

# Pattern and process in Norwegian upland grasslands: an integrated ecological approach

Vigdis Vandvik

## INTRODUCTION

Over the past two centuries there has been an increasing awareness of the enormous influence that humans, and human activities, may exert on nature. This awareness was initially made possible by parallel changes in our economies and in our intellectual world-views during the late 18<sup>th</sup> and early 19<sup>th</sup> century. In this period, rapid developments in our political systems, economies, and technological status took place, and this resulted in industrialisation, urbanisation, and a rapid human population growth. In the course of a few decades, these changes dramatically affected landscapes that had previously been conceived as unchangeable (Worster 1994, Lawton 1999). At the same time, there was a shift in how history itself was intellectually conceived, a shift from an analytical and mechanistic world-view to a historical and process-oriented world-view (Randall 1926).

Since that time, much public and scientific attention has focused on the destructive effects human activities inflict on natural habitats (Worster 1994). The very dramatic changes resulting from urbanisation, industrialisation, and new infrastructure were first acknowledged. Later, we came to realise that factors such as intensified agricultural practices, nutrient leaching, and pollution may exert strong negative effects on the survival and persistence of species populations in the physically unaffected landscapes surrounding the actual impact. Today, the effects of species invasions, often due to deliberate or accidental introductions by man, and the effects of the increasing habitat fragmentation are receiving considerable attention (Hobbs and Hunneke 1992, Harrison and Bruna 1999). Along with the developing awareness of the vulnerability of nature came the idea that pristine landscapes have an intrinsic value, indeed so high that they could, and should, be protected from destruction (McIntosh 1985, Worster 1994). These ideas spread from the USA to Europe in the beginning of this century (Fægri 1988, Worster 1994). Nature conservation developed out of these traditions, and was mainly concerned with the protection of unspoilt, pristine nature from the depredations of man. In Norway, these insights arrived comparably late, and while a localised occurrence of rare plants was protected

for the first time at Dovre in 1922, the protection of larger areas, as national parks, did not start until the Rondane National Park was established in 1962 ([www.dirnat.no](http://www.dirnat.no)).

One of the earliest detailed 'ecological' publications describing a pre-industrial landscape is Gilbert White's *The Natural History of Selbourne* published in 1789. The book, a collection of letters written to the scientific nobility of the time, presents White's life-long fascination with, and detailed observations of, the natural world of his church parish in southern England. White presents a picture of an integrated, unchangeable, wholesome nature, where the needs of all species are provided for, and where man is free to harvest for his needs, to observe, and to enjoy. We have later come to realise, however, that humans also exerted an influence on what was perceived as the pristine landscapes of the past, and it has gradually emerged that these effects were more far-reaching than originally acknowledged. Ironically, these insights were sparked by some rather unexpected consequences of early attempts to conserve and protect these idyllic 'natural' landscapes. Rapid successional change occurred within carefully fenced off and protected reserves (Fægri 1988, citing experience from Sweden in the early 20<sup>th</sup> century). We now know that many of the important habitats for wildlife and biodiversity throughout Europe are semi-natural: they have been created and maintained by millennia of extensive, low-intensity land-use (Lawton 1999). Indeed, "The 'natural' landscapes of earlier times are now understood for what they really are: relics of earlier types of land-use" (Fægri 1988), or Cultural Landscapes. The long ecological histories of these formerly widespread habitats have evolutionary and ecological consequences: these landscapes typically harbour a great biological diversity. Calcareous grasslands may serve as a paradigmatic example. The conservation value of these relatively uncommon but visually attractive and floristically diverse grasslands was early valued (Sernander 1920) and the importance of land-use practices for their long-term sustainability appreciated (Selander 1955). The extremely high fine-scale diversity of chalk grasslands has intrigued ecologists for decades, and prompted theoretical developments in many branches of ecology, including the expansion

of niche theory to include the regeneration stage (Watt 1947, Grubb 1977, Rusch and Fernández-Palacios 1995), the consequences of fine-scale mobility (van der Maarel and Sykes 1993, Gigon and Leutert 1996), and the relationship between diversity at local and regional scales (Eriksson 1993, Zobel 1997). The emerging results are far from clear-cut, and can be summarised by quoting Michael Crawley, who in his preface to the 1986 edition of *Plant Ecology* (reprinted in Crawley 1997) coined the 'MC&I School' of ecology: "The factors responsible... are many, complex, and interacting".

Today, such semi-natural habitats are doubly threatened. On one hand, they are still being destroyed by new, increased, or intensified human activities such as urbanisation, intensified crop production, overgrazing, pollution, fertilisation, nutrient leaching, and species introductions. At the same time, the extensive, low-intensity land-use practices necessary to maintain these habitats are no longer economically feasible, and are therefore discontinued. The result is a general trend for areas of no- or high-intensity land-use to increase at the expense of areas of (traditional) extensive low-intensity land-use (e.g. WallisDeVries et al. 2002). Changes in disturbance regimes often have dramatic effects on community composition and structure, especially in natural or semi-natural systems with high diversity and long ecological histories (Hobbs and Hunneke 1992, Milchunas et al. 1988). Accordingly, the non-continuation of low-intensive land-use in semi-natural grassland has recently been identified as one of the major factors adversely affecting the flora and fauna in Europe (Stanners and Bordeau 1995) including Scandinavia (Bernes 1993, Fremstad and Moen 2001).

## SUMMER FARMS – MOUNTAIN LAND-USE SYSTEMS

The historical agricultural systems of temperate regions depended on livestock farming, as the animals served a dual function as food and as a supplier of the manure necessary to sustain the production of crops for human consumption. Such agricultural systems depend on large areas of unfertilised, fodder-producing habitats such as grassland pastures and mown hay-meadows. In regions with steep altitudinal gradients, the necessary extensive areas could not be found near the lowland settlements, so animals were transported up to the mountains during summer. The advantages, from an agro-economic point of view, are two-fold. First, the human population that narrow valleys and fjords could support was increased. Second, the animals could 'follow the spring' up into the mountain during the summer, and make use of the high nutrition quality of early-

season plant material for an extended period. This practice, essentially an altitudinal transhumance system, is known as 'summer farming' in Scandinavia, but is also known from mountainous regions elsewhere in Europe and Asia (Frödin 1929, Reinton 1961, Szabó 1970, Rhinschede 1988, Bonard and Dubost 1992, Amiaud et al. 2000). Ethnological (e.g. Reinton 1955, 1957, 1961, Bryn and Daugestad 2001), archaeological (e.g. Bjørge et al. 1992, Randers and Kvamme 1992), and pollen-analytical (e.g. Kvamme 1988, Kvamme et al. 1992) studies suggest that the practice dates back to prehistoric times, and that the extent of summer-farming areas has varied greatly through time, depending on population size and economy.

At the summer farms (sæter, støl, Fig. 1), the domestic animals were gathered in milking sheds or enclosures for milking and shelter at night, but were allowed to range freely in the mountains during the day. This created a landscape with large variation and strong gradients in grazing animal effects, which again resulted in very distinct vegetation patterns (Resvoll-Holmsen 1920, Nordhagen 1943, Spatz 1980, Bonard and Dubost 1992, Austrheim et al. 1999, Bryn and Daugestad 2001, Vandvik and Birks 2002). Weedy communities and productive manured grassland dominate the area immediately surrounding the houses and enclosures. As one moves away from these most heavily influenced areas, this heavily disturbed and manured vegetation gives way to extensive low-productive perennial grasslands. During centuries of continuous low-intensity land-use, the perennial grasslands at summer farms have become characteristic and stable vegetation types that are often very rich in species. Different floristic elements meet here; generalist grassland herbs and grasses, more demanding semi-natural grassland specialists, alpine plants that take advantage of the open vegetation structure created by the grazing animals, and common subalpine plants. Further away from the summer farms, these grasslands blend into the surrounding low-alpine dwarf-shrub heaths or subalpine birch woodland.

At the landscape scale, these grasslands at summer farms appear as 'habitat islands' that are scattered throughout extensive sub- and low-alpine heaths and woodlands. In the mountains of Norway, the total biomass harvested by grazing and mowing has decreased by 61% from 1939 to 1996 (Edelmann 1997). There is no uniform trend, however, as the intensity of land-use varies at all spatial scales, from regions and landscapes to individual summer farms. Many summer farms of today are in different stages of secondary succession after abandonment (Spatz 1980, Austrheim et al. 1999, Austrheim and Eriksson 2002, Vandvik and Birks 2002), and this variation is often more related to the interests and private economy of different landowners than to any



**Figure 1.** Summer farms and the subalpine landscape in the study area in Vangrøftdalen valley (see Fig. 2). The valley system covers an area of ca. 60 km<sup>2</sup> at altitudes between 700 – 800 metres above sea level (m.a.s.l.), and is surrounded by mountains reaching 1100 – 1200 m.a.s.l. The landscape is characterised by semi-natural subalpine birch forest and extensive mire systems, with summer farms scattered throughout. The 87 historical summer farms in the area are in different secondary successional stages from farms in current use, with free-ranging grazing animals, to farms abandoned more than 100 years ago.

ecologically relevant characteristics of the individual summer farms (*personal observation*). Despite their importance both for traditional agricultural practices and as an integral part of the mountain landscape, and the threat posed by the recent land-use changes, summer farms in the Scandinavian mountain range have received surprisingly little attention in the ecological literature (Nordic Council of Ministers 1989). The work presented here was initiated to contribute in the recent effort (Olsson 1998, Austrheim et al. 1999, Austrheim 2001, Austrheim and Eriksson 2001) to reduce this gap in knowledge.

## OBJECTIVES AND APPROACHES

This thesis aims to contribute to the understanding of the ecological patterns and processes of semi-natural grasslands in the mountain summer farming landscapes of Norway. These grasslands are shaped and maintained by centuries of continuous low-intensity land-use, but the land-use regimes are now changing as many summer farms have been abandoned through the last 50 to 100 years. The ecology of semi-natural grasslands and the effects of land-use change in subalpine and alpine areas have been comparatively little studied. It is therefore poorly understood how ecological

processes in semi-natural vegetation are affected by the constraints of cold climates.

I have chosen to approach the general aims and the study system from several different angles. The biological responses monitored range from floristic composition via field recruitment to the timing of germination in individual seeds, and the data originate from observational field studies via field experiments to phytotron experiments. The temporal scales and resolutions range from snapshot studies via day-to-day monitoring of germination and four-year field experiments to 40-year chronosequences. The data are analysed using different univariate and multivariate statistical procedures. A summary of the data, approaches, and major statistical methods used in each of the five individual papers is given in Table 1. The motivation for this integrated approach was two-fold: By comparing results emerging from different ecological approaches, spatial and temporal scales of investigation, and statistical testing procedures, I hope to maximise the scientific soundness of the conclusions and increase the ecological understanding emerging from this work. The aims of the individual papers are summarised below:

**PAPER I** The total floristic variability of a summer farm landscape is partitioned into within-farm and between-farm components, and the explanatory power of different environmental and land-use history variables at these two scales is investigated.

**PAPER II** The general effects of summer farming on the vegetation are delimited and interpreted on the basis of vegetation-environment relationships and functional trait responses along the farm-to-surrounds gradient.

**PAPER III** The revegetation of experimentally created fine-scale disturbances is monitored over four years. The compositional responses to gap, size, and edge effects and differences between successional stages are quantified and tested.

**PAPER IV** The phytotron germination responses of 11 grassland herbs are used to predict field regeneration strategies in relation to gap detection and seasonal timing of germination. These predictions are tested in a field experiment.

**PAPER V** Between-population variation in the phytotron germination responses of *Knautia arvensis* is investigated, and the results are related to climatic gradients within Norway.

The studies were carried out within subalpine grasslands at mountain summer farms in western (Paper I, Paper II) and eastern (Paper III, Paper IV, Paper V) Norway, and on seeds from five perennial grasslands in different regions of Norway (Paper V) (Fig. 2).

## THE ECOLOGICAL EFFECTS OF SUMMER FARMING

### *The farms-to-surrounds gradient*

The papers in this thesis investigate the effects of summer farming on vegetation at a series of scales over space and time. Up to recently, studies of the vegetation in these landscapes have mainly used phytosociological methods (e.g. Resvoll-Holmsen 1920, Nordhagen 1943, Knatterud 1974), and a first step in this work was therefore to carry out a general ecological analysis of the floristic variability and vegetation-environment relationships (Paper I). Relatively coarse-scale data, 4m<sup>2</sup> plots, were placed subjectively in order to ‘sample the variation’ at a number of summer farms, and a relatively large number of potential explanatory variables were measured. The vegetation types delimited within these data, based on a TWINSPAN classification (Vandvik and Birks 2002), match the results of previous studies (Nordhagen 1943, Knatterud 1974). The general gradient structure in these data suggests a picture of an ecological system with strong floristic gradients, and many potentially important environmental factors (Paper I). It is apparent that a relatively large fraction of the variance occurs within the individual summer farms, structured along a spatial farm-to-surrounds gradient. Within the data, floristic composition is more strongly related to this gradient than to gradients such as soil moisture, microclimate (as measured by a radiation index), altitude, bedrock, or land-use history. At one scale this is a relatively clear-cut result: it shows that the summer-farm areas are floristically distinct from the surrounding heathlands. The interpretation and evaluation of different potential causal factors become difficult, however, because many potentially important causal factors, including soil nutrient status, slope, and the spatial gradient are correlated (Paper I), and because the effects of grazing and trampling are very difficult to measure in observational studies.

In order to try to tease apart these different potential explanatory factors, a ‘functional approach’ study of these observational data was performed (Paper II). The idea behind such a study is that the identification of gradients in plant form and function makes it possible to relate directly to the ecological processes underlying the floristic gradients (Thompson et al. 1996, Campbell et al. 1999). While there has been considerable debate

GEOGRAPHICAL LOCATION	Røldal	Dalsbygda	Dalsbygda <sup>§</sup> Norway <sup>#</sup>	Dalsbygda <sup>§</sup> Norway <sup>#</sup>
NUMBER OF SITES	12 summer farms** 10 summer farms*	6 summer farms	1 summer farm <sup>§</sup> 2 localities <sup>#</sup>	1 summer farm <sup>§</sup> 5 localities <sup>#</sup>
OBSERVATIONAL UNITS	130 plots** 107 plots*	216 / 540 plots (at different spatial scales)	220 plots <sup>§</sup> 20 plots <sup>#</sup>	528 batches <sup>§</sup> 168 batches <sup>#</sup>
DATA RESOLUTION	4m <sup>2</sup>	39cm <sup>2</sup> , 625cm <sup>2</sup> (4m <sup>2</sup> )	625cm <sup>2</sup>	50 seeds per batch
SAMPLING DURATION AND RESOLUTION	1 census	4 years (7 censuses)	2 years (3 censuses)	30 days (7 censuses)
NUMBER OF TAXA	144 species** 189 species*	86 species	11 species <sup>§</sup> 2 populations <sup>#</sup>	11 species <sup>§</sup> 5 populations <sup>#</sup>
BIOLOGICAL RESPONSE MONITORED	Floristic composition (including bryophytes and lichens*)	Floristic composition Seedlings Vegetative recruits	Seedling emergence Seedling mortality	Time to germination
OBSERVATIONAL PREDICTORS	Environment Land-use Spatial location Functional traits*	Time Recruitment mode	Time Species <sup>§</sup>	Time Species <sup>§</sup> Population <sup>#</sup>
SUCCESSIONAL SEQUENCE SAMPLED	0, 10, 20, and 40 Years	0, 10, and 40 Years		
EXPERIMENTAL TREATMENTS		Gaps vs. Controls Gap size Edge effects	4 microsites (Gap, cut, controls)	Light Temperature Cold-stratification Gibberillic acid
MAJOR STATISTICAL METHODS	Ordination Variance partitioning Classification **	Principal Response Curves	ANOVA	Repeated- measures ANOVA
RESULTS REPORTED	<b>Paper 1*</b> <b>Paper 2**</b>	<b>Paper 3</b>	<b>Paper 4<sup>§</sup></b> <b>Paper 5<sup>#</sup></b>	<b>Paper 4<sup>§</sup></b> <b>Paper 5<sup>#</sup></b>

**Table 1.** A summary of the field and laboratory sampling and experimental designs, the spatial and temporal resolution of the data, experimental and observational predictors available, the biological response monitored, and the major statistical methods used in each of the five papers.

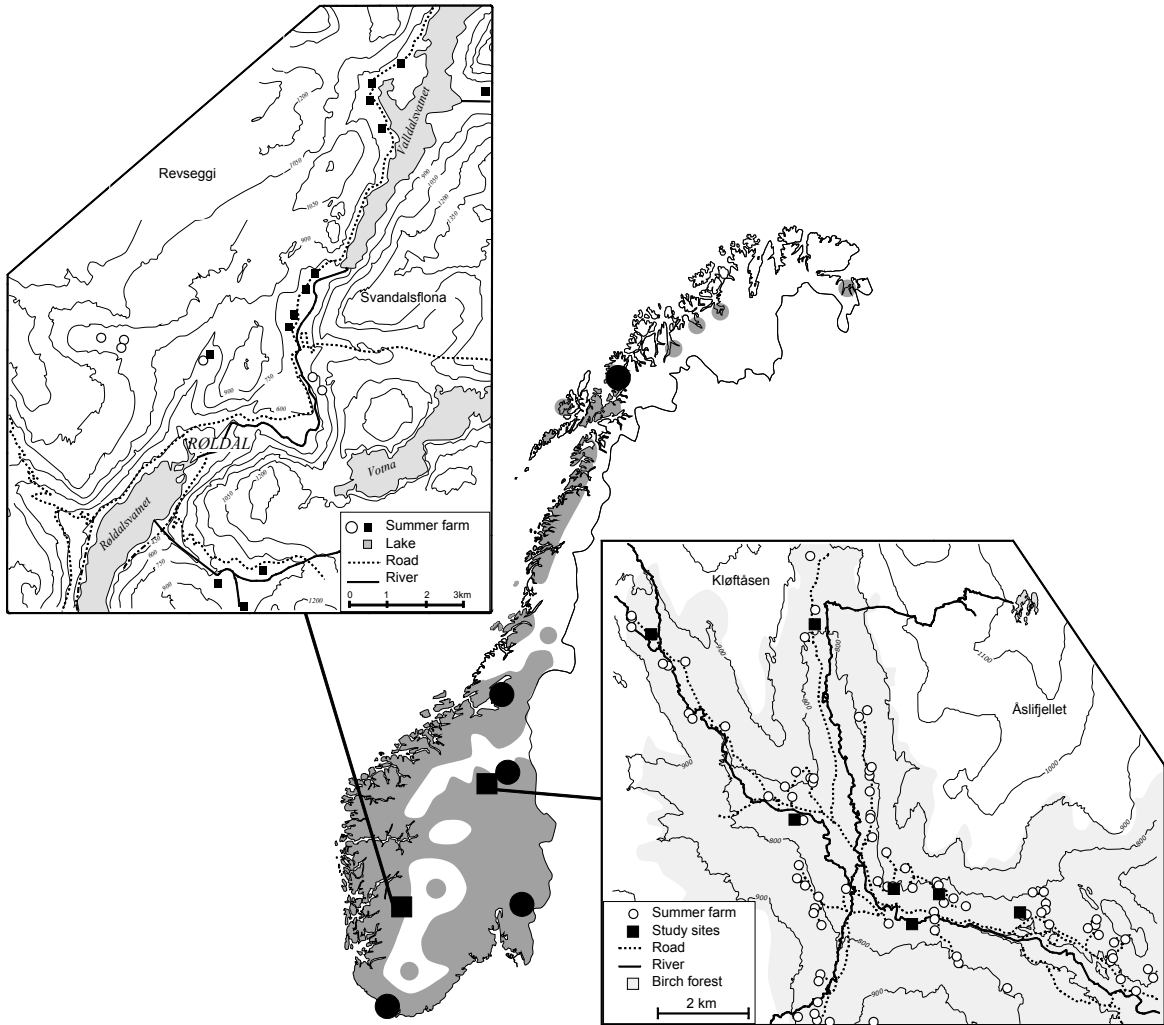
concerning the details, such as the expected inter-relationship between different classes of functional traits (Wilson 1990, Zobel 1992, Mabry et al. 2000) and the optimal level of detail (Grubb 1985, Grime 1989, Mabry et al. 2000), the advantages of the general approach are widely acknowledged (e.g. Díaz and Carbido 1997, McIntyre et al. 1999, Ducksworth et al. 2000). Here I essentially used this approach to ‘ask the plants how they perceive summer farms’. The interpretation, based on the concurrent use of environmental and functional explanatory variables, suggests that the gradient is one of decreasing disturbance and increasing environmental stress caused by decreasing grazing and manure effects away from farms (Paper II). The ‘functional approach’ is further elaborated in Paper III, where I investigate the differences between seed and vegetative recruits, and in Paper IV and Paper V where I focus specifically on traits of the seed regeneration phase in the plant life cycle.

The results of the ‘functional approach’ study in Paper II illustrate an important pitfall in vegetation science, namely that when ecological gradients are correlated (at summer farms: slope, soil fertility, and disturbance), this may introduce a bias into the analysis and interpretation of biological patterns. This becomes especially problematic if some potential causal factors are

more easily measured, at the scale of study, than others. The influence of the factors that are more difficult to measure and quantify may then tend to be systematically underestimated, or even ignored.

### *The effects of fine-scale disturbances*

Watt’s (1947) seminal paper on pattern and process in vegetation has inspired considerable research interest into how the creation, colonisation, and filling of fine-scale disturbances may influence the composition and structure of grasslands (Grubb 1977, see review by Bullock 2000). The general theme of disturbance was investigated, at different scales and in different degrees of detail, in Papers I, II, III, and IV. The broad-scale studies indicate that the overall disturbance regimes have considerable effects on the floristic composition, both between summer farms with different land-use histories (Paper I), and between 4m<sup>2</sup> plots along a farm-to-surrounds gradient (Paper II). Grazing animals may act as disturbance agents in vegetation through defoliation of established plants (Huntly 1990, Hulme 1996), as well as through the creation of bare-ground gaps by uprooting or trampling. In Paper III, I investigated the potential importance of this latter effect by following the revegetation of experimentally created gaps over three years (Fig.



**Figure 2.** A map of Norway, and of the two study areas, Vangrøftdalen, Os Municipality in eastern Norway (10°49'E, 62°37'N) (Paper I, Paper II), and Valldalen, Røldal Municipality in western Norway (6°55'E, 59°55'N) (Paper III, Paper IV, Paper V). Within each study area, major roads and waterways indicated. Contour intervals are in 100m (Vangrøftdalen) and 150m (Valldalen). All investigated summer farms are indicated with filled symbols. Additionally, all summer farms that have been in operation at some time after 1900 are indicated on the maps. The geographical distribution of *Knautia arvensis* is shaded on the map of Norway (Mossberg et al. 1992, Lid and Lid 1994), and the geographical locations of the populations used for Paper V are indicated.

3). The results show that recruitment into gaps is not directly proportional to the species abundances in the closed vegetation, resulting in a considerable and very persistent effect of gaps on the composition of the disturbed microsite (Paper III). Further, there is more to gap dynamics than simple on-off effects, as gaps of different sizes, and the edge-to-centre gradient within gaps are colonised by partially distinct assemblages of species, and as species responses are not constant across landscapes.

Overall, the gap-increasing species tend to colonise gaps from seeds rather than from clonal ingrowths (Paper III, see also van der Maarel and Sykes 1993, Gigon and Leutert 1996). A mechanism that could contribute to the high colonisation success of seedlings, both in absolute numbers and relative to clonal ingrowths, is the

very specific germination requirements found in many grassland species (Grubb 1977, 1985, Grime et al. 1981, Baskin and Baskin 1998). Such responses may function to inhibit germination of a subset of the species in closed vegetation, resulting in the accumulation of seed banks, and higher overall germination rates as well as differences in the relative abundance of species in gaps (e.g. Hutchings and Booth 1996). Once germinated, seedlings cannot rely on support or provision from the maternal plant during establishment, and competitive effects of established plants in a closed vegetation sward should therefore be more deleterious for seedlings than for clonal recruits. The high fraction of seed recruits appearing in these gaps contrasts the findings from many studies within perennial grasslands elsewhere (Rapp and Rabinowitz 1985, Coffin and Lauenroth 1989,

Milberg 1993, Arnthórsdóttir 1994, Kotanen 1997). The low productivity of summer farm grasslands, resulting from the relatively cold subalpine climate (Marchand 1996, Körner 1999), in combination with the relatively infertile soils of perennial grasslands at summer farms (Knattreud 1974, Austrheim et al. 1999, 2001, Paper I, Paper II), may contribute to explain these differences. This results in relatively slow vegetative growth and clonal encroachment, and the gaps will therefore be open to colonisation for extended periods of time, increasing the probability that seeds may reach them, germinate, and establish before the vegetation closes.

#### *Seed germination of subalpine grassland species*

Upon seed germination, the plant individuals pass from a relatively safe to perhaps the most vulnerable stage in the plant life cycle. Clearly, strategies or life-history traits that decrease the probability of encountering unacceptable growth conditions during germination and establishment may have a strong selective advantage (Kitajima and Fenner 2000). Generally, the germination of seeds may be regulated through two mechanisms: the seeds may have specific germination requirements or they may be dormant (defined as the non-germination under conditions that are suitable for germination, Vleeshouwers et al. 1995). Under stochastic environmental variation bet-hedging strategies (Venable and Brown 1988, Philippi 1993), that leave a fraction of the seeds dormant through periods of good germination conditions, ensure a carry-over of seeds across years and the build-up of persistent seedbanks that may buffer populations against years of high stochastic mortality. Seedling mortality risk is often not randomly distributed in space and time, however, but varies between vegetation types, between microsites with different water, light, and nutrient availabilities, and throughout the year (Mack and Pyke 1984). In such cases, seeds may exhibit environmental cueing responses, where very specific germination requirements may function to restrict germination onto times or places with relatively low mortality risk. Seed germination and dormancy has been intensively studied, it has been demonstrated that it may respond to a range of environmental factors, including temperature regime, light intensity or spectral quality, soil nutrients, moisture, and cold- or warm-stratification (reviewed by Baskin and Baskin 1998 and Fenner 2000).

These general considerations inspired some more detailed studies of the germination ecology of some characteristic plants of these grasslands (Paper IV, Paper V). As the germination ecology of plants growing in the Scandinavian

subalpine region has not previously been investigated (but see Anderson and Milberg (1998) for a study including boreal plant populations), a relatively broad approach was chosen. Eleven species that coexist within these grasslands, but otherwise represent as wide as possible ranges of seed sizes and also different established plant sizes, distributional patterns (alpine, lowland, or ubiquitous), regional abundances (scattered or common), habitat preferences (strictly grassland or generalist), bedrock requirements (basic or indifferent), and soil fertility requirements (low or high) were chosen for the study (Mossberg 1992, Lid and Lid 1994). The species were *Campanula rotundifolia*, *Gentianella amarella*, *Gentiana nivalis*, *Geranium sylvaticum*, *Knautia arvensis*, *Potentilla crantzii*, *Primula scandinavica*, *Ranunculus platanifolius*, *Trollius europaeus*, *Veronica alpina*, and *Viola biflora*. The germination responses and dormancy levels of seed batches from subalpine grassland populations of these species were investigated in a series of phytotron experiments (Table 1), and the germination responses were related to regeneration behaviour in contrasting microsites in the field (Paper IV, Paper V). The results show that these species differ in seed germination responses, that these differences cannot be explained by seed weight alone, and that germination responses relate to regeneration behaviour in gaps in the field (Paper IV).

#### *Regeneration ecology in subalpine perennial grasslands*

Seen together, the strong and interpretable differences in germination responses between the 11 grassland herbs (Paper IV), and strong and persistent floristic response to gaps (Paper III), indicate that gap creation and revegetation contribute to the vegetation structure and floristic composition of these grasslands (Paper II). The two studies are fairly consistent. Five of the 11 species investigated in the phytotron experiments (Paper IV), also occurred relatively frequently in the natural (unsown) gap revegetation experiments (Paper III), and these species behaved in the unsown plots as predicted by the phytotron responses. *Trollius europaeus*, *Campanula rotundifolia*, and *Gentiana nivalis* had strong positive gap responses, while *Geranium sylvaticum* and *Viola biflora* were more common in the closed sward. An equally clear pattern to emerge from these two studies, however, is that the species in these grasslands do not have any absolute gap or closed-sward requirements (Paper IV, Paper V), or responses (Paper III, Paper IV) but exhibit a range of behaviours ranging from positive via neutral to negative. This supports the view that gap responses should be seen as continuum rather than as on-off



**Figure 3.** A photo of one of the experimental blocks used for Paper III in the spring census 1998, the first time the gaps were sampled after the experiment was initiated. The large photo shows an experimental block with 3 + 3 large (25 x 25 cm) gaps and controls and 3 + 3 small (6.25 x 6.25 cm) gaps and controls created and marked in random positions in 1997. As small gaps are  $\frac{1}{16}$ <sup>th</sup> of the large gaps, the metal frame is used to analyse gaps of both sizes, and the presence-absence data from each of the 16 sub-plots within large gaps are the same size as small gaps. The small photo shows a close-up of one of the large gaps. On the blue background there is a seedling (note the cotyledons) and a vegetative recruit of *Knautia arvensis*.

effects (Hubbell et al. 1999, Bullock 2000). The trend for rare species to increase in relative importance in gaps (Fowler 1981, Milberg 1993, Lavorel et al. 1994, Paper III) suggests a mechanism by which gap revegetation can contribute to the survival of infrequent species and can increase diversity of vegetation and landscapes.

#### *Regeneration ecology compared to other regions and climates*

As seedlings are smaller and physiologically more vulnerable than established adult plants, the seed and seedling stages can be expected to respond

relatively strongly to environmental variation (Marchand 1996, Kitajima and Fenner 2000). For example, the factors and processes controlling seedling mortality risk may not be constant along broad-scale climatic or altitudinal gradients. Consequently, germination responses (Meyer and Monsen 1991, Meyer et al. 1995, Schütz and Milberg 1997, Pérez-Fernández et al. 2000, Cavieres and Arroyo 2001) or seed dormancy levels (Venable and Brown 1988, Philippi 1993, Milberg and Andersson 1998) may vary along these gradients. Perennial grassland species may be particularly well suited for comparisons across broad scales because these species and ecological



systems have wide geographical distributions. At the same time, the germination responses of many of these species are well studied in temperate regions. These ideas were explored in Paper VI and Paper V. Compared to other populations in Norway (Paper V) and grassland species from temperate regions (Grime et al. 1981, Washitani and Masuda 1990, Olff et al. 1994, Baskin and Baskin 1998, Kotorová and Lepš 1999), summer-farm populations (Paper VI, Paper V) had consistently high temperature thresholds for germination and low dormancy levels (as indicated by weak cold-stratification responses). These differences could have at least three explanations. First, the very short growing season in subalpine grasslands, where monthly mean temperatures typically exceed 5°C for about five months a year only, synchronises vegetative development. Second, the high levels of stochastic variation in weather between and within years in mountains (Marchand 1996, Körner 1999), coupled with the relatively low thermal amplitude through the frost-free season greatly reduce the physiological possibility for precise timing of germination. Third, the factors controlling seedling mortality risk may not be the same across climatic regions, so that differences in germination strategies may actually be expected. For example, drought is generally less problematic in mountain climates because the lower air temperatures decrease evaporation (Körner 1999). At the same time, late-spring or early autumn frosts are more frequent and the frost-safe part of the season is much shorter. Here, strategies that restrict the frost-sensitive seedling stage to the safer mid-season while avoiding the threats of early spring and late autumn may have selective advantage.

In the field, germination of the native plants was very slow (Paper IV, Paper V), compared to studies elsewhere, suggesting that the build-up of persistent seed banks may be considerable in these habitats. The seed banks of the six grasslands used for Paper III are actually relatively extensive, as they contain 66 species, 39 of which also appear in the gap revegetation data, at a mean density of 2131 seeds per m<sup>2</sup>, and change less during secondary succession than the established vegetation (*unpublished data*). The species richness is similar to lowland cultural landscapes (Berge and Hestmark 1997), unfertilised haymeadows (Kirkham and Kent 1997), and limestone grasslands (Milberg and Hanson 1993). The seed bank densities are approximately 1/5 lower, however, and are comparable to lowland acidic grassland (Edwards and Crawley 1999), and meadows (Falińska 1999), and alpine herb fields in Montana (Chambers 1992, Zabinski et al. 2000). Dormant seeds in the soil serve a dual function in plant populations. They are ‘memories of populations and communities past’, and at the same time a potential for future persistence and survival.

A consequence of this is that the longevity of seeds in the soil affects the resilience of plant communities. This applies both to ecological timescales, where seedbanks offer a potential for re-establishment if the grown plants go locally extinct, and to evolutionary timescales, where they are a potential source for the re-emergence of ‘old’ genotypes (McGraw and Vaverek 1989, Thompson et al. 1997, Bekker et al. 1997, Baskin and Baskin 1998, Cavieres and Arroyo 2000). If the magnitude and temporal dimensions of seed-banks vary throughout the species range, this will affect the local potential for ecological persistence and evolutionary change will be affected.

## QUESTIONS ABOUT TIME AT DIFFERENT SCALES

Succession is an important paradigm because it encapsulates the idea that although populations and communities may be intrinsically dynamic, it is possible to understand, or even predict, how they will change over time (Underwood and Anderson 1994). In other words, different patches of vegetation, when subjected to a change in some environmental or biotic factor, will respond in similar ways. But how similar do we expect these responses to be? Clements’ (1916) classical theory of succession states that it is an orderly, directional process that inevitably takes place as pioneer species invade new sites, grow, and modify their environment, thereby making way for later-successional species, and that the vegetation would therefore predictably proceed through different stages. This particular cause of successional change was later termed ‘*facilitation*’ by Connell and Slatyer (1977) who pointed out that other relationships between species, including ‘*inhibition*’ and ‘*tolerance*’ might have an influence on community change. With time we have come to realise that successional change may result from a range of different processes, and that these processes may be considerably modified by site characteristics, chance effects, and the non-equilibrium status of most communities (Glenn-Levin et al. 1992).

In this study I am asking *if* - or more correctly *to what extent* - the opening of a gap in the vegetation, or the change in a disturbance regime at a summer farm, produces a community response that is repeated across different sites (Paper I, Paper III, cf. McCune and Allen 1985)? How important is history relative to other environmental factors (Paper I, Paper III)? What is the covariation between history and other environmental factors (Paper I)? What is the effect of broad-scale history on fine-scale temporal trends (Paper III)?

At the broad scale, I investigate the effect of farm-scale land-use history (0 – 40 years of abandonment) on the vegetation of summer farms. The summer farms are floristically and ecologically distinct (Paper I, Paper II), and may be seen as scattered habitat islands in a ‘sea’ of heath or woodland (Figure 1, Figure 2). From an ecological point of view, these habitat islands with different successional histories can be seen as broad-scale natural – or semi-natural (sic) – experiments. In this study, I used a chronosequence approach (Matthews 1992) to investigate changes along successional sequences of up to 40 years of abandonment (Paper I, Paper III), a longer time-sequence than can normally be accomplished in formally designed experiments.

At the fine scale, I investigate temporal trends (7 sampling dates over 4 years) in the micro-successions occurring within fine-scale disturbances (Paper III). The statistical modelling approach used to analyse the gap revegetation data, Principal Response Curves (van den Brink and ter Braak 1997, 1998), treats time, and gap effects through time, as a series of dummy variables. Hence, there is no expected underlying response model (e.g. linear, unimodal, etc.) through time, and the methodology can essentially be seen as a way of implementing repeated-measures-ANOVA but in an ordination multivariate framework. This is appropriate for the general line of enquiry outlined above.

At both scales, and in both studies, there was a significant compositional response to the explanatory variable representing time (time since land-use change, time since gaps were opened). In other words, these are, by definition, successional systems. The actual fraction of the compositional variance that could be accounted for by successional time differs greatly between studies, and ranged between 3.1% (Paper I) to nearly 50% (between experimental blocks in Paper III). These differences do not merit interpretation, however, because they are affected by, among other things, the relationship between the numbers of species, plots, sites, and successional stages investigated (Table 1), the modelling of time (linear or classes), and the very different sampling or experimental designs resulting in different variance structures in the data sets (cf. Økland 1999).

An interesting line of enquiry may be to investigate the relative influence of different potentially important factors for vegetation development and successional change (Paper I). This brings me back to the theme briefly introduced in the section on gradients, namely the lack of a link between the potential importance and the measurability of explanatory variables. Although many different factors may affect the measurability – and the popularity of measuring – various explanatory variables, McCune and Allen’s (1984)

distinction between ‘site factors’ and ‘historical factors’ is important in this context. ‘Site factors’, they claim, are more or less constantly observable characteristics of the sample units (typically: slope, altitude, soil chemistry, etc.). ‘Historical factors’, in contrast, are instant or short-term effects that may exert a strong and persistent effect on vegetation, but leave little or no direct, independent, and measurable evidence on the site. Fine-scale disturbances, and disturbance regimes may in many ways be seen as typical examples of such ‘historical’ factors. At the time they are created, fine-scale disturbances may be easily observable, but their compositional effects persist as the gap closes (Paper III), and probably remain long after the gap has visually blended into surrounding undisturbed vegetation. At the scale of landscapes, land-use regimes, both past and present, are typical ‘historical’ factors that are difficult to measure and express (Paper I, Paper II). This is especially true in grazed systems, because grazing animals utilise landscapes in highly selective ways at spatial scales ranging from individual plants via vegetation patches to landscapes (Wielgolaski 1976, Bakker et al. 1983, Sævre and Baadshaug 1984, deLeuw and Bakker 1986, Glenn and Collins 1990, Huntly 1991). Further, land-use is not an on-off effect, but includes a range of different practices, local histories, and ways of reporting to authorities or researchers (Reinton 1955, Kvamme 1988, Edelmann 1997). Precise quantifications of the ecologically relevant local land-use history, based on interviews and agricultural statistics, have been attempted (e.g. Olsson et al. 2000, Losvik 1988, Kaland and Vandvik 1998), but the reliability and utility of such data are difficult to assess. The dichotomy between historical and site characteristics relates to some important questions, such as the degree of convergence expected between ‘replicate’ sites (McCune and Allen 1985, Samuels and Drake 1997), and the relative importance of historical contingency and the ecological rules that transcend these contingencies for the emerging patterns in nature (Samuels and Drake 1997, Vermeij 1999).

Several aspects of the results suggest that the actual course and direction of the vegetation change at abandoned summer farms do not behave as classical ‘secondary successions’, at least not on relatively short temporal scales of years to decades. First, successional change is exceedingly slow in these grasslands (Paper I, Paper III, cf. Spatz 1980), relative to the rapid changes that have been reported from abandoned lowland semi-natural grasslands in Norway (e.g. Losvik 1988, 1996, Norderhaug et al. 1996) and elsewhere (e.g. Peart and Foin 1985, Marrs et al. 1988). This is probably related to the general decrease in productivity levels with increasing altitude (Chapin 1987, Marchand 1996, Körner 1999). Second, the 40-year successional

stages do not revert towards the 'natural' surrounding vegetation (Paper I, Paper III), and abandoned summer farms are still visible in the vegetation up to 100 years after abandonment (*unpublished observations*). Third, the effects that summer farms have on the local soils are very strong and persistent (Paper I). Fourth, many heath and woodland species do not seem to readily colonise the successional grasslands, even in experimental gaps (28 species, 33% of the total flora, disappear while only 7 new species appear along the successional sequence, Paper III). Fifth, some species change in their ecological behaviour and disturbance responses along the successional sequence (Paper III). It has long been acknowledged that changes in disturbance regimes may function as a driving force in succession (Denslow 1980, Pickett et al. 1987, Milchunas and Lauenroth 1993, Kotanen 1995, Blatt et al. 2001). Disturbance regimes do not operate in isolation, however, and following Zobel (1992, 1997) we may see them as one of many biotic and abiotic 'environmental sieves' that function to exclude a subset of the species in the regional species pool from the local communities at particular sites. At summer farms, other potentially important 'sieves' could be related to soil pH and productivity, climatic constraints on flowering and seed set, and between-site dispersal.

#### SOME DIFFERENCES BETWEEN SUMMER FARMS IN EASTERN AND WESTERN NORWAY

Some species found at summer farms in eastern Norway (Nordhagen 1943, Knatterud 1974, Austrheim et al. 1999, Paper III) were not found, or were much less common in Røldal in western Norway (Paper I, Paper II). Several of these, e.g. *Betula nana*, *Polygala amarella*, *Potentilla crantzii*, *Trollius europaeus*, *Viola biflora*, and *V. rupestris*, have their distributional centres east of the Scandes (Mossberg 1992, Lid and Lid 1994, Pedersen 1990). Furthermore, some species with a western distribution in Norway, e.g. *Galium saxatile*, *Festuca vivipara*, and *Carex pilulifera*, occur exclusively, or are more common, in Røldal than in summer farms further east. There also seem to be systematic differences between the summer-farm soils. The pH values in eastern Norway are higher by ca. 0.7 pH units, base saturation is higher by 20%, and soil N is slightly higher, whereas soil LOI is ca. 20% lower (Knatterud 1974, Austrheim et al. 1999, Paper I, Paper II). There may be at least three explanations: First, the study areas have different site characteristics such as bedrock. Second, the higher precipitation and lower summer temperatures in an oceanic climate (Fægri 1960) decrease the rate of mineralisation of organic matter, whereas leaching is accelerated

(Etherington 1975). The result is lower pH, base saturation, and soil N, and higher organic content in the west. Third, soil acidity has changed during the 20 years separating Knatteruds (1974) investigation from the more recent studies. Soil acidification in southern Sweden (Tyler 1987) and southern Norway (Dahl 1988, Bjørnstad 1991) has occurred during the last few decades. Several hypotheses have been put forward to explain this phenomenon, including the decrease in pastoral activities, an increase in atmospheric acid deposition, and long-term successional changes (see Birks et al. 1990).

#### CONCLUSIONS AND PERSPECTIVES

In this study I have investigated general vegetation patterns, and some potentially important processes within the subalpine grasslands, at summer farms in Norway. Three major findings have emerged from the study. First, I have demonstrated that disturbance, at scales ranging from the disturbance regimes of entire summer farms, via gradients in disturbance intensity in the landscape, to fine-scale gaps in the closed vegetation sward, exert considerable influence on the floristic composition at these various scales (Papers I, II, III, IV). Second, I have found that the processes operating at broad- and fine- scale spatial and temporal scales are not independent, as overall disturbance regimes and the dynamics within individual disturbances affect each other (Paper I, Paper III). Third, the biological processes monitored in this study were exceedingly slow. This applied to the secondary successions (Paper I, Paper III), to gap revegetation (Paper III), to seed germination in the field experiment (Paper IV, V), and to the germination of seeds from subalpine populations in the phytotron (Paper IV, Paper V). Together, these findings suggest that summer farm grasslands share some common characteristics with semi-natural vegetation elsewhere, but that they also have their own particularities.

The patterns and processes investigated in the five papers that make up this study are by no means meant as an exhaustive survey of the ecology of summer farms. The study is based on field data from 19 summer farms in two valleys in western and eastern Norway. Clearly, studies including a larger number of sites, and wider geographical ranges, are necessary to determine patterns and variation at the scales of landscapes and regions. The diverse flora of summer farms, including species with predominantly alpine, subalpine, and lowland distributions, and semi-natural grassland specialists together with common grassland plants, suggests that between-site dispersal and regional dynamics may be important. Within landscapes, the relative importance of spatial constraints on dispersal, local environment, and land-use history for species distributions and

community patterns would make another interesting line of enquiry. Further, the density, composition, and longevity of seed banks will have important bearings on the potential for vegetation change and recovery. In addition to the bare-ground gaps, grazing animals defoliate mature plants, and this will affect mature plant performance, survival, and seed set. Neither is disturbance the only ecological factor affecting vegetation at summer farms. Small-scale variability, for example in soil nutrients, may also have strong effects. The summer farms are not the only ecological system in these landscapes that are changing. Succession is also affecting the floristic composition, vegetation structure, and plant populations, in the extensive, formerly mown, subalpine mires (Øien and Moen 2001, 2002), and the subalpine forests are expanding as tree-lines are climbing due to a combination of climate change and a decrease in pastoral activities (Hofgaard 1997).

This study contributes to the knowledge of these systems by demonstrating that changing the disturbance regimes of landscapes, resulting from land-use change, have dramatic effects on the vegetation and flora of subalpine semi-natural landscapes. The slow secondary successional rates in the mountains (Paper I, Paper III), may explain why upland semi-natural vegetation is regarded as less immediately threatened than its lowland counterparts (Fremstad and Moen 2001).

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