Temporal and spatial effects of climate fluctuations on population dynamics of vertebrates
2006	Jafari R Kideghesho	Ph.d Biology	Wildlife conservation and local land use conflicts in western Serengeti, Corridor Tanzania
2006	Anna Maria Billing	ph.d Biology	Reproductive decisions in the sex role reversed pipefish *Syngnathus typhle*: when and how to invest in reproduction
2006	Henrik Pärn	ph.d Biology	Female ornaments and reproductive biology in the bluethroat
2006	Anders J. Fjellheim	ph.d Biology	Selection and administration of probiotic bacteria to marine fish larvae
2006	P. Andreas Svensson	ph.d Biology	Female coloration, egg carotenoids and reproductive success: gobies as a model system
2007	Sindre A. Pedersen	ph.d Biology	Metal binding proteins and antifreeze proteins in the beetle *Tenebrio molitor* - a study on possible competition for the semi-essential amino acid cysteine
2007	Kasper Hancke	ph.d Biology	Photosynthetic responses as a function of light and temperature: Field and laboratory studies on marine microalgae
2007	Tomas Holmern	ph.d Biology	Bushmeat hunting in the western Serengeti: Implications for community-based conservation
2007	Kari Jørgensen	ph.d Biology	Functional tracing of gustatory receptor neurons in the CNS and chemosensory learning in the moth *Heliothis virescens*
2007	Stig Ulland	ph.d Biology	Functional Characterisation of Olfactory Receptor Neurons in the Cabbage Moth, (*Mamestra brassicae* L.) (Lepidoptera, Noctuidae). Gas Chromatography Linked to Single Cell Recordings and Mass Spectrometry
2007	Snorre Henriksen	ph.d Biology	Spatial and temporal variation in herbivore resources at northern latitudes
2007	Roelof Frans May	ph.d Biology	Spatial Ecology of Wolverines in Scandinavia
2007	Vedasto Gabriel Ndibalema	ph.d Biology	Demographic variation, distribution and habitat use between wildebeest sub-populations in the Serengeti National Park, Tanzania
2007	Julius William Nyahongo	ph.d Biology	Depredation of Livestock by wild Carnivores and Illegal Utilization of Natural Resources by Humans in the Western Serengeti, Tanzania
2007	Shombe Ntaraluka Hassan	ph.d Biology	Effects of fire on large herbivores and their forage resources in Serengeti, Tanzania
2007	Per-Arvid Wold	ph.d Biology	Functional development and response to dietary treatment in larval Atlantic cod *(Gadus morhua* L.) Focus on formulated diets and early weaning

2007	Anne Skjetne Mortensen	ph.d Biology	Toxicogenomics of Aryl Hydrocarbon- and Estrogen Receptor Interactions in Fish: Mechanisms and Profiling of Gene Expression Patterns in Chemical Mixture Exposure Scenarios
2008	Brage Bremset Hansen	ph.d Biology	The Svalbard reindeer (*Rangifer tarandus platyrhynchus*) and its food base: plant-herbivore interactions in a high-arctic ecosystem
2008	Jiska van Dijk	ph.d Biology	Wolverine foraging strategies in a multiple-use landscape
2008	Flora John Magige	ph.d Biology	The ecology and behaviour of the Masai Ostrich (Struthio camelus massaicus) in the Serengeti Ecosystem, Tanzania
2008	Bernt Rønning	ph.d Biology	Sources of inter- and intra-individual variation in basal metabolic rate in the zebra finch, (*Taeniopygia guttata*)
2008	Sølvi Wehn	ph.d Biology	Biodiversity dynamics in semi-natural mountain landscapes. - A study of consequences of changed agricultural practices in Eastern Jotunheimen
2008	Trond Moxness Kortner	ph.d Biology	"The Role of Androgens on previtellogenic oocyte growth in Atlantic cod (*Gadus morhua*): Identification and patterns of differentially expressed genes in relation to Stereological Evaluations"
2008	Katarina Mariann Jørgensen	Dr.Scient Biology	The role of platelet activating factor in activation of growth arrested keratinocytes and re-epithelialisation
2008	Tommy Jørstad	ph.d Biology	Statistical Modelling of Gene Expression Data
2008	Anna Kusnierczyk	ph.d Bilogy	*Arabidopsis thaliana* Responses to Aphid Infestation
2008	Jussi Evertsen	ph.d Biology	Herbivore sacoglossans with photosynthetic chloroplasts
2008	John Eilif Hermansen	ph.d Biology	Mediating ecological interests between locals and globals by means of indicators. A study attributed to the asymmetry between stakeholders of tropical forest at Mt. Kilimanjaro, Tanzania
2008	Ragnhild Lyngved	ph.d Biology	Somatic embryogenesis in *Cyclamen persicum.* Biological investigations and educational aspects of cloning
2008	Line Elisabeth Sundt-Hansen	ph.d Biology	Cost of rapid growth in salmonid fishes
2008	Line Johansen	ph.d Biology	Exploring factors underlying fluctuations in white clover populations – clonal growth, population structure and spatial distribution
2009	Astrid Jullumstrø Feuerherm	ph.d Biology	Elucidation of molecular mechanisms for pro-inflammatory phospholipase A2 in chronic disease

2009	Pål Kvello	ph.d Biology	Neurons forming the network involved in gustatory coding and learning in the moth *Heliothis virescens:* Physiological and morphological characterisation, and integration into a standard brain atlas
2009	Trygve Devold Kjellsen	ph.d Biology	Extreme Frost Tolerance in Boreal Conifers
2009	Johan Reinert Vikan	Ph.d Biology	Coevolutionary interactions between common cuckoos *Cuculus canorus* and *Fringilla* finches
2009	Zsolt Volent	ph.d Biology	Remote sensing of marine environment: Applied surveillance with focus on optical properties of phytoplankton, coloured organic matter and suspended matter
2009	Lester Rocha	ph.d Biology	Functional responses of perennial grasses to simulated grazing and resource availability
2009	Dennis Ikanda	ph.d Biology	Dimensions of a Human-lion conflict: Ecology of human predation and persecution of African lions (*Panthera leo*) in Tanzania
2010	Huy Quang Nguyen	pd.d Biology	Egg characteristics and development of larval digestive function of cobia (*Rachycentron canadum*) in response to dietary treatments -Focus on formulated diets
2010	Eli Kvingedal	ph.d Biology	Intraspecific competition in stream salmonids: the impact of environment and phenotype
2010	Sverre Lundemo	Pd.d Biology	Comparative studies of genetic structuring in Scandinavian populations of Arabidopsis thaliana and A. lyrata
2010	Iddi Mihijai Mfunda	ph.d Biology	Wildlife Conservation and People’s livelihoods: Lessons Learnt and Considerations for Improvements. Tha Case of Serengeti Ecosystem, Tanzania
2010	Anton Tinchov Antonov	ph.d Biology	Why do cuckoos lay strong-shelled eggs? Tests of the puncture resistance hypothesis