



Life after fire: smoke and ash as germination cues in ericads, herbs and graminoids of northern heathlands

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Nomenclature

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Abstract

Question: What is the impact of the fire cues smoke and ash on seed germination of important functional groups in the heathland system, namely ericads, herbs and graminoids? We predict that if germination from heathland seed banks is in part regulated by fire cues, there should be stronger responses to fire cue treatments in seed bank samples taken from heath that has not been recently burned in comparison with samples taken from newly burned heath, where seed banks have been exposed to the same cues *in situ*.

Location: Lygra, Lindås commune, western Norway.

Methods: The efficacy of smoke, charred wood, ash and heat in promoting germination has been documented in a wide range of species and systems, but relatively little work has been done on fire-related cues in northern European heathlands under anthropogenic fire regimes. We studied fire experimentally by testing the effects of aqueous smoke solution, ash and a combination of the two treatments, on the germination of graminoids, herbs and ericads. A greenhouse germination trial compared seed banks from old heath (28 yr since the last fire) with seed banks from newly burned heath (burned the previous year), where we expected that fire-cued germination had already occurred.

Results: We found that both ericads and graminoids responded to fire cues, whereas herbs did not. In line with our predictions, responses were stronger in the old heath than in the young heath. Further, the smoke treatment is a more effective cue than ash across all functional groups.

Conclusions: The prevalence of positive fire cue responses across functional groups underscores the importance of fire in the ecology of these heathlands, and hence of burning as a central tool for their management. The finding that the germination response is stronger in naïve seed banks than in seed banks that have already been exposed to recent fire cues through *in situ* fires further supports the role of fire in the successional dynamics of these heathlands.

Introduction

Fire is an important disturbance factor in many terrestrial ecosystems all over the world (Keeley et al. 2011a; Pausas & Keeley 2009). It determines community assemblages and plant and animal distributions both directly after a fire event, but also in the long term, for example by guiding the evolution of fire adaptations (Bond & Keeley 2005; Keeley et al. 2011b; Vandvik et al. 2014). The selective use of fire, in combination with grazing and/or cutting, has been central to heathland management for centuries, and is essential in maintaining the semi-natural heathland

landscapes of Europe (Fagúndez 2013; Kvamme et al. 2004; Mallik & Gimingham 1983; Prøsch-Danielsen & Simonsen 2000; Webb 1998).

It is reasonable to assume that habitats which are prone to fires, be they natural or man-made, will also be home to species that tolerate or are facilitated by fire. This has been shown in heathlands that are naturally prone to fires, such as the Mediterranean Basin (Moreira et al. 2010), South African fynbos (Brown 1993; Lange & Boucher 1990), Californian chaparral (Keeley & Bond 1997; Keeley & Fotheringham 1997; Wicklow 1977) and Australian heath (Dixon et al. 1995). However, while a vast amount of

research has been conducted on the responses and evolutionary adaptations of plant species to burning in naturally fire-prone areas (Bell 1999; Brown & Van Staden 1997; Dixon et al. 1995; Gilmour et al. 2000; Keeley & Bond 1997), comparatively little focus has been on the fire response under anthropogenic fire regimes, such as in northern European heathland ecosystems (but see Måren & Vandvik 2009; Måren et al. 2010; Vandvik et al. 2005).

There are many different ways in which fire can promote germination of dormant seeds, including physical, physiological and morphophysiological. Fire cues are very complex, and while the exact mechanisms for germination responses are not completely understood, there are many specific underlying cues that have been documented. One example is dry heat, which fractures the seed coat of certain hard-seeded species (Jeffery et al. 1988) and can stimulate embryo development of species with morphophysiological dormancy. Chemical substances such as ethylene and various nitrogenous substances (Keeley & Fotheringham 1997; Van de Venter & Esterhuizen 1988), as well as ash (Reyes & Casal 1998) and smoke (Lange & Boucher 1990), can stimulate germination in species with physiological dormancy. In our study, our focal fire cues are smoke and ash, which have been found to stimulate germination in a wide range of species, including the dominant species in our study system, *Calluna vulgaris* (Måren et al. 2010).

Smoke has long been suggested to promote germination (Lange & Boucher 1990), but it is also known to be rather complex, and composed of many compounds, such as nitrates, ethylene, cyanohydrins and nitric oxide, that are likely to promote germination in different plant species (Nelson et al. 2012). Relatively recently, an important active compound found in smoke has been identified as karrikinolide (Chiwocha et al. 2009; Flematti et al. 2004). Karrikinolide is a simple organic compound that promotes seed germination, seedling vigour and growth in a variety of different plant species (Light et al. 2010; van Staden et al. 2006), and has thus been hypothesized to be one of the major fire-related germination stimulants (Flematti et al. 2013; Nelson et al. 2012). However, other species respond to compounds that remain unidentified (Downes et al. 2010, 2013). Måren et al. (2010) showed that smoke can promote seedling germination in *C. vulgaris* in anthropogenic heathlands, and as fire is an important but also contested part of the recommended management regime for northern heathlands, it is important to investigate the fire responses of a wider range of plants characteristic of the heathland habitat.

Ash and charred wood are also known to be important in germination regulation, although the mechanisms behind the germination responses to these substances are not well understood (Franzese & Ghermandi 2011; Reyes

& Casal 1998). Ash has been known to reduce germination, and has been proposed to do so by increasing the pH of the soil (Thomas & Wein 1990) and, when present in large quantities, poisoning the seed, and reducing water potential, thus impeding water flow to the embryo (Neéman et al. 1993, 2002). Conversely, charred wood has been shown to promote germination. Zackrisson et al. (1996) suggest that charred wood can reduce the phytotoxic effects of phenolic compounds produced by heathland species by effectively absorbing them. Further, charred wood can increase soil fertility by increasing the soil pH. Similarly, it has been suggested that ash adds nutrients to the soil and that ethylene, which is a by-product in wet ash, is a promoter of germination (Neéman et al. 2002). However, while evidence is conflicting, and the germination response to ash is not well understood (Reyes & Casal 1998), it is important to keep in mind that due to its complex molecular nature, ash may capture many different potentially important cues, including, but not limited to, those that are captured by smoke.

Fire is an important but also contested part of the recommended management regime for the anthropogenic heathlands of northwest Europe, and it is important to investigate the role of fire in the ecological dynamics of these habitats. This study therefore aims to investigate the impacts of smoke and ash on seedling recruitment of important functional groups in the heathland system, namely ericads, herbs and graminoids.

We used burned heather biomass to test for the effect of ash, and *Themeda triandra* smoke bubbled through water to test for the effect of smoke. As it has been shown that the active compounds in aqueous smoke extracts derived from cellulose and a range of species are all able to promote germination, and are thus likely to be ubiquitous in plant material (Jäger et al. 1996), we expect that the result of using heather to produce the smoke solution would be similar. We predicted that if germination from heathland seed banks is in part regulated by fire cues, there should be stronger responses to fire cue treatments in seed bank samples taken from old heath in comparison with samples taken from newly burned heath, which have been exposed to the same cues *in situ* more recently.

Methods

Study area

The study was conducted at the island of Lygra (60°42'N, 5°5'E), about 40 km north of Bergen in western Norway. The area has an oceanic climate with a mean June temperature of 12 °C and a mean January temperature of 2 °C. Mean annual precipitation is at ca. 1600 mm yr⁻¹, and the growing season is ca. 220 d (www.met.no), defined as the number of days with a mean temperature above 5 °C.

The landscape is dominated by *Calluna* heath, mires and mixed grass heaths, with some smaller patches of forest (mainly *Betula pubescens* and *Pinus sylvestris*). The clearing of forests that gave way to anthropogenic heathlands in western Norway occurred mostly during the Bronze and Iron Ages, between 6000 and 3300 BP (Prøsch-Danielsen & Simonsen 2000). However, the process of forest clearance occurred in small patches and took more than 4000 yr, with the youngest dated deforestation occurring 800–900 yr ago (Kvamme et al. 2004). Complete deforestation and establishment of *Calluna* heath has been dated to ca. 1300 BP on the nearby island of Lurekalven, where the landscape has also been kept open ever since (Kaland 1986). The exact date of forest clearance could not be determined at Lygra specifically, due to the common practise of peat collection in the bogs of the area. Nevertheless, as archaeological findings have dated farming practises back to the late Neolithic (ca. 3500 BP) in this particular area, it is likely that Lygra has been at least partly deforested since then (Kvamme et al. 2004). Recent fire history at Lygra is also well documented, and patches have been subjected to controlled burning almost every year since 1992. In accordance with traditional management methods in Norway, burning is always done in winter or early spring to ensure that the ground is still frozen, so that the fire does not burn away the soil and soil seed bank. Typical Norwegian management fire temperatures, measured in the centre of the canopy, are between 680 ± 98 °C (\pm SD) and 740 ± 54 °C (Nilsen et al. 2005).

Functional groups

This study covers three functional groups; ericaceous dwarf shrubs, graminoids and herbs. Common ericads found on Lygra include *Arctostaphylos uva-ursi*, *Calluna vulgaris*, *Empterum nigrum*, *Erica tetralix*, *Vaccinium myrtillus*, *V. oxycoccus*, *V. uliginosum* and *V. vitis-idaea*. Common graminoids are *Agrostis canina*, *Anthoxanthum odoratum*, *Carex panicea*, *C. pilulifera*, *Luzula multiflora*, *Molinia caerulea* and *Trichophorum cespitosum*. Common herbs include *Anemone nemorosa*, *Campanula rotundifolia*, *Chamaepericlymenum suecicum*, *Dactylorhiza maculata*, *Lotus corniculatus*, *Potentilla erecta* and *Trientalis europaea*. *Anemone* and *Campanula*, as well as the latter three species have been found to be abundant in newly-burned heather while the building phase (6–15 yr after fire) of heathland growth is more species-rich, with both graminoids and herbs dominating before *Calluna* and other shrubs become dominant in the mature phase (16–25 yr after fire; Måren & Vandvik 2009). A previous extensive study of the area by Måren & Vandvik (2009) provides a full species list of both the vegetation and the seed bank (see Appendix S1).

Experimental setup

In order to test the germination responses of the functional groups to smoke and ash, 20 soil seed bank samples were taken from Lygra in March 2008, when cold stratification had already taken place naturally. Ten soil seed bank samples were taken from a mature to degenerate heath (28 yr old, referred to as 'old heath' hereafter), and ten were taken from an adjacent heath that was burned in April of the previous year (2007, referred to as 'new heath' hereafter). Each of the 20 soil samples taken had a volume of 2000 cm³ and was taken down to 5-cm depth. As management fires were re-introduced to Lygra in the early 1990s, it was not possible to replicate burn age numbers.

The prescribed fire regime at Lygra is similar to the patchy fire regimes characteristic of traditional heathland management of western Norway (Webb 1998), where small patches of typically 0.5–2 ha (Måren 2009) are burned in winter/early spring. In our study, samples were collected at the centre of each of the two burn patches (one newly burned and one degenerate), at least 10 m from the edge of the patch, thus minimizing edge effects and avoiding contamination by seeds dispersed in from the surrounding habitats. The ten replicated soil seed bank samples were taken at least 10 m apart in a systematic grid pattern, starting 10 m from the edge of the patch, to sample as much of the natural variability in the heathland as possible. Both litter and humus layers were sampled in accordance with Leck et al.'s (1993) definition of soil seed banks.

Each of the 20 samples was mixed and split into four equal parts. In accordance with Ter Heerdt et al.'s (1996) improved seedling emergence method, the samples were then washed over a fine sieve (0.4 cm) to remove roots, twigs and stones, contributing to a bulk reduction, no later than 48 h after collection. In order to optimize light exposure and temperature, each of the four resulting concentrated parts was then spread in a thin layer of ca. 0.1 cm on top of 5 cm of sterile subsoil in 30 × 60 cm trays, and assigned one of the following treatments: (1) control, (2) aqueous smoke solution, (3) ash or (4) both aqueous smoke solution and ash. An additional six control trays were also prepared in order to control for airborne contaminants, and all 86 trays were then placed randomly in an unheated greenhouse. In addition to natural light, SON-XL high-pressure sodium lamps (400 W) were set up with an 8-h dark/16-h light regime. All trays were watered regularly from above with tap water.

The smoke solution used in the experiment was made using standard *Themeda triandra* smoke bubbled through water, in accordance with previous studies (Brown 1993; Lange & Boucher 1990; van Staden & Light 2004), and

was supplied by Kirstenbosch Botanic Gardens and the University of Kwazulu Natal, South Africa. The solution was diluted 1:1000, as higher concentrations of smoke solution have been shown to have an inhibitory effect (Brown 1993), and a previous trial (1:100, 1:500, 1:1000, 1:2000, 1:5000 and 1:10000) with *Calluna* sampled from our study system showed that this dilution provided the best results (Måren et al. 2010). Each sample receiving smoke treatment was dosed once with 0.05 L of the solution using a pressurized spray bottle at the onset of the experiment. Ash was produced by drying 300 L of compacted mature heather from Lygra at 80 °C for 4 h, and then burning it at ca. 600 °C until ash was formed. The 1 L of ash produced was then spread in a thin layer (ca. 1 mm) over all sample trays receiving ash treatment. Seedling recordings were conducted approximately every 2 wk where emerging seedlings were identified to functional group (trees, ericads, herbs or graminoids), counted and removed from the trays. As ericads only constituted *Calluna vulgaris* and *Erica tetralix*, which are easily distinguishable as young seedlings, these species were recorded separately. *Potentilla erecta* was the most common herb and was also recorded to species. All other germinating seeds were recorded to functional group. During the course of the germination experiment, bryophytes emerged in the sample trays. Consequently, we recorded moss cover in sample trays on a scale of 0–4 (0 = 0–1%, 1 = 1–5%, 2 = 5–25%, 3 = 25–75% and 4 = 75–100%). Recordings were carried out for a total of 4 mo, when no more seeds germinated.

As it was difficult to remove moss from the trays without damaging the emerging seedlings, and germination can be affected by an extensive moss cover, trays that had a moss cover of above 75% at the sixth count were not included in the analyses. This resulted in the exclusion of 13 trays, leaving 73 trays in the analysis. The sixth count was conducted 3 mo into the experiment, and was considered a reasonable cut-off point because at this time more than 75% of the seedlings (out of the total seedling counts) from each functional group had germinated.

Data analysis

The seedling count data were analysed using linear mixed effects models. Analyses were run separately for seedlings of each functional group (ericads, graminoids and herbs) as well as for the two most common ericaceous species (*C. vulgaris* and *E. tetralix*). For each of these response variables, the full factorial model included the following predictors; ash treatment (+/–), smoke treatment (+/–), and heathland age (newly burned/old heath), as well as all two- and three-way interactions. A Poisson error distribution was used and each seed bank sample (n = 20) was included as a random effect in all analyses. The full model

for each response variable was thus: counts~ash × smoke × age + (1|sample).

Complex two- and three-way interactions involving the predictor variable 'age' were found in all analyses, confirming that germination responses to the investigated fire cues differ between old and new heath samples. To aid ecological interpretation, analyses of the smoke and ash responses were therefore carried out for each age group separately, to enable testing of the significance of the fire cue effects within each functional group and heath age group. This gave the following final model for each age group: counts~ash × smoke + (1|sample). All analyses were done in R v 2.14.1 (R Foundation for Statistical Computing, Vienna, AT), using the package lme4 and the default contrast matrix in R (treatment contrasts).

Results

A total of 21 244 seedlings were recorded. Overall, the responses to the fire cues used in this experiment were positive, and there were complex two- and three-way interactions involving heath age and all of the fire cues for most of the functional groups and species (Appendix S2). The exceptions were the herbs, where the only significant interaction was for the ash:age interaction, and *E. tetralix*, where the ash:age interaction was not significant. The strongest responses to smoke and ash treatments were observed for the ericads and for the graminoids, while the herbs were less affected (Table 1, Fig. 1). Both the ericads and the graminoids responded significantly positively to both smoke and ash treatments in the old seed bank samples, whereas the responses were generally weaker and not always significant in the new seed bank samples.

The ericads responded positively to smoke in the new heath samples, but this response was driven by *Erica*, as *Calluna* did not respond significantly to smoke in this age group. Both species responded strongly to the smoke treatment in the old heath samples, however. The graminoids presented an interesting response pattern, as they responded negatively to the smoke treatment in the new heath samples and positively in the old heath samples. Finally, the herbs responded slightly positively to the smoke treatment, but only in the new heath samples.

The ericads in the new heath samples generally did not respond to ash treatment at all, while they responded positively in the old heath samples. However, the lack of an overall response to the ash treatment within the new heath samples is caused by a negative response in *Calluna*, and a positive response in *Erica*. Both species responded positively to the ash treatment in the old heath samples. Ash also caused higher germination for the graminoids in old heath samples, but not in new heath samples.

Table 1. Estimates and *P*-values for germination counts from soil seed banks of each of the functional group responses to smoke and ash, and the ash: smoke interaction, as predicted by a linear mixed effects model with a Poisson family distribution. Values refer to samples of heath from Lygra, in Hordaland, Norway, that were burned in the previous year, and samples that were burned 28 yr ago. Estimates for the treatments should be compared to the corresponding intercepts. Significance codes: *P* < 0.001 = '***', 0.001–0.01 = '**', 0.01–0.05 = '*', >0.05 = '.'

	Newly Burned Heath				Heath Burned 28 Yrs Ago			
	Intercept	Ash	Smoke	Ash:smoke	Intercept	Ash	Smoke	Ash:smoke
Ericads	4.63	0.03	0.19***	−0.10.	4.90	0.25***	0.38***	−0.41***
Calluna	4.22	−0.18***	0.01	0.21**	4.53	0.18***	0.17***	−0.16**
Erica	3.14	0.28***	0.41***	−0.82***	3.22	0.39***	0.74***	−0.48***
Graminoids	4.06	−0.06	−0.10*	0.31***	3.95	0.13*	0.20***	−0.25**
Herbs	−0.23	0.37	0.75.	−0.04	0.21	−0.55*	0.10	−0.17

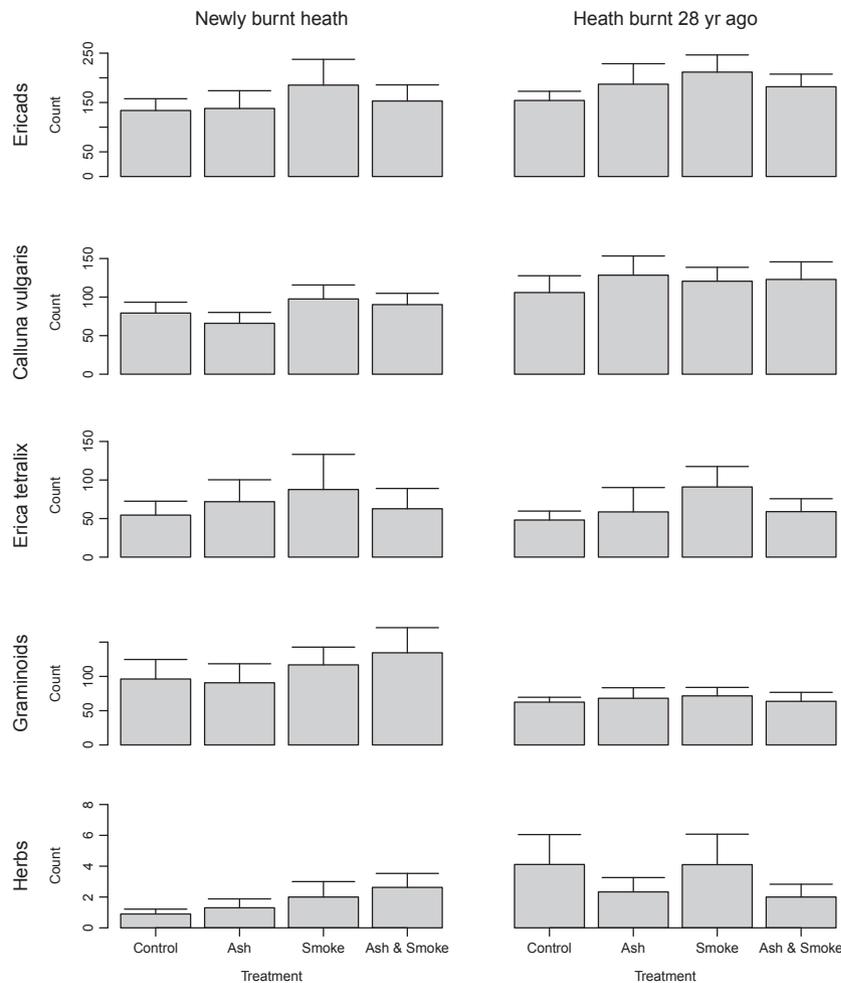


Fig. 1. Mean seed bank germination counts of ericads, graminoids and herbs, +5D, from heathlands on Lygra, in Hordaland, Norway. The seed bank samples were subjected to four different treatments; control, ash, smoke and smoke and ash combined. Graphs on the left show germination counts in heath samples burned in the previous year, while those on the right show samples taken from heath burned 28 yr previously.

Conversely, herbs did not exhibit a response in the new heath samples, but responded negatively to the ash treatment in the old heath samples.

There were differences in the smoke and ash interaction between age groups for *Calluna* and the graminoids. While the interactions were generally positive in the new heath

samples, they were negative in the old. *Erica* showed negative interactions for both age groups, while the herbs did not show any interaction of the treatments.

Discussion

Responses across functional groups

Seed germination of many species is known to respond positively to fire-related cues such as high temperatures, smoke, ash or charred wood. In our study, the smoke effects tended to be stronger and more positive than the ash effects in both the old and the new heath samples across all functional groups. This suggests that chemical substances present in smoke are a dominating fire cue in promoting germination within our heathland system. Further, smoke and ash cues generally resulted in increased germination from the investigated seed banks, particularly in old heath. This means that the time since the last exposure to fire is important for the germination response to fire cues. As the samples from newly burned heath have recently been exposed to fire, and all the seeds in the seed banks, including those in the controls, have already been exposed to the same fire cues, this may explain the weaker or negative responses to fire cues in the newly burned heath. The difference between newly burned and old heath samples was especially evident in *Calluna* and the graminoids. This is not surprising with respect to *Calluna* in particular, as it is the dominant species in European heathlands, and is frequently exposed to fire as part of the management regime. As a result, *Calluna* can be expected to be more adapted to utilizing fire cues as a means to promote germination in a post-fire environment. The germination response of the graminoids from the old heath samples is also in accordance with a previous study, which found that the graminoids generally are among the more positively affected by smoke when compared to other plant groups (Brown 1993).

Combinations of fire cues may sometimes be more or less effective in promoting germination than a single cue (Keeley & Fotheringham 1998, 2000). The combination of cues may function to increase germination independently and additively (Keith 1997; Kenny 2000) or synergistically (Gilmour et al. 2000; Kenny 2000). Therefore, although combined cues can result in improved germination, as in Tieu et al.'s (2001) study of heat and smoke cues in Australian heath, they may work independently. In the present study, the combination of smoke and ash treatments resulted in negative interactions in the old heath samples for all groups, as well as in the new heath samples of *Erica*. A probable explanation for the negative interactions is that the smoke and ash cues trigger the same underlying response and therefore cancel each other out in the combined treatment. Smoke is consistently the more effective

germination cue, and the smoke and ash treatments are not additive. This is consistent with a scenario where it is smoke molecules leached from the ash that is the effective cue, rather than some unique properties of ash, that promote germination. If this was the case, the mean counts in the independent and combined treatments could be expected to be similar. This is not always the case in our data (although the parameter estimates in the interactions, are mostly of the same magnitude as the ash or the smoke effect). Higher taxonomic resolution and/or better replication may be necessary to establish to what extent and in which taxa smoke and ash do trigger the same underlying response. In contrast, *Calluna* and the graminoids in the new heath samples exhibited positive interactive effects of the treatments. This could reflect true interactive effects or additive effects where a lack of significance in the single treatment was due to low seedling counts (i.e. below the detection threshold). The latter is particularly likely in the case of the herbs.

Ericads

It has been suggested that the distribution of fire-cue-related germination traits is not random between plant groups, but rather common in annual species, as well as perennial shrubs, uncommon in trees and rare in perennial herbs (Keeley 1991, Keeley 1995; Keeley & Bond 1997). While some patterns in germination response to fire cues do seem to exist, there is still a variation in the responses of species within plant groups and even genera. We found that *Erica tetralix* responded positively to both smoke and ash treatments, regardless of the age of the heath sample, but other studies have shown that species of the genus *Erica* vary in their responses to fire cues. *E. arboorea* and *E. australis* have been shown to be unaffected by heat (Valbuena & Vera 2002), whereas *E. umbellata* and *E. ciliaris* have been shown to germinate more readily as a result of heat treatment (González-Rabanal & Casal 1995). However, another study by Moreira et al. (2010) showed that *E. umbellata* is stimulated to germinate only by smoke, and not by heat, while two further *Erica* species (*E. multiflora* and *E. terminalis*) responded positively to both. The differences in responses to fire cues between species of the same genus further emphasizes the need for species-specific investigations of germination responses.

Like *E. tetralix*, *Calluna* responded positively to both treatments in the old heath sample, however, it responded negatively to the ash treatment and not at all to the smoke treatment in the newly burned heath samples. While the negative response to the ash treatment is in accordance with a previous study of *Calluna*, which showed that ash is strongly inhibitive to germination (González-Rabanal & Casal 1995), our different result

for the old heath samples shows that the time since the last fire is of importance.

The difference in response to ash and smoke between *Calluna* and *Erica* could, in part, be explained by their respective habitat niches. While *Calluna* is found in comparatively drier areas of heathland, *E. tetralix* is more common in wetter areas, and may thus not have had as much exposure to fire and resulting fire cues caused by management fires over the course of heathland history. In addition, management fires are typically not hot enough to destroy the seed bank and underground stems or rhizomes, and both vegetative re-sprouting and germination from seed can occur (Mallik & Gimingham 1983), but some plants are very effective at vegetative re-sprouting after burning, while others rely on fire either as a direct or indirect germination cue. For example, Valbuena et al. (2000) found that fire treatment reduced the number of germinable seeds in *E. australis*, and that it tended to recover by vegetative sprouting as opposed to from seed, whereas the number of germinable seeds in *C. vulgaris* increased as a result of fire.

Graminoids

The positive responses to fire cues in the old heath seed banks are of particular interest in the case of graminoids, as graminoids are largely absent in persistent seed banks (Fenner & Thompson 2005), and are thus often found exclusively in the vegetation (Holmes & Cowling 1997). However, Fenner & Thompson (2005) point out that habitat types with frequent disturbance regimes, such as heathlands, may support species with both long-term persistent and short-term persistent seed banks. In support of this, Måren & Vandvik's (2009) study of the same area (Appendix S1) revealed that different graminoid species were found in the vegetation, in the seed bank, or in both, showing that a generalization cannot be made. This is important to keep in mind, as the persistence of some species in the seed bank will affect what is left to germinate in the older vs the newer heath after fire treatments. While there was clearly more overall germination from the new vs the old heath samples for the graminoids, our results suggest that the graminoids remaining in the persistent seed bank are also more likely to be stimulated by fire cues. However, as graminoids were not recorded to the species level, it is not possible to tell whether the species composition varies between age groups, or whether fire cues promote germination in the same species more effectively in old heath samples when compared with the new. The significant negative response to smoke in the new samples is difficult to explain, but may be due

to the large range, including some very high germination counts, in the controls.

Herbs

The herbs responded positively, albeit weakly, to the smoke treatment, but in contrast to our predictions, this was only observed in the newly burned heath samples. While it has been suggested that herbs are rarely triggered to germinate by fire cues (Keeley & Fotheringham 2000), an Australian study found that one-sixth of their perennial herbs responded positively to smoke (Read et al. 2000), and Keeley et al. (1985) emphasize that herbs respond very differently from one another to fire cues. As *Potentilla erecta* was the most common herb to be recorded in this experiment, it should be noted that while this species may germinate more readily as a result of smoke exposure, this does not apply to all species within these samples. It is possible that the response of *P. erecta* is overriding the responses of other species in this group. Therefore, it would be useful to increase the resolution of this study by distinguishing between species-specific responses in future studies of fire responses in herbs.

In contrast to the graminoids, ash had the reverse effect on the germination of herbs, with no effect in the new heath samples, and a negative effect in the old heath samples. Ash has been reported in different studies to reduce germination (Neéman et al. 1993, 2002; Thomas & Wein 1990), as well as to promote it (Neéman et al. 2002; Zackrisson et al. 1996). Interestingly, our study shows that while ash does not have a significant effect on the germination of herbs and graminoids in recently burned heath, seeds that have not experienced fire cues for a longer period of time do in fact respond to ash. This may reflect that samples from newly burned heath have already been exposed to fire cues *in situ*, however, herbs are apparently inhibited in their germination, whereas graminoids benefit. This is consistent with the point made previously, that herbs are rarely promoted in their germination by fire cues, whereas graminoids are more likely to be. Unfortunately, we cannot ascertain if reducing the quantity of ash would promote germination in the herbs. The amount of ash provided in the treatment may simply have been higher than is required by herbs or more than is produced by natural fire events.

Conclusions

This study highlights the prevalence of fire cue-induced germination across functional groups in northern European heathlands, as ericads, graminoids and, to some extent, herbs, respond positively to smoke and ash treatments. This is highly relevant within a system that is

periodically exposed to prescribed burning. Even though both ericads and graminoids are often observed to resprout vegetatively (Mallik & Gimingham 1985), and graminoids are often thought to have low persistence in the seed bank (Fenner & Thompson 2005; Holmes & Cowling 1997), fire clearly plays a central role in seed recruitment of ericads and graminoids in heathlands. Further, the time dimension of this study shows that seeds may be more sensitive to fire cues when the time since the last exposure is long, both by increasing and by decreasing germination responses. It is important to note, however, that since this study did not distinguish between species within functional group (apart from *Calluna vulgaris* and *Erica tetralix*), it is possible that species also respond to fire cues differently within functional groups. Although it is unlikely that the species found in northern heathlands have evolved in these systems, they have probably benefitted from the management regimes that have been used to maintain them (Måren et al. 2010; Vandvik et al. 2014). It is therefore reasonable to believe that these species are adapted to using fire cues to their advantage in order to utilize areas that have been recently disturbed, and hence provide more nutrients. This study found that germination is particularly promoted by fire cues when the time since the last burning is long, further supporting the necessity for rotational burning within heathlands. This is in line with present heathland management guidelines for Norway. Further, the findings of this study imply that within this anthropogenic system, it is not only *Calluna vulgaris* that benefits from fire, but rather a large range of species.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Modified species list from Måren & Vandvik (2009), showing species that are present in the vegetation and in the seedbank at Lygra and Lurekalven, western Norway.

Appendix S2. Significances for the age interactions with the full model (counts~ash x smoke x age + (1|sample)) for each of the functional groups.