Fire as a management tool in coastal heathlands: a regional perspective

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Contents

Abstract

Velle, L.G. 2012. Fire as a management tool in coastal heathlands: a regional perspective. PhD Thesis, Faculty of Science, University of Bergen, Norway.

Background and aims:

The coastal heathlands of north-western Europe is an old cultural landscape that has been maintained by burning and grazing for at least 5000 years. Heathland communities vary among geographical regions and in response to land-use regimes, and although some heathlands are still well-managed, many heathlands are now abandoned or have low management intensities. Today, abandonment of traditional land-use is considered one of the major threats to coastal heathlands, which are classified as endangered and considered a habitat of high conservation importance throughout its geographic range. Understanding the implication of prescribed burning along the geographic and land-use gradients in coastal heathlands is important for conservation, restoration and management of these landscapes. The antiquity of the system rise the question if the smoke-induced germination found in coastal heathland populations of *Calluna* might be an evolutionary impact of human land-use. Moreover, it is open to debate if prescribed burning still has a place in this management regime, or if it should be discontinued due to its roles in increasing human disturbances in landscapes, which has been shown to lead to increased invasiveness of generalist species, biotic homogenization and habitat degradation. This PhD thesis examines the role of prescribed burning as a management tool in Norwegian coastal heathlands.

Methods:

The main research approach has been the analysis of post-fire vegetation dynamics after experimental fires set in coastal heathlands. Dynamics after fire was studied along a 340 km north-south latitudinal gradient. In addition, data from a previous study was available, which extended the gradient to 470 km. Permanent vegetation plots were followed over time in 6 sites; A (Lygra), B (Aursnes), C (Nerlandsøy), D (Smøla), E (Tarva) and F (Kalvøya). Based on these field data, variation have been explored due to sites, habitats, age and homogenization. Smoke-induced seed germination in *Calluna* was tested in a laboratory experiment, and seeds from two contrasting gradients was compared; a latitudinal gradient along the coast (6 sites) and an altitudinal gradient from the coast into the mountains (5 sites).

Major results:

(i) Prescribed burning caused consistent post-fire trends along the gradient, but also patterns that were site- and habitat-specific. Specifically, regeneration rates decreased from south to north, and along the entire gradient wet heath stands regenerated faster towards the pre-burned community composition than the dry stands. (ii) Young heath had a faster succession towards the pre-fire community composition and a less pronounced overall community response to fire than old heath. Despite slower rates, old stands developed characteristic heathland vegetation and structure after fire, and showed a high restoration potential. (iii) Prescribed burning caused taxonomic differentiation after fire, rather than homogenisation. Species that increased after fire were natural constituents of the community, and not widespread generalist species. At the landscape scale dry and wet heaths became more compositionally similar after fire, a pattern that will become differentiated again over time. (iv) Smoke-induced germination in *Calluna* were found in populations from the coastal heathland, but the adaptation lacked form populations outside the coastal heathland region, and implies that evolutionary responses to fire also exist in a culturally fire-prone ecosystem.

Implications for management and conservation:

Prescribed burning in combination with grazing fulfils its traditional role as an important management tool in coastal heathlands; burning removes standing biomass, and thereby halts the secondary succession towards shrubs and woodlands, it causes taxonomic differentiation in early successional stages, and rejuvenates the *Calluna* stands. Moreover, evolutionary adapted smoke-induced germination in *Calluna* seeds in coastal heathlands illustrates the important historically role of prescribed burning in this system. Geography, habitat and age influence post-fire regeneration rates, and these differences should be implemented in local and regional management plans and strategies. Specifically, the variation in regeneration strategy and rates of *Calluna* among sites and habitats suggest that burning rotations must be based on the cover of the vegetation canopy in combination with *Calluna*'s morphological growth form, instead of the age of the *Calluna.* Recourse utilization and conservation management in heathlands must be adapted to the regional differences.

Samandrag

Velle, L.G. 2012. Lyngsviing som eit skjøtselstiltak i kystlynghei: eit regionalt perspektiv. PhD syntese, Det matematisk-naturvitskaplege fakultet, Universitetet i Bergen.

Målsetting:

Kystlyngheiane i nordvest Europa er eit gammalt kulturlandskap som har blitt kontinuerleg skjøtta gjennom sviing og beiting i minst 5000 år. Kystlyngheiane varierer mellom geografiske regionar og i forhold til ulik bruk, og med varierande skjøtselsgrad. I dag utgjer opphøyr av tradisjonell bruk ein av dei største truslane i kystlyngheia. Dette gamle kulturlandskapet er klassifisert som truga og har høg verdi gjennom heile si geografiske utbreiing. Det er viktig å forstå korleis variasjonar i geografi og bruk påverkar effekten av lyngsviing, og dette er kunnskap av interesse for dei som vil skjøtte og ta vare på kystlyngheiane. Den høge alderen til kystlyngheiane gjer at ein kan stille spørsmål om røykindusert frøkvile hos røsslyng kan vere eit resultat av ei evolusjonær tilpassing til lyngsviing. Vidare kan ein spørje om lyngsviing framleis fungerer som ein del av lyngheiskjøtselen, eller om sviing i dag opnar opp for at fleire artar med stor utbreiing (generalistar) kjem inn i lyngheia og gir meir lik vegetasjonssamansetting (homogenisering) og at naturtypen vert øydelagt. Denne PhD syntesa undersøker rolla til lyngsviing som ein del av skjøtselen i norske kystlyngheier.

Metode:

Undersøkingane omfattar vegetasjonsanalysar før og etter lyngsviing i kystlynghei. Vegetasjonsdynamikkar etter sviing har blitt studert langs ein gradient på 340 km i nord-sør retning. I tilegg har data frå ein tidlegare studie vore tilgjengeleg og utvida gradienten til 470 km. Seks lokalitetar med fastruter har vore følgt over tid; A (Lygra), B (Aursnes), C (Nerlandsøy), D (Smøla), E (Tarva) og F (Kalvøya). Basert på feltdata har variasjonar i vegetasjonssamansettinga i forhold til lokalitetar, habitat, alder og homogenisering blitt studert. Røykindusert frøspiring hos røsslyng har blitt testa i eit laboratorieforsøk, og frø frå to ulike gradientar blei samanlikna; ein nord-sør gradient langs kysten (6 lokalitetar) og ein aust-vest gradient frå fjell til kyst (5 lokalitetar).

Hovudresultat:

(i) Lyngsviing førte til både konsistente vegetasjonsdynamikkar langs heile gradienten, men også til ulikskapar knytt til lokalitet og habitat. Vekstraten minka nordover, og langs heile gradienten utvikla den fuktige lyngheia seg raskare i retning av vegetasjonssamansettinga slik ho var før sviing, enn i den tørre lyngheia. (ii) Ung lynghei utvikla seg raskare i retning av plantesamansettinga før sviing, og synte over tid ein samla mindre påverknad av lyngsviinga enn den gamle kystlyngheia. Sjølv om vekstraten var noko seinare i gammal kystlynghei, kom den opphavlege vegetasjonen og strukturen tilbake, og dette synleggjorde restaureringspotensialet i gammal kystlynghei. (iii) Lyngsviing førte til ei meir variert vegetasjonssamansetting (heterogenisering) etter sviing. Dei nye artane var artar som er ein naturleg del av vegetasjonen i kystlynghei og ikkje generalistar med vid spreiing. På landskapsskala blei tørr- og fuktheia meir lik i vegetasjonssamansettinga etter sviing, eit mønster som vil bli forskjellig igjen over tid. (iv) Røykindusert frøspiring hos røsslyngfrø vart berre funne i kystlyngheia, og ikkje i lokalitetane utanfor kystlyngheiregionen. Dette kan tolkast som ei evolusjonær tilpassing til eit menneskeskapt brannregime.

Betydning for skjøtsel og ivaretaking:

Saman med beiting oppfyller lyngsviing rolla si som ein viktig del av den tradisjonelle skjøtselen av kystlynghei; sviinga fjernar den ståande biomassen og stoppar den sekundære suksesjonen i retning av buskar og tre, fører til meir variasjon i artssamansettinga etter sviing, og til fornying av røsslyngen. Vidare viser den evolusjonært tilpassa røykinduserte spiringa hos røsslyngfrø kor viktig lyngsviinga har vore over tid. Geografi, habitat og alder påverkar vekstraten og vegetasjonssamansettinga etter sviing, og desse forskjellane må ein ta omsyn til i utarbeiding og oppfølging av skjøtselsplanar. Ulikskapar i regenereringsevne hos røsslyngen mellom lokalitetar og habitat, gjer at brannrotasjonar bør bestemmast ut i frå vegetasjonsdekke og røsslyngen si vekstform, og ikkje ut i frå alder. Ressursutnyttinga i kystlyngheia må tilpassast dei regionale forskjellane.

Acknowledgements

My first introduction to coastal heathlands was in 2001, and I was immediately fascinated by the open landscape with *Calluna*-heaths and their management regimes. Since this, coastal heathlands have been an important part of my job.

This PhD started in 2006, and has been part of the interdisciplinary project “Old Norse Sheep in coastal heaths – developing a sustainable local industry in vulnerable cultural landscapes”. Throughout my work I have had excellent guidance from my supervisors Vigdis Vandvik (University of Bergen), Liv Nilsen (The Norwegian Directorate for Nature Management) and Ann Norderhaug (Bioforsk). Their advice and encouragement have been of utmost importance, and I am very thankful for the time they have spent on my work.

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List of papers

The thesis is based on the four following papers which will be referred to their Roman numerals hereafter.

Paper I: Velle, L.G. & Vandvik, V. Post-fire succession in coastal *Calluna* heathlands along a 340 km latitudinal gradient. Manuscript.

Paper II: Velle, L.G., Nilsen, L.S. & Vandvik, V. (2012). The age of *Calluna* stands moderates post-fire regeneration rate and trends in northern *Calluna* heathlands. *Applied Vegetation Science,* 15, 119-128.

Paper III: Velle, L.G., Nilsen, L.S., Norderhaug, A. & Vandvik, V. Does prescribed burning result in biotic homogenization of coastal heathlands? Manuscript.

Paper IV: Vandvik, V., Spindelböck, J.P., Cook, Z., Daws, M.I., Heegaard, E., Måren, E.I., & Velle, L.G. Smoke-induced germination in *Calluna vulgaris* – a case of management-induced evolution? Manuscript.

The International Association of Vegetation Science and Wiley-Blackwell have given permission to print the paper: "Velle, L.G. Nilsen, L.S., Vandvik, V. 2012. The age of *Calluna* stands moderates post-fire regeneration rate and trends in northern *Calluna* heathlands. *Applied Vegetation Science*, 15, 119-128" as part of this PhD thesis.

Declarations

Paper I: Velle, L.G. & Vandvik, V. Post-fire succession in coastal *Calluna* heathlands along a 340 km latitudinal gradient.
Velle, L.G.: Experimental design, field work, data processing, statistical analyses, writing
Vandvik, V.: Experimental design, analytical design, statistical analyses, editing

Paper II: Velle, L.G., Nilsen L.S. & Vandvik, V. The age of *Calluna* stands moderate post-fire regeneration rate and trends in Northern *Calluna* heathlands.
Velle, L.G.: Project design, field work, data processing, statistical analyses, writing
Nilsen, L.S.: Experimental design, field work, editing
Vandvik, V.: Analytical design, statistical analyses, editing

Paper III: Velle, L.G., Nilsen, L.S., Norderhaug, A. & Vandvik, V. Does prescribed burning result in biotic homogenization of coastal heathlands?
Velle, L.G.: Experimental design, field work, data processing, statistical analyses, writing
Nilsen, L.S.: Heathland ecology, field work, editing
Norderhaug, A.: Cultural landscape ecology, editing
Vandvik, V.: Experimental design, analytical design, statistical analyses, editing

Paper IV: Vandvik, V., Spindelböck, J.P., Cook, Z., Daws, M.I., Heegaard, E., Måren, I. E., & Velle, L.G. Smoke-induced germination in *Calluna vulgaris* – a case of management-induced evolution?
Vandvik, V.: Project design, experimental design, writing
Spindelböck, J.P.: Germination experiments, statistical analyses, writing, editing
Cook, Z.: Germination experiments, data summary, editing
Daws, M.I.: Germination experiment design, editing
Heegaard, E.: Statistical design, statistical analyses, editing
Måren, I.E.: Experimental design, field work, laboratory work, editing
Velle, L.G.: Historical data, field work, writing, editing

Introduction

Fire: an important disturbance mechanism

Fires, whether they are natural or anthropogenic, constitute one of the major disturbance agents shaping vegetation, and they play an important role in maintaining the structure and function of plant communities world wide (Bond & Keeley 2005; Bond, Woodward & Midgley 2005). Some ecosystems have evolved with natural fire regimes, and harbour many plant species that rely on recurrent fires for their population persistence (Keeley, Fotheringham & Baer-Keeley 2005; Archibald *et al.* 2010). In such systems, species may occupy distinct niches in the post-fire successional dynamics, resulting in characteristic spatial and temporal dynamics (Keeley, Fotheringham & Baer-Keeley 2005) and predictable patterns of functional type distribution, species occurrence and diversity after fire (Pausas, Keeley & Verdu 2006; Keeley *et al.* 2011). Fire can be seen as an evolutionary pressure shaping plant traits, such as re-sprouting and germination by heath and smoke, traits that provide fitness advantage in fire-prone environments (Pausas *et al.* 2004; Keeley *et al.* 2011).

In prehistoric Europe, our ancestors developed burning techniques evolved to meet their livelihood needs. Accordingly, this prescribed burning varied due to different intents, geographical and climatic conditions and to the respective ecosystems they inhabited (Castellnou, Kraus & Miralles 2010; Lazaro 2010). Prescribed burning can be characterized as a careful application of fire under specified fuel and weather conditions to meet specific resource management objectives and long-term management goals (Castellnou, Kraus & Miralles 2010). Most European countries experienced significant socioeconomic changes in the 20th century resulting in major land-use changes and abandonment of traditional land-use techniques. The changes in fire-cycles has caused disruption of community and ecosystem processes including decreased diversity (e.g. Hobbs & Huenneke 1992; Schwilk 2003) and increased fire risks due to accumulation of fuel (Keane et al. 2004). A growing awareness of these problems has caused an interest to restore fire in some ecosystems or land-use systems (Goldammer & Montiel 2010). Biotic homogenisation due to human disturbances causes growing conservation concern (McKinney & Lockwood 1999; Olden & Poff 2003; Rooney et al. 2004) suggesting potential conservation challenges in cultural landscapes were disturbances are needed for maintaining the dynamics and functioning of the ecosystems.

Coastal heathlands: an old cultural landscape

The coastal heathlands of north-western Europe is a cultural landscape where anthropogenic fire regimes play an important role in maintaining vegetation composition and successional dynamics (Gimingham 1972; Kaland 1986). They originated soon after the introduction of livestock husbandry to western Europe, and palynological data have demonstrated heathland establishment 6000 years ago (Prøsch-Danielsen & Simonsen 2000). Heathland establishment followed human settlement, and this explains the spatially and temporally metachronous pattern of establishment (Gimingham 1972; Kaland 1986; Bennett *et al.* 1992; Odgaard 1994; Bunting 1996; Hjelle, Halvorsen & Overland 2010). In Norway, the first anthropogenic heathlands were recorded in the south-west c. 4000-3600 cal. B.C. (Prøsch-Danielsen & Simonsen 2000) and somewhat later northwards (Kaland 1979; Moe 2003; Tveraabak 2004; Hjelle, Halvorsen & Overland 2010). The Late Bronze Age and Iron Age seem to be important time periods in the final heathland development along the Norwegian coast (Hjelle, Halvorsen & Overland 2010). The heathlands evolved as a result of human-induced forest clearance in order to provide pastures, and around 1800 AD coastal heathlands had their largest distribution (Haaland 2002) (Fig. 1). Coastal heathlands once covered several million hectares, but have been considerably degraded throughout their distribution area. Today, this unique nature type is classified as endangered (EN) (EC habitats Directive 92/43/EEC, Webb 1998; Aarrestad, Fremstad & Skogen 2001; Lindgaard & Henriksen 2011), and abandonment of traditional use is one of the major threats (Thompson *et al.* 1995; Fremstad & Moen 2001).

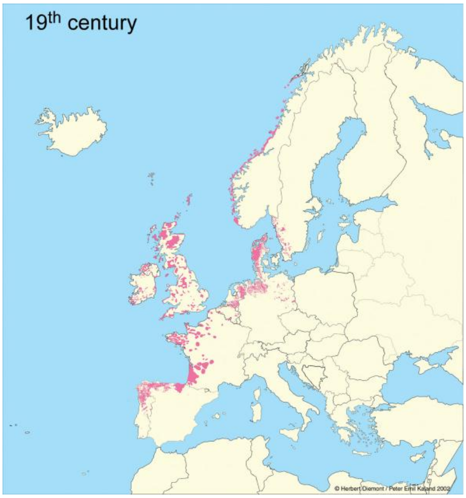

Figure 1. The distribution of coastal heathlands along the Atlantic coast from Portugal to northern Norway around 1800 AD (Illustration: HEATHCULT/The Heathland Centre).

The coastal heathlands are distributed on poor soils along the Atlantic coast from Portugal to northern Norway, and are dominated by Ericaceous species, especially *Calluna vulgaris* (L.) Hull (hereafter *Calluna*) (Gimingham 1972). Although the heathlands have a wide geographic distribution, ca. 3600 km from south to north, some common patterns are found in the heathland farming systems throughout Europe (Gimingham 1992; Webb 1998). Most importantly, the coastal heathlands have been an integrated part of the agricultural system. They formed large outfields where livestock (e.g. sheep, goats, cattle, horses) were kept, whilst arable crops were produced close to the settlement (Fig. 2). In this system, a flow of nutrients were transported from the heathlands to the arable fields in the form of manure. The humid temperate climate with mild winters characteristic of the oceanic climates of western Europe made it possible to establish year-round grazing systems, with low labour-intensity regarding fodder collection. The evergreen *Calluna* constituted an important grazing resource during wintertime and prescribed burning was used to manage the heaths by rejuvenating *Calluna* and to optimise the fodder throughout the year (Gimingham 1992; Webb 1998; Haaland 2002; Kvamme, Kaland & Brekke 2004).

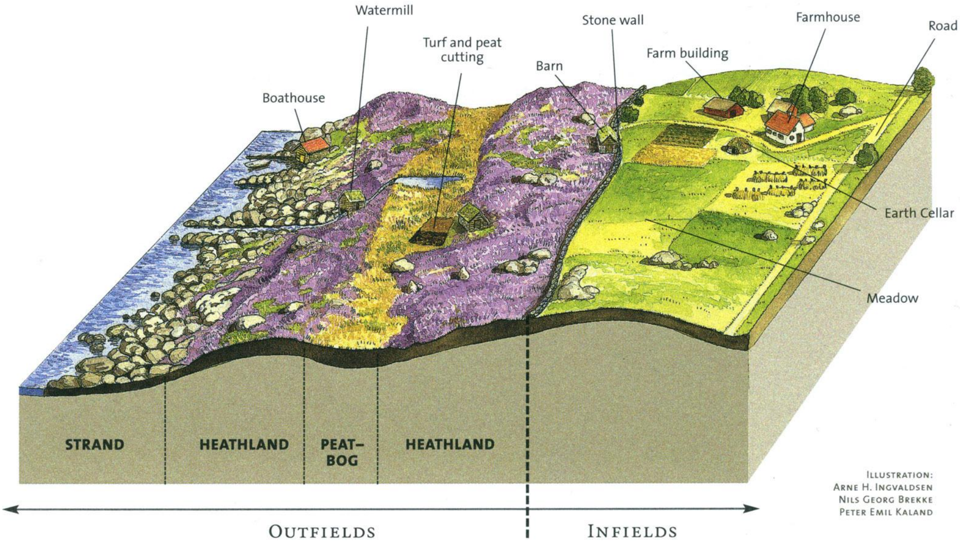

Figure 2. Illustration of a typical heathland farm in Norway with small infields and large outfields. Coastal heathlands and peatbogs are found in the outfields (Illustration: A.H. Ingvaldsen, N.G. Brekke and P.E. Kaland/The Heathland Centre).

Differences in natural conditions and climate have resulted in regional variation in heathland management and use (Webb 1998). In Norway, heathland farming was often combined with fishing, and most farms had easy access to the sea. The small stock (sheep and goats) grazed outdoors throughout the year, while cattle and horses were taken indoors during the coldest winter months. Peat bogs were an important source of fuel, and crumbled peat together with dried straw, bracken, heather and seaweed were used as bedding in the byres, and later as fertilizer on the arable land (Kaland 1999; Haaland 2002; Kvamme, Kaland & Brekke 2004). Old Norse Sheep is an ancient sheep breed, and the most common breed in coastal heathlands today. Adaptations to oceanic climate, ability to utilize relatively nutrient-poor pastures, low rates of complications during lambing and high mobility in heath-vegetation make these animals especially valuable as part of the heathland management (Kvamme, Kaland & Brekke 2004).

Burning and post-fire vegetation dynamics

Prescribed burning has been used as a tool to manage heathlands, and has important implications for the heath vegetation; i) it removes old vegetation and prevents shrubs and trees from re-establishing in the habitat; ii) it provides a flush of nutrients and stimulates new growth, including a number of grasses and herbs; and iii) it rejuvenates *Calluna* either by resprouting or from seeds (Hobbs & Gimingham 1984a; Gimingham 1994; Gimingham 2002). Over time, prescribed burning in combination with grazing formed complex vegetation mosaics (Barclay-Estrup & Gimingham 1969; Gimingham 1992; Vandvik *et al.* 2005). As vegetative regeneration results in faster build-up of biomass, burning practices that maximise vegetative regeneration of *Calluna* have often been preferred (Kayll & Gimingham 1965; Mohamed & Gimingham 1970). Heath burning was carried out when the soil was wet or frozen from late autumn to early spring, as this prevented damage to the seed bank in the upper layer of the soil (Gimingham 1972; Kaland 1999). Traditionally, burning has been performed in order to optimise the production in the heaths, and burning rotations of 10-20 years have been common, though there are regional and local variations (Gimingham 1972; Yallop *et al.* 2006).

The vegetation dynamics of the traditional heathland farming are strongly related to the heathland cycle (Fig. 3). In this cycle, four phases have been recognised; pioneer, building, mature, and degenerative (Watt 1947; Barclay-Estrup & Gimingham 1969; Gimingham 1988). Although the phases are not sharply defined, they are relatively easily recognized, and have been used as a proxy for successional dynamics in a number of ecological studies (e.g. Barclay-Estrup & Gimingham 1969; Hobbs & Gimingham 1984b). The phases span the early stage of establishment and growth, via a phase where *Calluna* becomes bushy with high productivity and vigorous flowering, to a period of decreased growth despite a high shoot production, and ends when central branches die and gaps in the *Calluna* cover is created (Watt 1947; Barclay-Estrup & Gimingham 1969; Gimingham 1988).

The heathland succession after burning is to a large extent related to the removal of the dominating key-species *Calluna*, and the changes in interspecific competition in new-burnt patches (Clement & Touffet 1981; Mallik & Gimingham 1983; Hobbs, Mallik & Gimingham 1984). Both species diversity and the abundance of other species are highest in the pioneer phase, when *Calluna* is young and occupies a relatively low proportion of the available space in the recently burnt areas. Diversity and abundance decrease as the *Calluna* density increases in the building- and mature phases, and increase again when *Calluna* enters a degenerative phase (Barclay-Estrup & Gimingham 1969; Gimingham 1978). Species respond in different ways to the *Calluna* development, either as competitor species or species with complementary strategies (Gimingham 1972). Most grasses and herbs are out-competed by *Calluna*, and have their peak abundances in early post-fire successional stage (Hobbs & Gimingham 1984b; Hobbs, Mallik & Gimingham 1984).

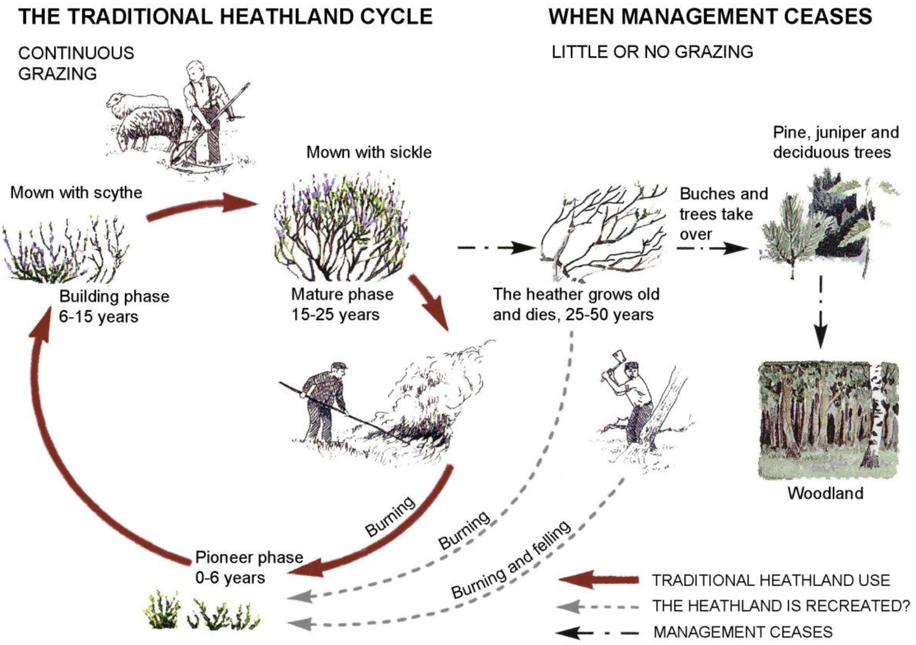

Figure 3. The traditional heathland cycle with the cyclical management regime illustrated to the left, and concequenses of management abandonment to the right (Illustration: P.E. Kaland and K. Isdal/The Heathland Centre).

Knowledge needs: geographical variations and land-use change effects

The degradation of the coastal heathlands is caused by a set of factors, including changes in management regimes (abandonment, under- and over-utilization), transition to arable land, urbanization, pollution, and invasion of native as well as non-native species (Thompson *et al.* 1995). Like other cultural landscapes in Europe, the heathlands developed as part of an agricultural regime that is no longer economically feasible (Vos & Meekes 1999; Goldammer & Montiel 2010). Thus, they are difficult to maintain in modern times (Webb 1998). However, there is renewed interest in traditional management techniques, partly related to conservation and management of especially valuable habitats, including coastal heathlands, and partly due to a new interest in Old Norse Sheep farming (Buer 2011). In Norway, the number of Old Norse Sheep has increased from 500-1000 in the 1950s to more than 40 000 sheep today (Velle & Øpstad 2009). In this connection, many farmers restore traditional heathlands along the coast, and thus require knowledge of appropriate management regimes.

Post-fire successional trends have received considerable attention in the heathland literature, and these are often described in terms of a consistent set of responses following the vegetation dynamics of the *Calluna*-cycle (Watt 1947; Gimingham 1988). However, variations in post-fire patterns are also described, for example by Britton *et al.* (2000) who compare two contrasting heathland sites and report surprisingly variable regeneration patterns, which they attribute to climatic, management, soil, nutrient, and seed input differences between sites (see also Motzkin *et al.* 2002; Oberndorfer & Lundholm 2009). Holden *et al.* (2007) point to the need for more holistic and spatially explicit approaches in studying moorland processes and management, including both social and natural processes. The coastal heathlands cover a long bioclimatic gradient from north to south, and variations in temperature and precipitation cause differences in community dynamics (Fremstad 1997; Moen 1999; Halvorsen *et al.* 2008) and production (Peñuelas *et al.* 2004), factors that influence the local management regimes (Webb 1998). Studies that examine the broad-scale spatio-temporal variation in post-fire regeneration dynamics may provide important knowledge to understand geographic variation in heathlands, and such knowledge is also needed to develop regionally adapted management regimes.

Because of decreased management intensities or land-use abandonment many heathlands are now old and in the degenerative stage, and information is limited of how to manage such heathlands in order to improve their conservation value (Hulme *et al.* 2002; Pakeman *et al.* 2003). Restoration efforts of old heaths have been challenging. Old heaths generally regenerate slowly after fire because of lack of vegetative regeneration by *Calluna* (Hobbs & Gimingham 1984b; Mallik, Hobbs & Legg 1984), they have relatively low biodiversity and changed vegetation composition (Hobbs & Gimingham 1984b). Build-up of biomass in old heath increases the risk for difficult-to-control wildfires, which again result in heterogeneous fire responses (Davies *et al.* 2009, 2010). Consequently, the regeneration rate, and hence the restoration potential, of late-successional heaths has been regarded as low, leading to the recommendation that young heaths should be prioritised for conservation management (Davies *et al.* 2010). However, the critical conservation status of coastal heathlands today implies that old and degraded heaths are of conservation interest, and their restoration potential needs to be explored. As farmers resume heathland management, an understanding of how stand-age influences regeneration rates is required also by them.

Vegetative regeneration of *Calluna* decrease as the plant becomes older (Kayll & Gimingham 1965; Miller & Miles 1970; Mohamed & Gimingham 1970; Hobbs & Gimingham 1984b). However, in a study from northern heathlands no vegetative regeneration was found, even in relatively young heaths (Nilsen, Johansen & Velle 2005), and similarly, *Calluna* is considered an obligate seeder in northwest Spain (Calvo, Tarrega & Luis 2002). This apparent lack of vegetative regeneration implies that management recommendations based on studies where vegetative regeneration is the dominant regeneration strategy are likely to be of little relevance in northern latitudes and at higher altitudes in the south. Studies that explicitly assess revegetation rates and dynamics in northern and alpine climates are therefore needed. At the same time, northern and alpine heathlands can provide a test case for the prevailing hypothesis that slower recovery after fire in old stands is caused by lack of vegetative reproduction in old *Calluna* individuals (e.g. Davies *et al.* 2010).

The invasion and spread of widespread generalist species replacing specialized native species is increasingly seen as a challenge in coastal heathlands. This type of development has been recognized to cause biotic homogenization in many ecosystems (McKinney & Lockwood 1999; Olden & Poff 2003; Rooney *et al.* 2004). Human disturbances have been shown to be a major driver of homogenization (Spear & Chown 2008; Marr *et al.* 2010; Ross *et al.* 2012), and this may cause conservation challenges in cultural landscapes. It can be questioned if traditional management regimes including grazing and burning will maintain the dynamics and functioning of these ecosystems. Perhaps environmental changes, or alterations in the heathland ecosystems due to management changes, cause new effects of traditional management techniques, such as increased invasion of unwanted species. During the last decades, characteristic heathland species have been gradually replaced by more competitive species such as *Molinia caerulea* and *Avenella flexuosa* in continental Europe (Chambers, Mauquoy & Todd 1999; Brys, Jacquemyn & De Blust 2005), and *Betula* ssp. in north-western Europe (Manning, Putwain & Webb 2004). Moreover, Chytry *et al.* (2012) predict that north-western and northern Europe is a region that will be exposed to higher levels of future invasions, due to the spread of alien plants to the landscape from plantations. Homogenization is a complex process that operates over different spatial and temporal scales (McKinney 2008). So far, most studies of biotic homogenisation have been conducted on large spatial scales, comparing extant and historic species lists among large scale units (La Sorte & McKinney 2008). It has been argued that local-scale studies are equally important, as changes in land use regimes often are implemented locally and because interactions between species and their physical environment are strongest at local scales (Buehler & Roth 2011). Furthermore, studies of homogenization at different scales in the same ecosystem, may add valuable knowledge to the understanding of the importance of scale.

Old Norse Sheep - project

The current heathland farming in Norway is to a large extent related to husbandry of Old Norse Sheep, an old domestic breed well adapted to coastal heathlands. Today the breed is found along most of the Norwegian coast, as far north as the Lofoten islands. A new interest in local foods by producers and consumers, in combination with new economic tools for the maintenance of valuable semi-natural habitats has created a positive trend and new possibilities for heathland management. However, while some heathland farmers are successful, others struggle with low slaughter-weights, failing markets, and fluctuating subsidies. Furthermore, there is an increasing awareness of animal welfare issues in our modern society. Animal conditions seen as normal and satisfactory some decades ago need to be adapted to today's welfare standards. In order to meet some of these challenges and contribute to further development of heathland farming, a project called "Old Norse Sheep in coastal heaths – developing a sustainable local industry in vulnerable cultural landscapes" was developed in 2006. The basic idea of the project is that a combination of local industry and heathland management will be the most efficient and cost-effective tool for the future conservation of the coastal heathland ecosystems. The project is interdisciplinary including researchers on landscape ecology, animal health, agronomy and agricultural economy, and has three main packages; (1) sheep holding, production, and animal welfare, (2) the effect of management on the coastal heathland vegetation, and (3) economy and development of local industry. This PhD degree is a part of the Old Norse Sheep project (project 178209/I10).

Aims of the study

The main objective of this PhD-study is to evaluate the role of prescribed burning as a management tool in Norwegian coastal heathlands. Heathland communities vary among heathland habitats, geographical regions, and in response to land-use regime and history. Understanding the implications of this variability for heathland dynamics and diversity is key to conservation, restoration and management.

To address the main objective, the following aims have been set up:

1) Explore if post-fire vegetation dynamics differ along a geographical gradient and quantify the relative magnitude of consistent vs. habitat-, site- and regionally-specific post-fire vegetation responses.
2) Assess the difference in post-fire vegetation dynamics and rates between young and old *Calluna* stand-age and assess how fast *Calluna* is able to regain its position as a dominant species in northern habitats, where vegetative regeneration is absent.
3) Assess if prescribed burning causes homogenisation in coastal heathlands, and if it is scale-dependent.
4) Explore whether *Calluna*-seeds along the coast have smoke-induced germination, and evaluate if this might be a result of human-induced evolution.
5) Evaluate the implications of our findings for heathland conservation and management.

Study areas

Post-fire regeneration

Dataset 1: Post-fire vegetation dynamics were studied in five heathland sites spanning a 340 km latitudinal gradient along the west coast of Norway (Paper I). In addition, data from a previous study have been available, which extended the gradient to 470 km (Paper III), from 60.70 N, 5.08 E to 64.98 N, 10.87 E (Fig. 5, Table 2). The sites were Lygra (A), Aursnes (B), Nerlandsøy (C), Smøla (D), Tarva (E) and Kalvøya (F). They were selected to cover a bioclimatic gradient, and the short geographic distance between sites B and C was selected specifically to capture variation at the border between the boreonemoral and south boreal vegetation zone (Moen 1999), and also because of reports of a shift in *Calluna* regeneration mode in this region from vegetative + seed in the south to seed only in the north (Nilsen, Johansen & Velle 2005). All sites were in acidic heathland vegetation, the most common heathland type along the Norwegian coast. Sites were selected to contain both wet and dry *Calluna*-dominated stands, the major vegetation types of acidic heath in western Norway (Fremstad 1997; Halvorsen *et al.* 2008).

Dataset 2: Post-fire vegetation development in young wet heath, old wet heath, and old dry heath were studied in site E (Tarva) (Paper II). Young dry heath should ideally have been included in the study, but such sites were not available in the study area. The old heath had not been burnt for at least 50 years, and young heath was 8 years.

The sites had to be large enough to harbor a nested design of plots within blocks within habitats, where each block was 100 m^2. In order to obtain as similar vegetation-structure as possible along the gradient, the blocks were selected to contain *Calluna*-stands of >75 % *Calluna* cover, <30 cm *Calluna* height and in mature to degenerative stage. We aimed to select heathlands that had been managed up until recent time; but due to practical constraints and availability this was not achievable, and all sites have been subjected to some changes in management during the last century, generally decreased grazing pressure and fire frequency. Land-use changes have been minor in sites A and E (Tretvik 2003; Kvamme, Kaland & Brekke 2004); sites D and F are still managed by grazing and fire, but with reduced intensity; whereas in sites B and C, burning has been discontinued and grazing pressure has been minimal over the last 40 years. While year-round grazing traditionally has been practiced in sites A-E, summer-grazing has been most common in site F.

Prescribed burning

The experimental fires in this PhD-project (Fig. 4, Table 1) were performed following traditional burning prescriptions (Kaland 1999), under as constant conditions as possible along the gradient. The heather stands that were burnt had approximately equal structure (>75 % *Calluna* cover, <30 cm height, mature to early degenerative morphological growth phase). Fires were set in March and April, in dry weather and when the ground was frozen or wet. The fires were set downwind under light wind speed (0.3-3.3 m/s). Due to practical and legal constraints, experiments were started in different years in the different localities; A: 2006, B: 2006, C: 2008, D: 2007, E: 2002.

Figure 4. Prescribed burning on frozen ground in March at site A, Lygra.

Table 1. Mean fire-temperatures (±SD) in wet and dry heaths in sites A-E. n = 150 measurements per habitat per site. Fire temperature was measured using high temperature Chromel-Alumel (Type K) thermocouples (Hobbs & Gimingham 1984a)

	A	B	C	D	E
Wet	632 (± 107)	630 (± 128)		692 (± 140)	700 (± 87)
Dry	605 (± 98)	658 (± 129)	648 (±110)	616 (± 85)	740 (± 54)

Seed-sampling

Dataset 3: The seed-sampling for paper IV was conducted along two gradients that span similar climatic variability but differ in land-use and fire history. The coastal *Calluna* heaths along the latitudinal gradient have been exposed to traditional heathland management, while the heaths along the altitudinal gradient from the coastal into pine forests and boreal heaths have not had burning as part of the traditional land-use. *Calluna* seed material was collected between Oct 20th and Nov 4th 2007 from 11 heathland populations along these two gradients. The latitudinal gradient (58°4'N to 69°38'N) comprised coastal heathland sites at Hidra (I), Fedje (II), Hjørungavåg (III), Smøla (IV), Bodø (V) and Tromsø (VI), and the altitudinal gradient (0 – 1000 m a.s.l.) *Calluna* heath sites at Lygra (a), Gullbotn (b), Kvamskogen (c), Vøringsfossen (d) and Ustaoset (e) (Fig. 5, Table 3).

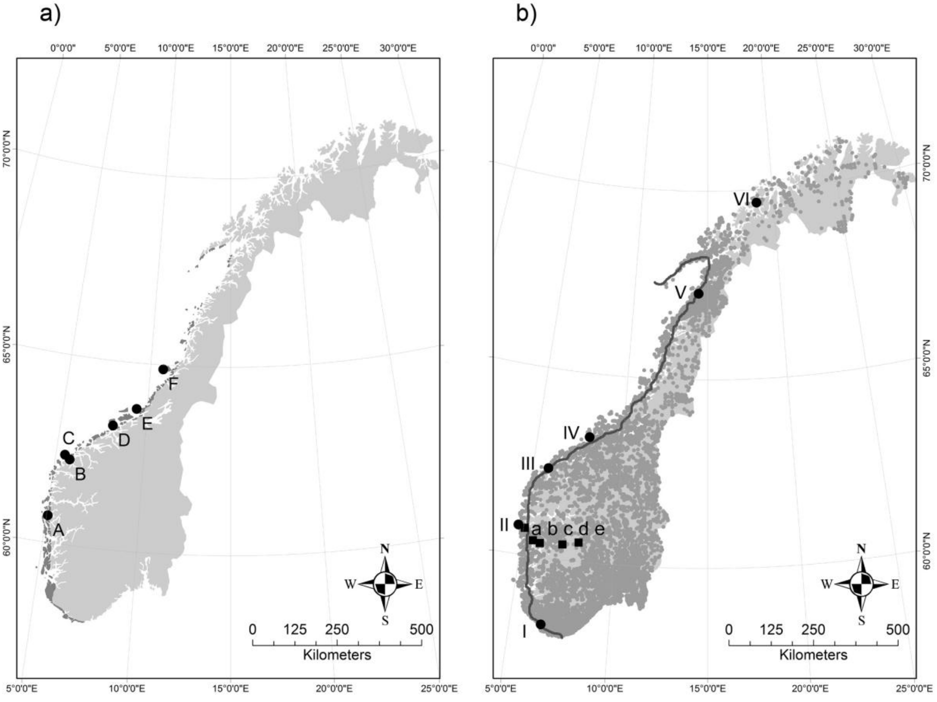

Figure 5. a) Study sites for dataset 1 and 2 vegetation analysis. For site details see Table 2. Darker colour represents coastal heathland distribution in Norway (after The Heathcult Project, see Kvamme, Kaland & Brekke 2004). b) Sample sites for dataset 3 *Calluna* seeds in smoke-induced germination experiment. For site details see Table 3. The coastal gradient is represented by circles, the altitudinal gradient by squares. Darker colour represents distribution of *Calluna vulgaris* (www.artsdatabanken.no).

Table 2. (a) Climatic conditions and biogeography and (b) bedrock and land-use in the six study sites along the 470 km latitudinal gradient in western Norway (dataset 1 and 2). The table is based on data on temperature (Aune 1993), precipitation (Førland 1993), vegetation-zone and section (Moen 1999), bedrock (Sigmond, Gustavson & Roberts 1984) and land-use (based on local management plans and interviews with local land-owners).

(a) Climate and biogeography

Site number	Geographic location	Mean annual temp. (°C)	Mean Jan. temp. (°C)	Mean annual precip. (mm)	Vegetation zone	Vegetation section
A	60.70 N, 5.08 E	7.3	2.5	1630	Boreonemoral	Highly oceanic
B	62.25 N, 5.83 E	6.7	1.2	2075	Boreonemoral	Highly oceanic
C	62.36 N, 5.52 E	6.9	1.8	1645	Boreonemoral	Highly oceanic
D	63.30 N, 8.06 E	6.9	2.0	1155	South Boreal	Highly oceanic
E	63.79 N, 9.39 E	6.2	1.1	1124	South Boreal	Highly oceanic
F	64.98 N, 10.87 E	6.0	0.5	850	South Boreal	Highly oceanic

(b) Bedrock and land use

Site number	Bedrock	Grazing pressure	Burning rotation last 50 years
A	Dioritic to granitic gneiss and migmatite	1 ewe ha^{-1}	Between 10-20 years
B	Dioritic to granitic gneiss and migmatite	Low pressure	> 20 years
C	Dioritic to granitic gneiss and migmatite	Low pressure	> 20 years
D	Dry heath: Conglomerate and sedimentary breccia		
	Wet heath: Mangerite to gabbro, gneiss and amphibolite	0.1 ewe ha^{-1}	> 20 years
E	Granitic gneiss and migmatite	0.5 ewe ha^{-1}	> 20 years
F	Calc-silicate schist and gneiss	0.7 ewe ha^{-1}	> 20 years

Table 3. Geographic and climatic characteristics of the sampled *Calluna* populations (dataset 3). Latitudinal gradient above the vertical line, and altitudinal gradient below. M.a.s.l. = metres above sea level.

Site number	Longitude	Latitude	Altitude (m.a.s.l)	Mean annual precip. (mm)	Mean annual temp. (°C)
Lat gradient					
I	6°48'E	58°40'N	1	1200	7.3
II	4°49'E	60°47'N	3	1680	7.2
III	6°10'E	62°20'N	20	1770	6.5
IV	8°40'E	63°17'N	1	1290	6.1
V	14°24'E	67°17'N	20	1040	4.5
VI	18°55'E	69°38'N	1	1020	2.7
Alt gradient					
a	5°50'E	60°42'N	1	1890	7.3
b	5°44'E	60°26'N	300	2960	4.9
c	5°58'E	60°23'N	500	3010	3.6
d	7°16'E	60°25'N	800	-	-
e	8°20'E	60°29'N	1020	750	-0.6

Experimental and analytical approaches

Paper I:

In the first paper we investigated revegetation dynamics after experimental burning in two habitat types; wet vs. dry *Calluna* stands, in five heathland populations along a 340 km long latitudinal gradient. Dataset 1 was used, with a repeated measures design, floristic data recorded in permanent plots (n = 20), and experimental post-fire successions were followed over a 3-year period. The data were analysed using multivariate ordination techniques; principal components analysis, partial redundancy analysis and principal response curves, and mixed effects models.

Paper II:

In paper II we investigated the effect of stand age on the direction and rate of post-fire successional dynamics in coastal *Calluna* heaths, and whether old degraded heath vegetation could be restored through the re-introduction of fire. Dataset 2 was used, and revegetation dynamics were studied after experimental fires set in young (8 years since last fire) and old (> 50 years since last fire) grazed *Calluna*-stands in site E. A repeated measures design was used, with floristic data recorded in permanent plots in the post-fire successions (n = 12) over a 7-year period. The data were analysed using multivariate ordination techniques; principal components analysis, partial redundancy analysis and principal response curves, and mixed effects models.

Paper III:

In this study we tested whether prescribed burning results in biotic homogenisation of heathlands. Dataset 1 was used, and beta-diversity was compared before and after fire at three spatial scales; within local vegetation patches, between wet and dry heathland patches in the same landscapes, and along a 470 km bioclimatic gradient. In the study of the compositional vegetation patterns we used full time series (n = 524), and in the tests of homogenization the datasets were balanced over time (0-2 years) and habitats (site C excluded) (n = 300). The result in this paper have been analysed by multivariate principal components analysis, partial redundancy analysis, calculation and tests of beta-diversity (vegan package in R) and multi-level pattern analysis (indicspecies package in R).

Paper IV:

In paper IV we tested smoke-induced *Calluna* germination in cultural vs. natural fire regimes, and used dataset 3. The seeds were sampled along two spatially independent geographical gradients in Norway; a latitudinal gradient along the coast (6 heathland populations) and an altitudinal gradient from the coast into the mountains (5 populations). The gradients covered comparable ranges in climatic conditions, but differed in historical land-use regime; burning has been a common and frequent land-use practice along the coast but not in the boreal and alpine heaths away from the coast. Seeds from ten maternal plants per population were used in the smoke-water experiment. The results were analysed by Generalized Linear Mixed Models.

Results and discussion

POST-FIRE DYNAMICS

Immediate and strong effects of fire

All sites showed an immediate and strong response to fire along the entire studied gradient, and all successional trajectories had the same general direction toward pre-burned controls. The distances between years on the trajectories illustrated that the first year (from control to first post-fire year) contributed the most to the compositional variation, and that the rate of succession decreased with time (Paper I-III). The species that were most strongly negatively affected by fire are *Hylocomium splendens*, *Hypnum jutlandicum* and *Calluna* (Figure 2, paper I), species of high abundance in pre-fire vegetation across all sites. No geographical patterns were found in species richness (paper I & III) or number of species that decreased (paper III) after fire. This confirmed a relatively uniform pre-burned vegetation composition, and the efficiency of the prescribed burning in order to remove standing biomass in *Calluna*-stands. The removal of the dominant *Calluna* in pre-burned vegetation caused a shift in species composition and opened the vegetation canopy for colonising species. After fire we recorded increased species richness (paper I & III) and a higher taxonomic dissimilarity within habitats and across sites (paper III). In particular, grasses and herbs constituted the groups of early colonizers in new-burnt flats (papers I & III) and *Carex pilulifera*, *Dactylorhiza maculata* and *Luzula multiflora* were the species most consistently positively affected by fire (Figure 2, Paper I).

These overall post-fire successional trends are in line with a number of previous studies (e.g. Mallik & Gimingham 1983; Hobbs & Gimingham 1984b), and the expectations of burning as a management tool in heathlands (Gimingham 1992). The predictability of this development is important in order to motivate burning, and make burning into an instrument that can be used to manage the spatial structure of the heathland pastures that contain patches of both grassland and heather of good fodder value. Such combinations are important for the grazers and influence the way the animals utilize the heathland pastures (Hester & Baillie 1998; Bokdam & Gleichman 2000). Grasses and herbs have high nutrient value, and are important for the animals from spring to autumn (Nedkvitne, Garmo & Staaland 1995). Results from the "Old Norse Sheep project" have demonstrated that the evergreen *Calluna*, that is crucial to the animals during wintertime, also is an important part of the sheep's diet throughout the entire year (Norderhaug & Thorvaldsen 2011).

Burning also strongly influenced the germination of *Calluna* seeds. The seed-germination experiment (Paper IV) showed that *Calluna* had a strong smoke-response along the entire geographical gradient that paralleled the historic land-use regime with prescribed burning. Smoke-induced germination has earlier been documented in *Calluna* populations from coastal heathlands (Thomas & Davies 2002; Måren *et al.* 2010), and provides an advantage in the form of increased recruitment from seed-banks in newly-burnt heaths (Måren *et al.* 2010; Harris *et al.* 2011), resulting in faster post-fire vegetation recovery. In contrast, we found that *Calluna* populations from the mountains, which have not been subjected to burning as part of a traditional management regime, did not have such germination responses to smoke. This implies that the smoke-induced germination in this study is likely to be a result of human-induced evolution (Paper IV).

Figure 6. The vegetation composition before burning (control) and the following three growth seasons after burning (year 1-3) at site A, Lygra.

Variations in fire responses due to geography, habitat and age

The vegetation dynamics after fire varied geographically both in species composition and in post-fire successional trends and dynamics. Although pre-burned vegetation was strongly dominated by *Calluna* (>75 % cover) across all sites and gave a similar impression in terms of vegetation type and structure, a number of regional patterns became apparent after fire.

Successional trajectories varied geographically: after accounting for the main post-fire successional trend (17.4%), site-specific fire responses explained a further 6.5% of the variation in community composition (Paper I, Table 2). In south-western sites, a number of frost-sensitive species appeared after fire, such as *Erica cinera*, *Hypericum pulchrum*, *Pedicularis sylvatica*, *Polygala serpyllifolia* and *Leucobryum glaucum*. From mid-Norway (sites B & C) and northwards this western element gradually declined and northern and more alpine species increased, for instance *Arctous alpinus, Carex bigelowii* and *Rubus chamaemorus.* The cover of lichens and *Racomitrium lanuginosum* increased, and *Empetrum nigrum* became more important (Paper II, Måren & Nilsen 2008; Nilsen & Moen 2009). This underlines that if we want to maintain the floristic variation of Norwegian coastal heathlands, it is important to conserve heathlands representing this north-south gradient. It is especially important to maintain coastal heathlands harbouring threatened species that have heathlands as their most important habitat. Two such species were recorded in this project, *Erica cinera* is considered as near threatened, and *Leptodontium flexifolium* (Aarrestad & Vandvik 1997) is categorised as endangered (Kålås *et al.* 2010).

Paper III ascertained that the species that increased after fire were native, mainly grasses and herbs, and there was no increase in potentially invasive species after fire. Interestingly, species characteristic of newly-burnt vegetation generally had a narrower geographic distribution than the species characteristic of unburnt vegetation. This contrasts the often-cited effects of anthropogenic disturbances such as fire in promoting biotic homogenization, which predicts that generalist species should enter the system after fire (Buehler & Roth 2011; Ross *et al.* 2012). Traditionally, prescribed burning has been used as a tool in heathland management to release nutrients captured in old vegetation (Webb 1998) and to promote a temporarily period of grasses and herbs that are typically more nutritious than Ericaceous species (Nedkvitne, Garmo & Staaland 1995). The vascular plants that increased after fire also had relatively high pH requirements. This is typical for species found in newly-burnt vegetation (Granged *et al.* 2011).

The most distinct geographical pattern in our post-fire vegetation trends and dynamics were faster succession in the southernmost sites, particularly prominent in wet habitats (Papers I & III). This can be explained by the rapid return of *Calluna* and bryophytes (Paper I). Moreover, the southern sites had a faster recovery of grasses and herbs, and the highest species richness (Paper I & III). The higher number of species in the south is probably linked to higher productivity in the warmer southern climate (Rustad *et al.* 2001; Peñuelas *et al.* 2004), and to a larger species pool, giving a higher number of potential post-fire colonizers in the south, related to the biogeographic diversity gradient (Nekola & White 1999; Whittaker, Willis & Field 2001). A number of species that were found in all sites also changed in abundance along the gradient. Differences in abundance can be linked to the bioclimatic production gradient and to a high grazing pressure that might have influenced the cover of grasses in site A.

Sufficient grazing pressure can promote grass and herb cover in newly-burned heath stands and delay re-establishment of *Calluna* dominance (Hulme *et al.* 2002; Pakeman *et al.* 2003; Vandvik *et al.* 2005). However, site E, with the second highest grazing pressure had the lowest cover of both grasses and herbs. The highest cover of herbs was found in the dry heath stand in site D, on slightly richer conglomerate bedrock. Rich heathlands often has higher species content than acidic heath (Nilsen & Moen 2009). In Norway, rich heathlands with high species diversity are found mostly north of the studied gradient, illustrating a diversity hot-spot uncorrelated with the north-south bioclimatic production gradient (Tveraabak 2004; Nilsen & Moen 2009).

The key species Calluna

In our study, vegetative regeneration was of importance in site A only, and observed in a few individuals in site C. Vegetative regeneration can be reduced if *Calluna* stands are exposed to high temperatures (800 ºC) in the canopy during burning (Mallik & Gimingham 1985), however temperature measurements in our sites did not reach this level (Table 1). Also, vegetative regeneration has been demonstrated to decrease in old *Calluna* stands (Kayll & Gimingham 1965; Miller & Miles 1970; Mohamed & Gimingham 1970; Hobbs & Gimingham 1984b; Davies *et al.* 2010) which can also be the case in some of our sites. However, lack of vegetative regeneration has previously been documented for both young and old stands in site E (Nilsen, Johansen & Velle 2005; Paper II). This lack of vegetative regeneration might potentially link *Calluna* regeneration strategies to environmental, climatic and/or genetic conditions, and further research is needed to unravel the specific drivers and mechanisms of these shifts in regeneration strategies along the bioclimatic gradient.

The regeneration rate of *Calluna* is essential in the heathland management, as it strongly influences the coexistence of other species, determines the length of burning rotations, and constitutes an important plant for pasture (Hobbs & Gimingham 1987; Gimingham 1992). In papers I-III we demonstrate considerable variation in *Calluna* regeneration rates, both among sites, between habitats and due to age. The regeneration rates documented in paper I demonstrate that *Calluna* decreased immediately after fire in all sites and increased from the second year onwards, with the southernmost site having the fastest return to pre-fire conditions. Here, *Calluna* covered 13-25% in the first growth season after fire, in contrast to less than 3% cover in all other sites. In the third growth season site E had the highest *Calluna* cover, exceeding 50%, despite regenerating from seedling only in this site. This was surprising, since vegetative regeneration generally results in the fastest build-up of biomass (Kayll & Gimingham 1965; Mohamed & Gimingham 1970). The slowest *Calluna* regeneration was found in dry heaths in sites B, C and D, relied on seedling requirement only, and illustrates, in accordance with other studies, that *Calluna* seedlings are drought sensitive (Gimingham 1972; Britton *et al.* 2003; Calvo *et al.* 2005).

LAND-USE CHANGES

Calluna *age moderates regeneration rates*

In paper II we addressed the specific challenge of longer burning rotation compared to the historic land-use regime, and we found to what extent the age of *Calluna* stands influenced post-fire succession. Young heath had a faster and more uniform succession towards the pre-burnt community composition, a pattern paralleled by the development of *Calluna*, grass cover, and species richness. Compared to southern sites, the cover of grasses in the old heath in site E was very low (Paper I), however, by adding a second burning rotation, the cover increased significantly (Paper II). The differences between young and old *Calluna*-heaths might be attributed to succession-related differences, as we find a lower cover of mosses and lichens in young pre-burned vegetation, which leads to a lower cover of litter in the early successional stage. Nilsen, Johansen & Velle (2005) describe how *Calluna* stems and mosses sometimes remained after fire in old heaths, but rarely in young heaths. Succession-related factors such as moisture content of the soil and ground-layer, ground-layer thickness and topography have been demonstrated to influence the biomass removed by fire (Forgeard 1990; Legg, Maltby & Proctor 1992). Further, Davies *et al.* (2010) link post-fire regeneration to pre-fire substrate type, and ascribe poor seedling establishment to post-fire substrate dominated by live or dead pleurocarpous moss mats. In line with previous work we also found that pre-fire species composition is a major determinant of community development after fire (Hobbs & Gimingham 1984b; Vandvik *et al.* 2005) but this effect was weak relative to the age effect.

Concerns have been expressed regarding loss of species diversity in old heaths (Hobbs & Gimingham 1984b; Mallik, Hobbs & Legg 1984). Grasses and herbs typically decline in the degenerate successional stage, especially in rich heath (Hobbs & Gimingham 1984b; Mallik, Hobbs & Legg 1984). In our study, species richness was habitat-specific, with dry heaths harbouring the highest diversity. Despite a faster recovery in the number of species in young wet heaths compared to the old wet heaths, all heath types developed towards the pre-burned condition, indicating no seed limitation during succession among the resident species. The seed bank may be of importance for species persistence during succession in both young and old blocks, and this is in accordance with Måren & Vandvik (2009), who found no drastic changes in the soil seed bank along a 24-year successional sequence.

Traditionally-managed coastal heathlands consist of a fine-scale spatio-temporal mosaic created by the interplay between environmental conditions and post-fire dynamics (Usher & Thompson 1993; Vandvik *et al.* 2005). Small-scale management is important in order to sustain the diversity in heathlands. To survive long term, early successional species that occur in mosaic vegetation must be able to colonize new patches before they are lost from existing vegetation. Among the species that increased after fire were a number of species that have coastal heathlands as their most important habitat i.e. *Galium saxatile*, *Hypochoeris radicata* and *Polygala serpyllifolia* (Paper III). They were especially distinct in southern sites, but sites A and E contributed almost the same number of unique (found in one site only) post-fire increaser species (Appendix 1 in paper III). Vegetative resprouting, seed dispersal, and longevity in seed banks are important contributors to population persistence in heathlands for the species found in early post-fire stages (Hobbs, Mallik & Gimingham 1984). Måren & Vandvik (2009) find that the seed bank can act as a temporal refuge for post-fire specialist species in coastal heathlands. Nevertheless, many grasses and herbs have relative short soil seed bank longevity (Hobbs & Gimingham 1984b; Måren *et al.* 2010) and thus rely on continued management that provides both a dependable seed bank and transient patch mosaics. Meulebrouck *et al.* (2009) demonstrate that cessation of management can be detrimental to short-lived species, and Piessens & Hermy (2006) link the loss of a few heathland species in Belgium to an extinction debt where the full effects of habitat loss have not yet been seen. These findings point to the small-scale management and spatiotemporal aspects in conservation strategies.

Succession cause homogenization

The successional dynamics after fire in coastal heathlands can be seen as a post-fire heterogenization-homogenization process driven by the re-establishment of *Calluna*, and the restoration of this species as the dominant species over a few years after fire (Paper I-III). Understanding how management regimes influence vegetation composition and diversity is therefore crucial to evaluate evidence for homogenization. In a study of alpine vegetation in Scotland, Britton *et al.* (2009) conclude that homogenization occurs in their system over a 20-40 year period, and northern and alpine species declined while lowland generalist species increased. In their studied *Calluna* heaths, species richness (higher plants and mosses), *Calluna* frequency, and cover increased, while beta-diversity decreased and *Calluna*-plots became more tightly clustered. The land-use was not specified in this article, but our results indicate that their observed homogenization might be related to successional dynamics inherent to the ecosystem.

Invasive species

Even though potential invasive species such as *Avenella flexuosa, Betula* ssp., *Molinia caerulea* and *Pteridium aquilinum* were present in our study sites, widespread generalist's species did not appear to constitute a problem in the studied post-fire vegetation dynamics along the gradient (Paper III), or after burning old heath (Paper II). However, their presence might constitute a future threat. Most importantly, a number of woodland species has established, especially near existing woodland and elsewhere where conditions are favourable for the spread of seedlings, establishment and growth (Hester, Gimingham & Miles 1991; Manning, Putwain & Webb 2004; Manning, Putwain & Webb 2007). Most heathlands in Norway have developed in close proximity to established woodland, and have thus not been as stable as further south or west in Europe (Skogen 1987). If these woodlands continue to spread, the coastal heathlands will disappear. In the northernmost site along our gradient (F), distinct changes in woodland and scrubland cover have been detected during the last 40 years (Moen *et al.* 2007). The reforestation accelerated over time in both cover and spatial occurrence, a typical pattern for secondary succession (Glenn-Lewin & Van Der Maarel 1992). Caution is needed when restoring heathlands that are only a short distance away from the nearest seed source for trees. Burning such heaths, with very low grazing pressure, or even no grazers at all, might cause accelerated clogging. In Italy, fire has become one of the main determinants that triggers transitions towards woodlands because of the continuance of frequent burning under low grazing pressure (Borghesio 2009; Ascoli & Bovio 2010). Spread of non-indigenous species from plantations is another threat to Norwegian coastal heathlands (Fremstad & Moen 2001; Chytry *et al.* 2012). A comprehensive forestation along the coast was carried out in the 1950s and 1960s, and among the introduced coniferous species, *Picea sitchensis* has the highest cover of approximately 50 000 hectare (Øyen *et al.* 2009). *P. sitchensis* spreads aggressively; in site E, Thorvaldsen (2011) has estimated that seedlings from a 1 ha large plantation have spread across an area of 8 ha, with a density of 15 500 plants per ha (Fig. 7).

Figure 7. Spread of *Picea sitchensis* in site E. Seedlings from a 1 ha large plantation have spread across an area of 8 ha, and with a density of 15 500 plants per ha (Illustration: P. Thorvaldsen, see also Thorvaldsen 2011).

Increased airborne nitrogen deposition is another threat to the heathlands, leading to acidification and eutrophication of the heathlands. The effect is generally decreased or changed biodiversity, especially an increase in grasses and a decline in sensitive herbs, bryophytes, and lichens (Fremstad 1992; Aarrestad & Stabbetorp 2010). Although Norway has not been exposed to as high depositions as further south or west in Europe, critical loads of nitrogen have been measured in south-western heaths, and the rates will probably increase further (Aarrestad & Stabbetorp 2010). Increased cover of *Molinia caerulea* and *Avenella flexuosa* have been linked to nitrogen depositions and changes in land-use (Chambers, Mauquoy & Todd 1999; Brys, Jacquemyn & De Blust 2005). Both species are present in our study sites, but do not currently appear to be threats as they have of low abundance and do not increase after fire (paper III). However, if the nitrogen deposition increases, this situation might change.

Another threat is *Pteridium aquilinum* (bracken), whose spread in heathlands has been linked to changes in land-use and climate (Marrs *et al.* 2000). Bracken is a common species throughout sites A-C, and has especially been considered a problem in the southernmost site, where control treatments have been tested (Måren, Vandvik & Ekelund 2008). However, bracken reaches its northern limit in the European *Calluna*-heaths in western Norway, and this might explain why it seems less vigorous and invasive here, compared to continental Europe and the UK (Måren 2009).

CONSERVATION AND MANAGEMENT

A new era for heathland conservation in Norway

The Norwegian coastal heathlands have received an increased interest during the past decades both nationally and internationally. They were formerly sparsely mentioned in the international heathland literature, but are now seen as an important part of the European heathland area. In Norway, the view of coastal heathlands went through an important paradigm-shift in the 1970s and 1980s, when Kaland (1979, 1986) by the use of palynological investigations in combination with archaeological data, demonstrated that the development of heathlands was human-induced and not a result of severe climatic conditions as previously thought. This knowledge made it clear that management is necessary to maintain the heathlands, and the knowledge came in a time when clogging already had started in abandoned heathlands (Steinnes 1988; Fremstad, Aarrestad & Skogen 1991). In 2001 the Norwegian coastal heathlands were listed as ‘endangered’ for the first time (Fremstad & Moen 2001).

Throughout the last 15-20 years an increased awareness of the critical conservation status of coastal heathlands in Norway has developed, based on mapping-projects and increased dissemination of knowledge about coastal heathlands as semi-natural vegetation. The Norwegian authorities has been criticised for leaving most nature reserves unmanaged, which has caused loss of biodiversity in semi-natural nature types inside reserves (Riksrevisjonen 2006). However, new legislation regarding the management of biological, geological, and landscape diversity (Nature Diversity Act 2009) has initiated new trends in nature conservation. Recently, a national action plan has been developed for the coastal heathlands (Norwegian Directorate for Nature Management, in prep.). The main objective is to secure maintenance of different types of Norwegian coastal heathlands and their biological diversity, together with traditional knowledge regarding sustainable land-use. Continued management is seen as a key component of this plan, and in congruence with our results (papers I & III) the action plan suggests the establishment of a number of heathland reference areas distributed along the north-south gradient in order to capture the geographical variation. Both protected and unprotected areas are included in the plan.

The action plan addresses the importance of local husbandry in order to secure the future of coastal heathlands. This is in congruence with others who point to considerable logistic and financial challenges in heathland management when traditional land-use ceases (Borghesio 2009). Our results (Paper II) shows that degraded and old heaths have restoration potential and can therefore also be of conservation interest. This implies that farmers that want to resume management in abandoned heaths should be encouraged to do so where it is feasible, and that abandoned sites should also be included in the subsidies schemes.

Management implications from our results

Prescribed burning in combination with grazing is an efficient tool in heathland management. Papers I-III demonstrate the importance of continuance for successful traditional management but also the possibility for restoration of degraded heathlands where it is feasible, and address the importance of targeted and knowledge-based management and support-policies. Burning efficiently removes standing biomass and thereby halts the secondary succession towards scrubs and woodland (Papers I-III). Burning rejuvenates the *Calluna* stands (Papers I & II), and the burning history of heathlands entails smoke-induced germination of *Calluna* seeds that results in increased germination rates and faster post-fire recovery (Paper IV).

The post-fire vegetation dynamics show considerable variation due to differences between sites and habitats (Paper I) and age of the pre-burnt stands (Paper II). Thus regional and even local knowledge about these differences must be taken into account in future management plans. Regeneration rates decrease from south to north, in relation to the bioclimatic productivity gradient and *Calluna*'s regeneration strategy (Paper II). However, even if regeneration is somewhat slower in the north, this does not inhibit the vegetation dynamics from developing toward pre-burned conditions (Papers I-III).

The variation in regeneration strategy and rates for *Calluna* among sites and habitats suggest that optimal burning rotations vary among sites and regions, and one way to achieve this is to base management plans and prescriptions on the cover of vegetation canopy in combination with *Calluna*'s morphological growth form (Papers I & II), instead of basing management on the age of the *Calluna* stands as is often currently advised. The early stages of the post-fire vegetation development are characterised by a number of native grasses and herbs (Paper II). Moreover, some of these species have heaths as their most important habitat and have regionally restricted geographical distribution patterns (Paper III). Prescribed burning seems, so far, not to cause homogenization in the form of invasion of generalist species into the Norwegian coastal heathlands. However, the heathlands contain species that can become future threats (e.g. *Avenella flexuosa*, *Betula* ssp., *Molinia caerulea*, *Picea sitchensis* and *Pteridum aquilinum*), especially when future changes in land-use, nitrogen deposition, and climate are considered. Such species need to be followed over time and, in sites where they occur, and management plans should contain strategies of how to deal with them.

Old *Calluna* heaths are shown to have restoration potential (Paper II), however, special consideration needs to be taken when restoring old *Calluna* heaths, in particular dry habitats where regeneration rates are slow, and in northern regions where seedling recruitment is the only mode of regeneration (Paper I). These sites provide poor winter pastures the first years after fire, and thus care is needed when setting grazing levels during winter-time. High cover of mosses and litter in pre-burned vegetation composition modify post-fire regeneration rates (Paper II), but these rates are expected to increase as new burning rotations are carried out (Paper II). As regeneration rates change, modifications in management plans should be undertaken to reflect the changes.

Based on the results of this project, small-scale burning in combination with grazing in order to create vegetation dynamics that vary both temporally and spatially is recommended, and burning rotations must be adapted to local conditions. This gives the manager good possibilities to control and limit potential problem species and will in addition create favourable conditions for year-round grazing.

Further perspectives

This PhD project has demonstrated regional variation in post-fire vegetation rates and dynamics along the studied bioclimatic gradient. It would be interesting to follow these dynamics for a longer time; especially in sites were *Calluna* regeneration has been slow. This will for instance make it possible to answer whether *Calluna* is able to re-establish a dense vegetation canopy in dry habitats that rely on seedling recruitment only. Moreover, it will provide information about possible changes in the vegetation composition, including potentially increased invasion of unwanted species to the ecosystem.

An expansion of the gradient by adding sites in both a southern and northern direction, including rich heaths, would provide a more complete picture of geographical variation in post-fire dynamics. Moreover, adding a second burning rotation to more sites will expand the understanding of the restoration potential of old heaths, as the effect of stand-age to post-fire regeneration has been assessed in one single site only in this project.

In order to increase the knowledge of phenotypic variation and biomass production in *Calluna* along the long biogeographical gradient in Norway, a greenhouse study of *Calluna* seedlings has been conducted parallel to this PhD-work. This dataset will add information to the variations seen in the field. The establishment of these *Calluna* seedlings in a garden experiment will give us the possibility to sample plant material for genetic analysis and to test the population's vegetative regeneration ability (burning experiment). Further studies might also show if genetic differences can explain the demonstrated variation in smoke-induced germination (north south gradient vs. east-west gradient) and the broad bioclimatic variations in regeneration rates and strategies of *Calluna*.

It will be important to follow the development of coastal heathlands along the Norwegian coast, as many future scenarios of changes might occur. Will the action plan for coastal heathlands secure sustainable management in the selected areas along the coast, and fulfil its objective? How will heathlands respond to possible future changes in land-use, nitrogen deposition and climate? The set-up of monitoring programmes in selected heathland sites could be an important tool allowing us to capture such changes.

For heathland farming it will be of importance to increase the knowledge of how to provide a sustainable husbandry in heathlands, and effort should be put into the dissemination of results from research projects to farmers, and managers as well as local and central government administrations.

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