

Prescribed burning and the role of seed banks in post-fire succession of northern heathlands, Lygra and Lurekalven islands, Hordaland, Norway

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SUMMARY

Variation in plant species composition, abundance of seeds in the soil seed bank and standing vegetation, over the course of a post-fire succession was investigated in coastal *Calluna*-heathlands in Western Norway. Vegetation and seed banks were analysed over a 24-year post-fire period. The total diversity of vegetation and seed bank were 60 and 54 vascular plant taxa respectively (39 shared species), resulting in 68% similarity. Over the 24 years the heathland community progressed from open newly-burnt ground via species rich graminoid- and herb-dominated vegetation to mature heather *Calluna vulgaris*-dominated heath. This post-fire succession was not reflected in the seed bank; the 10 most abundant species constituted 98% of the germinated seeds. The most abundant were *Calluna* (49%; 12,018 seeds/m²) and cross-leaved heath *Erica tetralix* (34%; 8,414 seeds/m²). *Calluna* showed significantly higher germination in the two first years following burning. Vegetation species richness (ranging 23 to 46 species/yr) was highest in the middle years of the post-fire succession period. In contrast, the seed bank species richness (21 to 31 species/yr) showed no trend. This suggests that the seed bank act as a refuge, providing a source of recruits for many species that colonize newly-burnt areas. The traditional management regime has not depleted or destroyed the seed banks, and continuing management is necessary to ensure perpetuation of the heathlands.

BACKGROUND

Due to their implications for plant species population persistence and community resilience, seed banks have been the subject of management, conservation and restoration research. Such studies, however, typically reach the conclusion that seed banks have little potential for the conservation and restoration of natural and semi-natural ecosystems (Mitchell *et al.* 2008). Many studies find lower species richness and higher proportions of weeds and early-successional species in the seed bank relative to the standing vegetation (Milberg 1995, Bekker *et al.* 2000). We therefore asked, what is the role of seed banks – do they act as a refuge for early successional species or can they simply be seen as a spillover from the extant local vegetation?

Heathlands are semi-natural habitats in which rotational burning and livestock grazing (both traditional management methods) significantly alter the species composition, biomass and plant growth forms. On heaths, fire acts as a re-setting

mechanism for secondary succession. Early successional high diversity, notably of graminoids and herbs is gradually outcompeted by a few species of ericaceous dwarf-shrubs; without suitable management succession proceeds to woodland. In cyclic vegetation types such as heathlands, seed banks are particularly important so that species can survive locally and re-establish over time (Thompson & Grime 1979, Meulebrouck *et al.* 2008) as studies of seed rain into burned areas have shown that few seeds enter from surrounding areas (Hobbs & Gimingham 1984). Both the size and quality of the viable seed bank may be determinants of successful restoration on successional sites (Granström 1987 and 1988, Hester *et al.* 1991, Pakeman & Hay 1996).

Prescribed burning and livestock grazing are still predominant management techniques of European lowland heathlands. The management history of Northern Europe's coastal heathlands is in many cases well known, hence they lend themselves to investigations on spatial and temporal processes. At

our study area at Lygra (www.lyngheisenteret.no) management history (Kaland 1986), vegetation development (Aarrestad & Vandvik 2000), microclimate, soil conditions and similarities in availability of propagules are quite constant through out the landscape, justifying the use of a chronosequence (space for time) approach. The regeneration of the key species in this system, heather *Calluna vulgaris*, (hereafter *Calluna*) in post-disturbance successions is of considerable interest to the conservation of these endangered habitats (Gimingham 1992, EU Habitats Directive 92/43/EEC). This is of particular relevance in northern regions (i.e. areas north of 62°N) as Nilssen *et al.* (2005) found that after fire *Calluna* regenerates from seed only, and not from vegetative resprouting as is the case in more southerly-lying heaths.

ACTION

Study sites: The islands of Lygra and Lurekalven (60°42' N, 5°5' E) are situated in the Lure fjord 20 km inland from the Norwegian west coast and 40 km north-west of the city of Bergen (Fig. 1). The climate is oceanic with mean temperatures of 12°C in June and 2°C in January, a long growing season of about 220 days, and mean annual precipitation of 1,600 mm evenly distributed throughout the year (www.met.no). *Calluna* heath dominates with mires and willow *Salix* shrubs in wetter areas, and mixed grass-heaths on nutrient-rich beaches and former cultivated areas. Additional main constituent ericaceous heath species (cross-leaved heath *Erica tetralix* (hereafter *Erica*), bilberry *Vaccinium myrtillus*, cowberry *V. vitis-idaea*, bog bilberry *V. uliginosum*, cranberry *V. oxycoccus* and crowberry *Empetrum nigrum*) occur throughout. Moisture is a major source of local environmental variability, with dry heath on shallow soils, ridges or south-facing slopes, and wet heath on deeper soils, north-facing slopes or, in poorly drained depressions. In western Scandinavia traditional coastal farming (a combination of mowing, rotational burning, turf-cutting and keeping several kinds of livestock) has resulted in a high diversity of semi-natural heath habitats at various successional stages over relatively small areas (Moen *et al.* 2006). This contrasts the situation on the continent and in the British Isles where stands tend to be larger and more even-aged (Gimingham 1972, Hobbs & Gimingham 1987). The outfields of Lygra and Lurekalven have been under continuous management for centuries up to the present day, and have the characteristic mosaic of different successional stages (Vandvik *et al.* 2005). Old Norse breed sheep *Ovis brachyura borealis* graze year around at a density of about 1 sheep/ha/year (S. Øpstad, unpublished data).

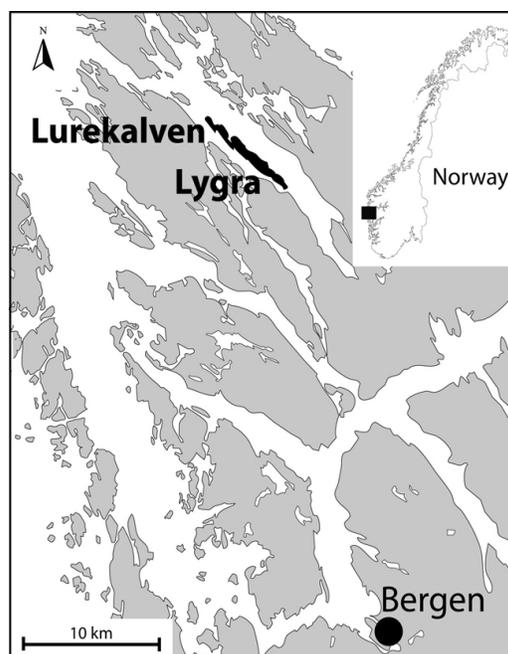


Figure 1. The neighbouring islands of Lygra and Lurekalven (separated by a narrow 20 m-wide strait) situated in the Lurefjorden fjord system of Western Norway (part of Europe's Atlantic coastal heathlands).

Vegetation and seed bank sampling: At Lygra and Lurekalven, yearly management fires have been carried out in small areas of mature to degenerate heath (*sensu* Watt 1955, Gimingham 1972) in late winter/early spring since 1992 (except in 1999 when wet weather did not permit burning). This gave a unique opportunity to study changes in seed bank and vegetation along a longterm fire chronosequence. As an earlier reference point, we also sampled mature to degenerate heath where the age of *Calluna* was estimated by dendrochronology (Bär *et al.* 2006); ring counts on a sample of 10 stems from 10 different individuals (at least 10 m apart), yielded an estimated age of 24 (± 1) years. The resulting fire chronosequence contains 13 burn years; 1980 (mature/degenerate phase), 1992-2004 (building – pioneer phases [except 1999]). For each burn year, we established two sites (each approximately 100 m² in area), one in wet north-facing heath and one in intermediately moist (hereafter 'dry') south-facing heath (*sensu* Fremstad *et al.* 1991). All sites were located below 100 m a.s.l. and less than 200 m from the sea. Within each site, five 1 m² quadrats were established for standing vegetation (percent cover of each vascular plant species) and soil seed bank sampling. To sample the seed bank, in each quadrat five soil cores (5 cm diameter; 6 cm depth) were taken (one from each corner and one from the centre) and combined into one bulk sample

representing a surface area of 98.2 cm² 589 cm³ in volume. Additional seeds may occur below 6 cm however, previous studies (Pywell *et al.* 1997, Miller & Cummins 2003) show that seed numbers are likely to be much lower at such depths.

Greenhouse germination trial: Within 48 hours of collection, soil samples were washed with water over a 0.4 cm meshed sieve to remove roots, twigs and stones, contributing to bulk reduction, in accordance with improvements to the seedling emergence technique recommended by Herdt *et al.* (1996). Each sample was thoroughly mixed and spread out in a thin layer of about 0.1 cm (so that most seeds were exposed to light and suitable temperatures for germination) on a tray (30 cm x 60 cm) filled with 5 cm of sterile growth substrate (equal amounts of sterile peat, perlite and soil). Trays were randomly placed in an unheated greenhouse and watered regularly from above with tap water. Additional light sources were SON-XL high pressure sodium lamps (400 watts) with a light regime of 8 h darkness and 16 h light (Fig. 2). Six control trays of sterile peat, perlite and soil were randomly placed to monitor any airborne contaminants. Emerging seedlings were identified, counted and removed. Unidentifiable seedlings, difficult taxa (i.e. Juncaceae, Cyperaceae and Poaceae), were transplanted to separate pots and grown to maturity under greenhouse conditions for subsequent identification. Recordings were carried out in three intervals, interrupted by two periods of cold stratification at 4°C for four months to ensure full germination. The experiment was terminated after 20 months when no more seedlings emerged. According to Thompson *et al.* (1997) these methods are capable of revealing all or nearly all species and individuals in the soil seed bank.



Figure 2. Seed bank trial set up at the greenhouses at the Norwegian Arboretum, Milde.

CONSEQUENCES

Standing vegetation: We recorded 60 angiosperm taxa in the standing vegetation (as opposed to the seed bank) of the Lygra and Lurekalven heathlands (Fig 3); 21 species occurred only in the vegetation. The newly burnt, pioneer phase (0-5 years) was characterized by bare soil, patches of accumulated litter and low abundances of all species except a few geophytes such as chickweed wintergreen *Trientalis europaea*, wood anemone *Anemone nemorosa*, tormentil *Potentilla erecta*, bird's-foot trefoil *Lotus corniculatus* and harebell *Campanula rotundifolia*, all of which have the capacity to regenerate vegetatively after fire. The building phase (6-15 years) was dominated by species-rich graminoid and herb-dominated vegetation, and soils had a high pH. The mature phase (16-25 years) was characterised by an increasing dwarf shrub layer, increasing height and cover of *Calluna*, increasing lichen cover and increasing soil organic content, and decreasing herb abundance and soil pH. Overall, herbs contributed the highest number of taxa, closely followed by graminoids; dwarf shrubs, bushes and trees were fewer in numbers.

Soil seed bank: In the germination trials a total of 31,414 seedlings, comprising 54 taxa, were recorded (Fig. 3) of which 15 species occurred only in the seed bank (as opposed to being recorded growing on the heaths). The post-fire succession was not reflected in the composition of the seed bank. The numbers of emerging seedlings were very variable and densities ranged from 3,873 to 69,300/m² per sample (mean 24,626/m²; median 19,975/m²). Thirty-eight of the seed bank species were also encountered growing on the heaths, and the most abundant taxa were generally also recorded with high densities in the soil seed bank. The main component was *Calluna*, constituting 49% (seed density varied from 2,854 to 33,733 seeds/m²). *Erica* was the second largest contributor; constituting 34%, but unlike *Calluna*, it showed large fluctuations both within years and between years, densities varying between 0 and 42,395 seeds/m². The third largest contributor, heath rush *Juncus squarrosus*, was highly over-represented in the seed bank relative to the standing vegetation, comprising 7% of the total counts but only present in six of the 130 vegetation quadrats. Toad rush *J. bufonius* was also over-represented in the seed bank. Several species conspicuous in the vegetation were grossly under-represented in or absent from the seed bank. For example, *Trientalis europaea* and heath milkwort *Polygala serpyllifolia* were common throughout the vegetation, yet only few seeds germinated, whereas the *Vaccinium* species failed to germinate from any of the soil samples. Initial germination counts after the first germination round yielded 86% of the total number of

germinated seeds succeeding two cold stratifications. New species after the first round of stratification were heath-spotted orchid *Dactylorhiza maculata* and round-leaved sundew *Drosera rotundifolia*, and after the second round, lousewort *Pedicularis sylvatica* and white clover *Trifolium repens*.

Seed bank and vegetation – species richness and similarity: Species richness was always higher in the vegetation in comparison to the corresponding seed banks. Species richness of the standing vegetation followed a significant unimodal pattern ($F_{2,127} = 23.38$, $p < 0.0001$ and $F_{2,10} = 10.51$, $p < 0.01$), while the corresponding seed bank showed no trend ($F_{1,128} = 0.4144$, $p = 0.52$ and $F_{1,11} = 0.4409$, $p = 0.5204$) over the course of the post-fire succession. The seed bank represents a rather large and constant proportion of total species richness in this system over time. There was a significant difference in vegetation species richness ($F_{1,64} = 3.2807$, $p < 0.01$) between wet and dry habitats, where richness was highest on wet sites, whereas no significant difference ($F_{1,64} = -0.6466$, $p = 0.5202$) in seed bank species richness between wet and dry habitats was apparent. The overall similarity of the soil seed bank and the standing vegetation in this heathland system indicated a 68.4% (IS) overall concordance and we see most shared species occurring in the middle of the building phase.

Abundance of *Calluna* in vegetation and seed bank over the post-fire succession: *Calluna* regained cover in the vegetation quite quickly (Fig. 4a), following a linear trend over time ($F_{1,128} = 173.8$, $p < 0.0001$), and by the fifth year it was up to c. 40%. *Calluna* vegetation cover was higher on dry sites ($F_{1,126.48} = 2.22$, $p < 0.05$). *Calluna* in the seed bank, on the other hand, showed a very different pattern, with much higher numbers of *Calluna* seeds germinating from years 0 and 1 after fire compared to the older sites (Fig. 4b). After these two years, densities of *Calluna* seed banks increased linearly with time ($F_{1,108} = 17.64$, $p < 0.0001$) over the remaining course of the succession. *Calluna* seed bank densities were higher in wet sites, but the differences were barely significant overall ($F_{1,128} = 3.87$, $p = 0.051$). However, when analysed for differences between pairs of wet and dry sites per year removing the effect of the chronosequence *per se*, the pattern is clearly significant ($F_{2,12} = -3.23$, $p < 0.01$).

The other large contributor to the heathland seed bank, *Erica*, did also show a trend of higher germination the two first years proceeding fire, but did not prove significant as seed germination varied greatly within and between years. We found no significant difference in *Erica* germination between wet and dry habitats ($F_{1,128} = -1.65$, $p = 0.1003$).

Despite the high overall similarity between vegetation and seed bank, a few species showed large differences. This was most extreme for Juncaceae, which contributed close to 10 % of the seed bank, but only 0.1 % of the vegetation cover. This is consistent with other studies (Chippindale & Milton 1934, Williams 1985, Bossuyt & Honnay 2008), and probably reflects the ‘weedy’ strategies of these species. Our study system is grazed, and it has been argued that grazing can diminish similarity by altering micro-environment conditions or by selective consumption of plants (Bakker & de Vries 1992). However, grazing has also been argued to have the opposite effect by increasing the seed bank and vegetation similarity, by promoting seedling recruitment and establishment of species that are otherwise inhibited by dense plant cover (Kitajima & Tilman 1996).

More species were recorded in dry heath, as also found in similar studies (e.g. Bekker *et al.* 2000), yet we found no difference in seedling diversity between wet and dry sites. Wet heath sites did however have slightly higher seedling densities (see also Legg *et al.* 1992, Pywell *et al.* 1997, Bekker *et al.* 2000), suggesting that seeds in wet soils are better preserved and/or germination is inhibited due to high moisture contents in the soil.

Conclusions drawn from chronosequence studies representing succession, dealing with changes of seed bank and vegetation, depend on the implicit assumptions that history, microclimate, soil conditions, predictable vegetation development and similarities in availability of propagules are similar at all sites (Pickett & McDonnell 1989, Milberg 1995). These assumptions might be difficult to meet in reality. In this study, we sought to minimise these problems by using an area where site management history and vegetation development are very well known and where environment and vegetation is rather similar throughout the study area, and by using replicate sites for each successional stage.

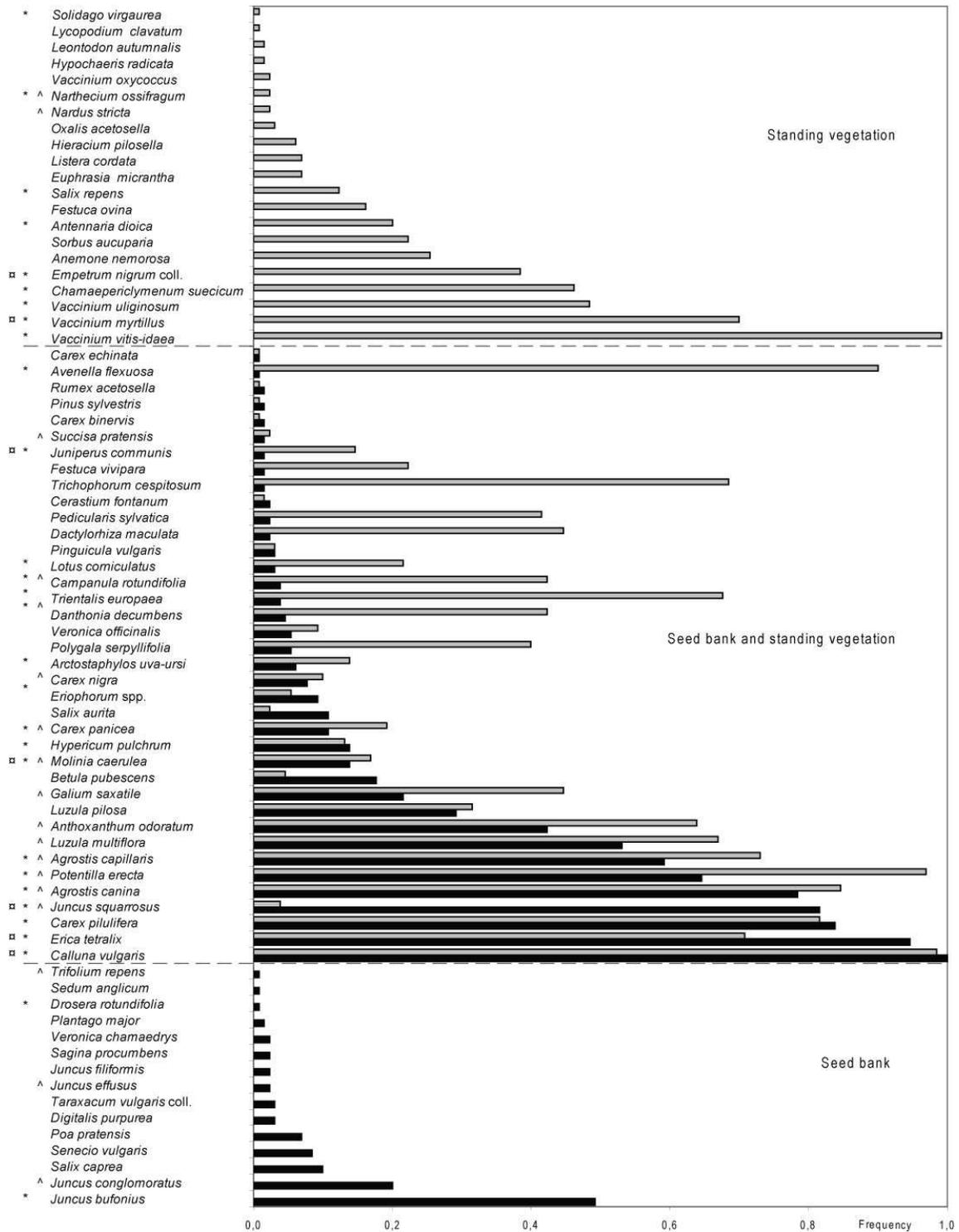


Figure 3. The frequency of occurrence of species registered in the 130 sampled quadrats as viable seeds in the soil seed bank (■) and/or in the standing vegetation (□), in the heathlands of Lygra and Lurekalven, managed by traditional heather burning. Dominating (■) and characteristic heathland species (*), and characteristic acidic grassland species (^) (Fremstad *et al.* 2001) are indicated.

Effects of fire on *Calluna* seeds in the soil seed bank: The seed bank of *Calluna* in *Calluna*-dominated heathlands is usually quite large (Nordhagen 1937, Granström 1988) but there may be striking fluctuations in time and space (Mitchell *et al.* 1998). As we explored the germinable (viable) soil seed stores of *Calluna* following prescribed burning we found surprisingly high densities of seeds germinating from the two first years (Fig. 4b). This trend was also seen in *Erica*. This pattern could not have been caused by differences in seed inputs, as all sites were burnt in the same successional stage (mature/degenerate phase), and as seed rain into newly burnt heathlands is minimal (Hobbs & Gimingham 1984). The alternative hypothesis is that *Calluna* and *Erica* seeds in newly-burnt soils germinate more readily than seeds in unburnt soils. Interestingly, Pons (1989) pointed out that the response of *Calluna* and *Erica* seeds to various environmental factors were strikingly similar. Seeds of many species of naturally fire-prone environments have been shown to be adapted to germinate in response to one or more physical cues produced by fire, or to chemical stimuli produced such as via ash, smoke, ethylene, ammonia and nitrogenous substances (Van Staden *et al.* 2000, Willis *et al.* 2003, Flematti *et al.* 2004). The increased germination of these two important heathland plants after fire could therefore give indications of fire-related adaptations. To investigate this, we have initiated two studies testing smoke and ash on fresh *Calluna* seed germination and on soil seed banks (Måren 2009, Måren *et al.* in press).

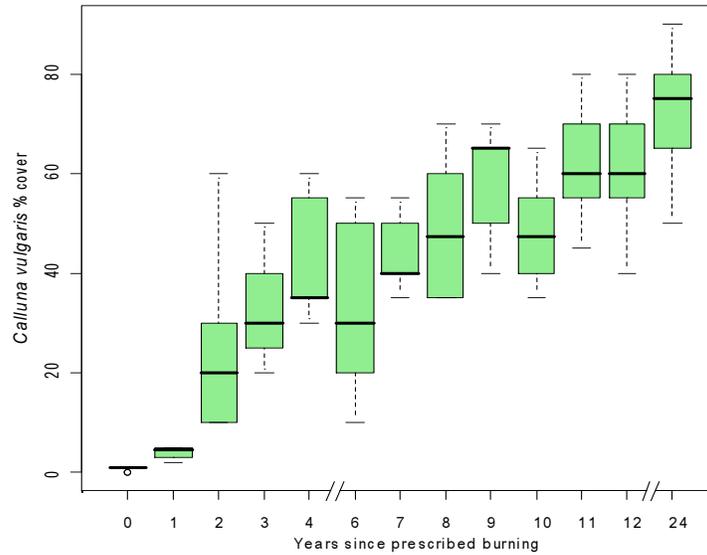
Implications for conservation: The capacity to form persistent seed banks allow plant species to survive episodes of disturbance and destruction, thus the understanding of the role of seed banks is key to many aspects of conservation management and formulation of conservation policies. Our heathland study shows that management by prescribed rotational burning and grazing creates a dependable seed bank for revegetation of bare ground after fire. In well managed heathlands, secondary succession following fire is often short

and *Calluna* recovers dominance after two to four growing seasons, which leaves little time for other species to establish. We found that the species richness in the vegetation and the vegetation-seed bank similarity reached the highest levels in the building phase, around 10 years after burning. This indicates relatively long fire return times in heathlands to achieve maximum plant diversity.

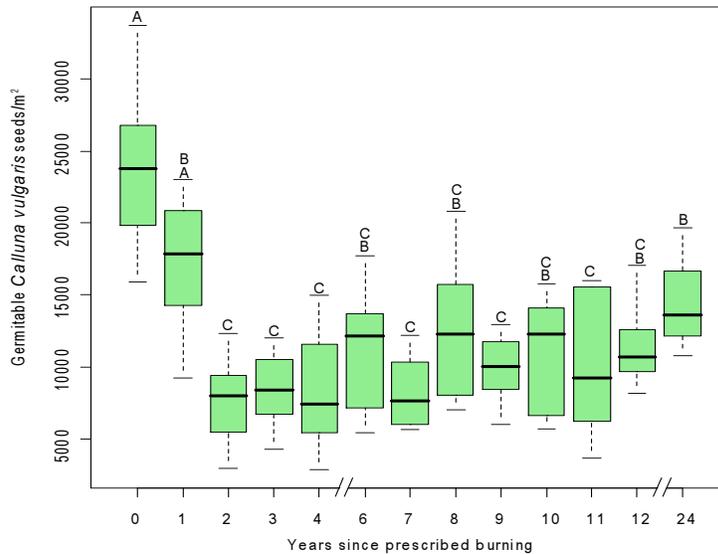
From a management point of view, prescribed burning of heaths is practical in many aspects, i.e. low cost, and not very labour intensive or time consuming. *Calluna* densities of about 12,000 seeds/m² contribute to natural recolonisation of bare ground after prescribed burning in northern heathlands, although a density of 40,000 seeds/m² has been suggested as desirable for successful *Calluna* restoration in the UK (Mitchell *et al.* 1998). The seed bank is, however, not the only source of revegetation after events of moderate disturbance. Several heathland species are capable of vegetative resprouting after fire, including *Calluna*. Resprouting may play an important role in vegetation dynamics after fire and should be investigated further, especially as Nilssen *et al.* (2005) found that *Calluna* lack vegetative resprouting in northern regions. We conclude, by the high species diversity of the seed bank and by the densities of emerging seedlings, that the traditional management regime at Lygra and Lurekalven has not depleted or destroyed the seed banks. On the contrary, their sustainability is dependent on continued management.

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a)



b)

Figure 4. *Calluna vulgaris* in (a) vegetation and (b) seed bank over the course of the post-fire succession following prescribed burning at Lygra and Lurekalven. The standing vegetation cover quickly increased after fire in a linear fashion, while the germinable *Calluna* seed densities show considerable higher germination in the two first years after fire. Equal letters in the lower figure (b) indicate years not significantly different at the 0.05 level using a Turkey HSD multiple comparisons test.

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