Fire increases aboveground biomass, seed production and recruitment success of *Molinia caerulea* in dry heathland

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Abstract

During the last decades, the perennial tussock grass *Molinia caerulea* has shown an increased abundance in European heathlands, most likely as a result of increased nitrogen deposition and altered management schemes. Because of its deciduous nature, *Molinia* produces large amounts of litter each year, which may affect the intensity and frequency of accidental fires in heathlands. These fires may influence plant population dynamics and heathland community organization through their effects on plant vital attributes and competitive interactions. In this study, fire-induced changes in competitive ability and invasiveness of *Molinia* through changes in biomass production, seed set and seed germination under both natural and laboratory conditions were investigated.We found that fire significantly increased aboveground biomass, seed set and germination of *Molinia*. Seed set was twice as high in burned compared to unburned heathland. Two years after fire, seedling densities in natural conditions were on average six times higher in burned than in unburned heathland, which resulted in increased abundance of *Molinia* after burning. The seed germination experiment indicated that seeds harvested from plants in burned heathland showed higher germination rates than those from unburned heathland. Hence, our results clearly demonstrate increased invasive spread of *Molinia* after large and intense fires. Active management guidelines are required to prevent further encroachment of *Molinia* and to lower the probability of large fires altering the heathland community in the future.

Keywords: Fire; Germination; Invasive species; Nutrient balance; Reproductive success

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1 Introduction

Fire is an important disturbance that affects vital attributes of plant species (e.g. Noble and Slatyer 1980; Silva et al., 1991; Canales et al., 1994; Kaye et al., 2001; Satterthwaite et al., 2002; Menges and Quintana-Ascencio, 2004), plant community organization and biodiversity (Whelan, 1995; Bond and vanWilgen, 1996) and large differences in fire response among plant communities exist. Generally, the effects of fire on plant diversity have been shown to increase with increasing productivity (Safford and Harrison, 2004). Moreover, high rates of biomass production and litter accumulation may lead to shorter time intervals between subsequent fires and a higher fire severity, both of which may negatively affect germination, survival rates in the dormant seed bank and plant growth after fire of residing plant species. Heathlands are generally known as low productive ecosystems characterized by dominance of typical dwarf shrub species such as *Calluna vulgaris* and *Erica tetralix*. Traditionally, these heathland systems were maintained by small-scale land use practices such as sod cutting, grazing by sheep or controlled burning in winter. During the last decades, however, typical heathland species have been gradually replaced by more competitive species such as Molina

caerulea and Deschampsia flexuosa. Especially, *Molinia* has shown a strong increase in distribution area in Western European heathands (e.g. Hansen, 1976; Berendse et al., 1994; Chambers et al., 1999). Increased nitrogen deposition and changes in management have been proposed as the main causes for this shift in species composition, particularly in dry heathland (Aerts and De Caluwe, 1989; Berendse, 1990; Aerts, 1993a).
As fire frequency and intensity may be related to biomass production and litter accumulation (Whelan, 1995; Bond and vanWilgen, 1996), the observed changes in species compo sition and the associated increase in productivity may increase the probability of intense accidental fires, which, in turn, may increase growth and spread of *Molinia* after fire. Aerts (1989) and Aerts and De Caluwe (1989) have demonstrated that *Molinia* shows a high phenotypic plasticity with respect to nutrient turnover and productivity. Increased soil nutrient levels after fire (Allen et al., 1969; Anderson and Menges, 1997) may, therefore, lead to vigorous (re)growth of *Molinia* plants when the vegetation has been burned. Moreover, burning removes all litter, which may also result in increased growth of *Molinia* due to higher midday soil temperatures (Grant et al., 1963). The increased aboveground biomass and associated litter production may, in turn, result in a competitive advantage to *Molinia* and, finally, in competitive exclusion of other heathland species.Although there is an extensive body of literature on the effects of nutrient availability and aboveground biomass production of *Molinia*, detailed investigation of the effects of fire on biomass production and post-fire seed set and seedling recruitment are lacking (but see Grant et al., 1963). Until now, most studies have focused on different management strategies, one of them being fire, to halt further invasion of *Molinia* and to restore heathlands (e.g. Grant et al., 1963; Todd et al., 2000; Ross et al., 2003; Milligan et al., 2003; Marrs et al., 2004), but they did not provide a mechanistic understanding of the effects of fire on *Molinia* dynamics. Moreover, data on natural fires affecting population attributes of *Molinia* are very scarce.
Hence, the aim of this study is to provide detailed insights in how fire affects population vital attributes (fecundity, germination and survival) of *Molinia*. Therefore, fire-induced changes in aboveground biomass production, seed set and seed germination, both in laboratory and under natural conditions, were compared between plants occurring in burned and unburned heathland. Data were collected in 1997 following a large fire in 1996 that burned almost one third of the Kalmthoutse Heide, a large heathland area in the Northern part of Belgium. This fire provided excellent opportunities to study the response of *Molinia* to spontaneous fires, which cannot be studied based on experimental, mostly low intensity burns. On the other hand, caution has to be made to extrapolate our findings to other heathland systems, since our study did not allow for proper replication (i.e. only one system was studied) (Oksanen, 2004). Nevertheless, the results of this study may reveal important information on the response of *Molinia* to fire and on future management guidelines for heathland areas where *Molinia* occurs and that are subject to frequent fires. First, we investigated whether fire increased biomass production, seed set and seed germination of *Molinia*. Secondly, we studied whether differences in nutrient conditions affected aboveground biomass production. Therefore, phosphorus and nitrogen concentrations and C:N ratios of different parts of the plant (seeds and leaves) were compared among plants occurring in burned and unburned sites (control plants). Finally, the results are evaluated with regards to the management of the studied area.

2 Material and methods

2.1 Study species and study site

M. *caerulea* (L.) Moench is a tall, deciduous, perennial grass species that occurs throughout much of Europe and that extends its distribution to North Africa, Caucasus and Siberia

(Taylor et al., 2001). The species occupies a wide range of habitats (ranging from forests, grasslands to heathlands) and soil types (ranging from dry acid sands to wet calcareous bogs). In Belgium, the distribution of *Molinia* is more or less restricted to heathland areas and pine plantations. *Molinia* forms swards or large tussocks from 8 to 20 (sometimes more than 30) cm in diameter at the base. Because of its deciduous nature, each year a large amount of litter is produced, which may burn quite easily in spring after prolonged periods of drought. *Molinia* has an enormous root system that forms a dense tangle at the top and can penetrate to a great depth (sometimes 100 cm) (Aerts, 1993a), which enables the species to survive intense fires. In contrast to many other grass species, the tufted growth form shows very little lateral vegetative spread, making colonization and spatial spread by the species dependent on sexual reproduction. Flowers are windpollinated and seeds are dispersed by wind. Mean seed production per plant is generally high (> 20,000 seeds per flowering plant) (Bruggink, 1993). Seeds are relatively small, have a mean air-dry mass of 0.53 mg (Grime et al., 1988) and are able to readily colonize bare ground (Taylor et al., 2001).
This study was carried out at the Kalmthoutse Heide (49°18′N, 4°25′E), a large heathland area (1020 ha) situated in the northern part of Belgium (near Antwerp). An intense and large, unintended fire on 24, April 1996, burned nearly a third of the total area. All investigations were performed in dry heathland (*Genisto pilosae-Callunetum*) on humus podsol. Based on soil and vegetation maps (De Blust and Slootmaekers, 1997), it was ascertained that the study was performed on a large, homogeneous site that showed no differences in soil conditions and vegetation characteristics between the burned and unburned sites before burning. In this way, plants in unburned sites could be treated as control plants. Before burning, the vegetation at the study site was characterized by relatively high dominance of *Calluna vulgaris*, whereas *Molinia* occurred in isolated tussocks. Other plant species occasionally observed at the study site were *Erica tetralix*, *Rynchospora alba*, *Festuca ovina*, *Carex pilulifera*, the mosses *Campylopus introflexus* and *Hypnum jutlandicum* and the lichens *Cladonia portentosa* and *C. floerkeana*. By the following year, burned *Molinia* plants had resprouted and produced seeds.

2.2 Aboveground biomass production and nutrient content

To investigate the impact of fire on aboveground biomass, 80 plants (40 in burned and 40 in unburned heathland) were randomly selected at the beginning of September 1997. For each plant, total aboveground biomass per plant and basal 300 R. Brys et al. / Acta Oecologica 28 (2005) 299–305 diameter were determined. Since *Molinia* shows hardly any aboveground mortality during the growing season, aboveground biomass at the end of the growing season (i.e. September) can be considered a good estimator of total aboveground net primary production (Aerts and De Caluwe, 1989). Total aboveground biomass was estimated for each plant by cutting all aboveground biomass and determining total dry mass after drying for 48 h by 70 °C. Besides biomass, the number and length of culms was also determined for generative and vegetative culms separately.
Nitrogen, carbon and phosphorus concentrations were measured for plants from both burned and unburned sites. Total nitrogen and carbon content were determined using a CNS analyzer (type NA 1500; Carlo Erba Instruments, Milan, Italy). Phosphorus content was analyzed colorimetrically; 150 mg of plant material was digested with sulfuric acid and a mixture of sodium sulfate, copper sulfate and copper. The diluted digestions were analyzed colorimetrically on a continuous-flow analyzer (Skalar SA-40) using the ammonium molybdate method. Measurements were performed for leaves and seeds separately. All measurements were repeated three times for each part of each plant and mean values were used for statistical analysis.

2.3 Seed quantity

To investigate the impact of fire on seed quantity (i.e. the number of seeds per reproducing plant), seeds were harvested at the end of September (1997) before seed dispersal. In both the burned and unburned site, 10 individual plants were randomly selected and per individual 10 inflorescences were harvested. For each inflorescence, all seeds were counted. Total seed production per plant was determined as the mean number of seeds per inflorescence multiplied by the number of inflorescences per plant.Afterwards, seeds were dried for 24 h at 70 °C and dry seed mass was determined.

2.4 Seed germination

Seed germination was determined both in laboratory and under natural conditions. First, in 1997 seeds originating from plants of the burned and unburned site, respectively, were germinated in controlled laboratory conditions. As soil substrate may influence seed germination rates, three different substrates were used: 1) a neutral, sterile substrate, 2) a burned soil core and 3) an unburned soil core. 100 *Molinia* seeds originating from five individuals were sown on each substrate. To avoid contamination by germination of seeds already present in the soil samples, samples were sterilized at 120 °C for 24 h prior to seeding. Each treatment was repeated three times. Seed germination rates were monitored every 4 days in the laboratory at 25/16 °C for 60 days in total.
Secondly, in order to study seed germination in natural conditions, eight 2 × 2 m^2 plots were laid out in pairs at the same study site, four in burned and four in unburned heathland. From 1997 until 2000, seedling recruitment was determined annually in each plot. For each year and for each plot seedling density (seedlings m^{-2}) was then calculated and used in all further analyses.

2.5 Data analysis

The effects of fire on total aboveground biomass production and the number and length of generative and vegetative culms were investigated using t-tests. t-tests were also used to investigate differences in nutrient conditions (C:N ratios, N-and P-concentrations) of different plant tissues among plants from burned and unburned sites. Analogously, seed production per culm and per plant, and seed mass were compared among plants from burned and unburned sites using t-tests. Differences in germination rates on different substrates among seeds originating from plants occurring in burned and unburned heathland were analyzed using a twoway analysis of variance (ANOVA) with substrate and fire (burned vs. unburned) as fixed factors. Differences in seed densities in natural conditions among burned and unburned plots were determined using repeated-measuresANOVA, with fire as a fixed factor and seedling densities in 1997, 1998, 1999 and 2000 as a repeated measure. Because the sphericity assumption was violated, the Greenhouse–Geisser method was used to adjust the numerator and denominator degrees of freedom. All statistical analyses were conducted using the SPSS statistical package forWindows (11.0).

Table 1
Total aboveground biomass per individual plant, basal diameter and the number and length of inflorescences for M. *caerulea* from burned and unburned heathland

	Burned	Unburned	*t*-value	*P*
Total biomass per plant (g)	126.64	77.98	3.108	0.003
Basal diameter (cm)	16.37	2.616	2.616	0.011
Number of inflorescences	209.30	134.00	3.305	0.001
Length of inflorescences (cm)	81.12	72.26	3.081	0.003

3 Results

At the end of the growing season of 1997 (i.e. 1 year after fire) total aboveground biomass per plant was significantly ($P < 0.05$) higher in burned than in unburned heathland (Table 1). Basal diameter, on the other hand, was significantlysmaller for plants of burned sites than that of unburned sites. The number and length of inflorescences were significantly larger for plants from the burned than those from the unburned site (Table 1). Nitrogen and phosphorus concentrations in leaves were higher in the burned than in the unburned situation (Table 2). The C:N ratio, on the other hand, did not differ between plants from the burned and unburned site. In contrast, no significant differences were observed in nutrient content of seeds among plants from the burned and unburned situation (Table 2).
Molinia produced significantly more seeds after fire ($t = 4.90$, $P = 0.001$). The number of seeds per culm was almost twice as high in the burned compared with the unburned site (mean number of seeds per culm: 460 and 241, respectively).As the number of inflorescenceswas larger after burning, total seed set per plant differed even more strongly between the burned and unburned situation (total seed set per individual plant: 96,000 and 32,000, respectively) (Fig. 1). On the other hand, no differences in seed weight were found ($t = 1.13$, $P > 0.05$).
Despite rather low seed germination rates under laboratory conditions (mean germination rate: 9.2%), significant differences were found between substrates on which seeds germinated and between seeds originating from the burned and unburned site (Fig. 2 and Table 3). Seed germination rates were significantly higher for seeds originating from plants growing in the burned site compared to plants from the unburned site (16.3% and 2.1%, respectively), and germination rates were highest on the control substrate.
Between 1997 and 2000, a total of 4527 seedlings were observed in eight 2 × 2 m2 monitoring plots. Mean seedling densities, however, varied tremendously among burned and unburned plots and among years (Fig. 3 and Table 4). Whereas the first year after fire (1997) mean seedling densities were comparable among burned and unburned plots, from 1998 onwards seedling density was much higher in burned than in unburned plots. Nevertheless, a decrease in seedling recruitment was observed in burned plots during the last 2 years of monitoring.

Table 2
C:N ratios (g g−1) and concentration of nitrogen (μmol g−1 dry wt.) and phosphorus (μmol g−1 dry wt.) in both leaves and seeds from M. *caerulea* occurring in burned and unburned heathland

Nutrient	Burned	Unburned	*T*	*P*
Seeds				
C:N	32.97	30.25	1.526	0.141
N	1390	1510	1.740	0.096
P	27.06	24.34	0.593	0.559
Leaves				
C:N	34.01	39.36	1.497	0.150
N	1440	1190	2.327	0.027
P	14.362	11.36	2.053	0.049

Fig. 1. The relationship between plant size (rosette circumference) and seed set for burned and control (unburned) plants.

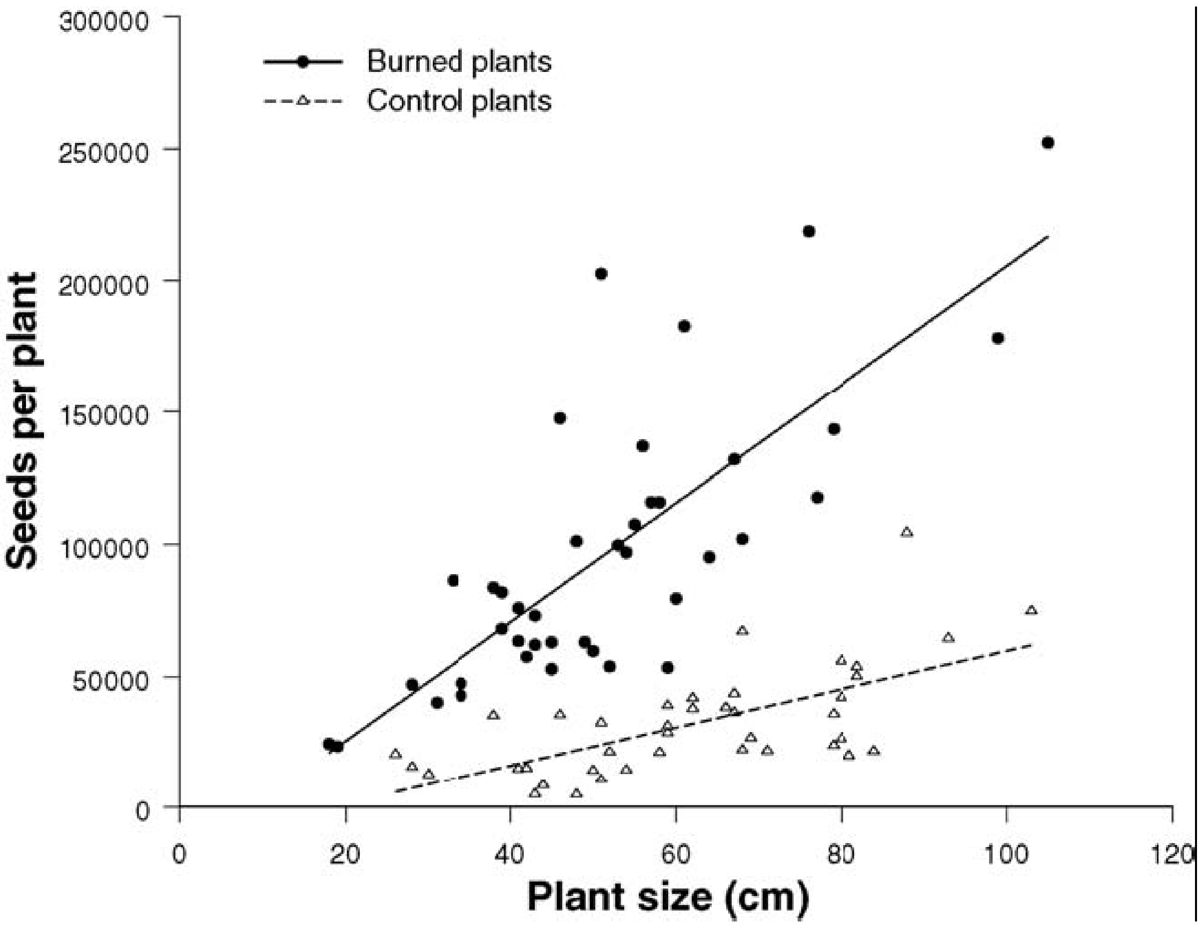

Table 3
ANOVA of the effects of soil substrate and fire treatment on seed germination rates (%) of M. *caerulea*

Source	Df	MS	*F*	*P*
Fire	1	0.091	60.681	0.000
Substrate	2	0.007	4.670	0.032
Substrate*fire	2	0.003	2.293	0.143
Error	12	0.002		

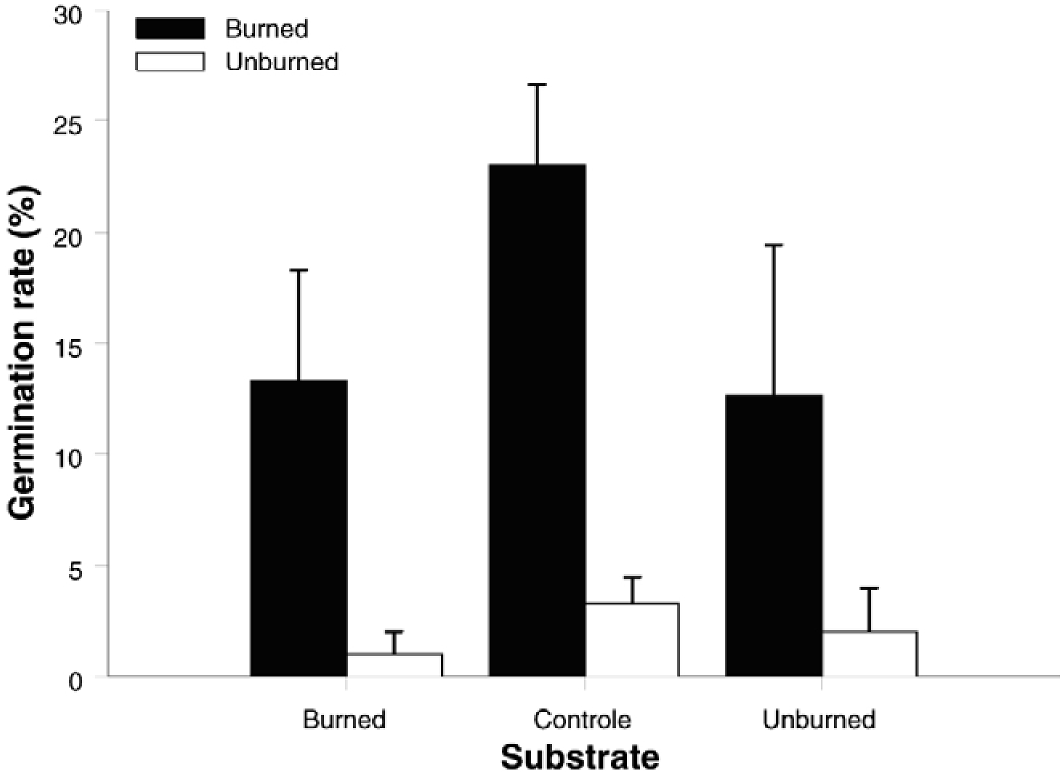

Fig. 2. Germination rates (%) of M. *caerulea* seeds from plants occurring in burned and unburned dry heathland on three different substrates (a neutral, sterile soil core (control), a burned soil core and an unburned soil core). Mean + S.D. (error bar) are given.

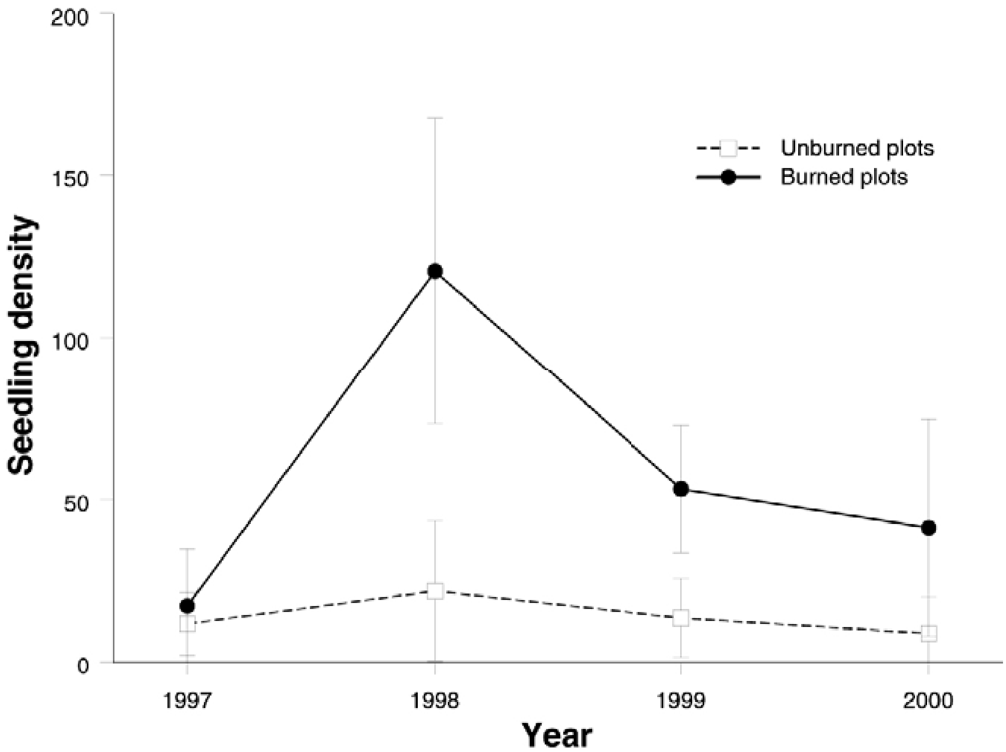

Fig. 3. Seedling densities (the number of seedlings per m2) of M. *caerulea* in burned and unburned 2 × 2 m2 plots (N = 4) from 1997 until 2000. Error bars represent the standard deviation of the four plots.

4 Discussion

4.1 Effects of fire on total aboveground biomass

production and seed set *Molinia* responded positively to fire as total aboveground biomass, the number of inflorescences and seed set, all strongly increased after fire. Several studies have already shown that *Molinia* shows a pronounced plastic response to nutrient enrichment (e.g. Aerts, 1989; Aerts and De Caluwe, 1989; Tomassen et al., 2003; Limpens et al., 2003). In all cases, nitrogen and/or phosphorus addition resulted in increased total aboveground biomass production of *Molinia*. In general, fire is known to result in a temporal increase of nutrient enrichment to the soil (e.g. Allen et al., 1969; Anderson and Menges, 1997). For dry heathlands for example, Aerts (1993a) found nutrient inputs after fire to be as large as 560 N kg ha−1, 23 P kg ha−1 and 63 K kg ha−1. As *Molinia* is able to respond quickly to increased nutrient inputs, fire resulted in a strong increase of *Molinia* biomass. Moreover, the increased levels of N and P in leaf tissue of the species also confirm rapid nutrient uptake and allocation by *Molinia* after fire. Analogously, fire resulted in a higher number of inflorescences per plant. Similar results were obtained by Grant et al. (1963), who demonstrated that fire increased the number of inflorescences per plant 2.3 times. According to Grant et al. (1963), this strong increase in flowering was mainly the result of litter removal, which resulted in higher soil temperatures that stimulated flowering. Similarly, the studied fire and associated removal of litter may have resulted in higher midday soil temperatures and increased flowering.

Next to the increased total aboveground biomass production, seed set per culm and per plant strongly increased after burning. These results are in accordance with findings of Aerts

(1993a), who found that *Molinia* showed a strong increased investment of biomass in reproductive tissues when nutrient supply was increased. Moreover, he reported that the percentage distribution of biomass to reproductive tissues increased significantly from 8% to 14% when nutrient additions increased 10-fold. Similarly, we observed a twofold higher seed set per culm in *Molinia* plants growing in the burned site compared to individuals of the unburned control situation. Several other grass species have also shown increased seed production rates after fire (e.g. Andropogon semiberbis and Sporobolus cubensis (Silva et al., 1990), A. brevifolius (Canales et al., 1994) and Hyparrhenia diplandra (Garnier and Dajoz, 2001)).

4.2 Fire and seed germination

The high seedling densities in burned plots may be explained by 1) a higher number of seeds produced, 2) higher seed germination rates and 3) reduced competition in the burned situation. Indeed, the germination experiment in laboratory conditions showed that, although seed germination rates were rather low, seeds from plants that occurred in the burned site showed higher germination rates than seeds produced by plants growing in the unburned site. The mean germination rates observed, however, largely correspond with values reported by Grime et al. (1981), who also found a very low percentage (only 3%) of freshly collected seeds that germinated immediately. The high seedling densities observed at the study site 2 years after burning may further be explained by the relatively large amount of bare soil and increased light penetration of the soil, since the germination of *Molinia* seeds is largely stimulated by light (Bruggink, 1993). In unburned plots, on the other hand, the thick litter layer diminishes light penetration to the soil and thus germination rates of *Molinia*. Moreover, as an increasing number of seeds have germinated over time in the burned plots, space and light became also more limiting, which may explain gradual reductions in seedling densities some years after burning. Nevertheless, seedling densities remained much larger in the burned than in the unburned treatment indicating that fire benefited seedling establishment. Analogous beneficial effects of fire on seedling recruitment have been reported for the perennial grass *A. semiberbis* (Silva et al., 1991).

4.3 Consequences for heathland conservation

The results of this study have demonstrated that large, unintended and intense fires benefit *Molinia* in at least two ways, both of which may affect heathland structure and plant diversity. First, it was shown that total biomass production following fire was nearly twice as high in the burned situation compared to the unburned situation. This massive fire-induced biomass production may result in a competitive advantage to *Molinia* with respect to other heathland species. Heil and Bruggink (1987) and Aerts (1993b) have demonstrated that at high levels of nutrient availability, heathland species such as Calluna will be outcompeted by *Molinia*. Similarly, fire may lead to absolute dominance of *Molinia*. Furthermore, high litter production rates after fire may further limit regeneration of heathland species, resulting in an extra competitive advantage of *Molinia*. Besides the increased biomass and litter production and the resulting build-up of organic material in the soil may also increase the frequency and intensity with which fires will occur (Whelan, 1995; Bond and van Wilgen, 1996). Increasing fire frequencies may again have a positive effect on *Molinia* encroachment and finally lead to, or maintain, absolute dominance of this species.

Table 4
Repeated-measuresANOVA for the effects of fire on seedling density of M. *caerulea* (the number of seedlings per m2) in eight 2 × 2 m2 plots monitored from 1997 until 2000

Source	Df	MS	*F*	*P*
Fire	1	15 488	9.92	0.020
Error	6	9369		
Year	1.08	4845	17.00	0.005
Year x Fire	1.08	8512	10.76	0.014
Error (Year)	6.48	791		

Both the between-subject main effect of fire as the within-subject main effect of year and the fire × year interaction are shown.

Secondly, higher seed production and seed germination rates after fire resulted in increased recruitment success and hence to an increased abundance of *Molinia*. Indeed, colonisation of new sites and invasive spread of *Molinia* are largely dependent on seed production, as the species shows little vegetative reproduction. Next to a higher number of seeds that are able to germinate and establish in heathland, high seed production may also increase the density of seeds reaching a certain distance (Nathan and Muller-Landau, 2000) and hence promote invasive spread of the species after fire (Neubert and Caswell, 2000; Caswell et al., 2003). Given the observation that fire regimes are expected to change over the next decades in response to global warming and land use changes (e.g. Piñol et al., 1998; Flannigan et al., 2000; Pausas, 2004), this urges for management interventions that reduce the probability of fires burning large heathland areas. The Kalmthoutse Heide may be exemplary, as the studied fire was clearly not an isolated case. During the last three decades, at least three large and intense fires (1976, 1996 and 1997) have burned substantial areas of the Kalmthoutse Heide and have led to an increased abundance of *Molinia*. In recent years, similar increases in fire frequencies have been observed in other heathland areas in Belgium too. Therefore, management should be directed in such a way that further increases in abundance of *Molinia* should be halted. Recent studies have shown that this can be best achieved by grazing in summer (Grant et al., 1996), selective herbicides (Milligan et al., 2003; Marrs et al., 2004) or to a lesser extent by controlled burning in winter (Ross et al., 2003), all of which reduce standing crop of *Molinia* and hence litter production.

5 Conclusion

The results of this study have demonstrated that intense, unintended fires largely increase growth and seed production of *Molinia* in dry heathland.Without management interventions aiming at decreasing litter accumulation and abundance of *Molinia*, large accidental fires are most likely to occur more frequently in the near future due to the increasing productivity of these originally nutrient poor heathland communities and the associated increase in litter production.

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