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Original article

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

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 van Wilgen, 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 van Wilgen, 1996), the observed changes in species compo-

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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 wind-pollinated 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