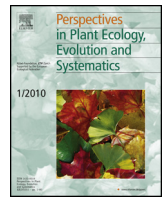


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Research article

## Shape determines fire tolerance of seeds in temperate grasslands that are not prone to fire

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## ABSTRACT

Prescribed burning is an important tool for nature conservation in many parts of the world. It is now also being increasingly proposed as an alternative to traditional management in temperate grasslands that are not naturally fire-prone. For effective biodiversity conservation, accurate knowledge about species responses to fire is indispensable. Plant diaspores are key elements in the long-term persistence of populations, but surprisingly, even in fire-prone ecosystems, little is known about traits that may influence seed responses to fire. In a comparative study, we assessed germination responses of 37 temperate European herbaceous species to experimental fires simulating grassland fires with moderate fuel loads and related these responses to the thickness, complexity and strength of the seed coat, diaspore type (seed vs. one-seeded fruit), size, shape, and heat tolerance, while accounting for the influence of phylogenetic relatedness. Seed traits like diaspore type, shape and heat tolerance were significantly related to seed responses to fire when considered in isolation. However, in multivariate models shape was the only factor explaining fire tolerance of seeds. More rounded seeds showed a higher fire tolerance. This can be explained by their smaller surface-to-volume ratio and/or because they are better protected by surrounding soil particles and hence tolerate fire more than elongated or flattened seeds. Our results show that species of non-fire-prone temperate grasslands display diverse germination responses to fire. The direction and magnitude of this response was best predicted by the shape of diaspores with elongated or flat seeds being most vulnerable to fire.

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### 1. Introduction

Prescribed burning is of great importance to nature conservation (Driscoll et al., 2010). Fire represents not only a major source of disturbance in natural environments (Bond et al., 2005; Bowman et al., 2011), but also a means of controlling the spread of invasive species (e.g. Cummings et al., 2007), community restoration (e.g. Baker, 1994; Pyke et al., 2010), reducing fire hazards (Baeza et al., 2002; Fernandes and Botelho, 2003) and conservation of endangered species (e.g. Pendergrass et al., 1999). As a consequence, prescribed burning is frequently used as a management tool in a variety of ecosystems, especially in North America and Australia (e.g. Russell-Smith et al., 2000; Fuhlendorf and Engle, 2001; MacDougall and

Turkington, 2007). Recently, it is increasingly being proposed as an alternative to traditional management (mowing and grazing) in temperate regions of Europe as well (Goldammer, 2013; Valkó et al., 2014). However, so far, long-term experiments in European temperate grasslands report undesired changes in species composition and a general decline in species diversity as a result of yearly burning (e.g. Moog et al., 2002; Köhler et al., 2005; Milberg et al., 2014). To meet management goals aimed at conserving all target species within a community or region, accurate knowledge about species responses to fire is indispensable (Keith et al., 2002).

Predicting the outcome of prescribed burning is often hampered by the complexity and variability in species responses to fire, i.e. plant survival and reproduction. Regeneration by seed is a key element in the long-term persistence of plant populations within a community. Previous experiments have shown great interspecific differences in the fire tolerance of seeds and their post-fire germination (e.g. Keeley and Keeley, 1987; Baskin and Baskin, 2001; Luna et al., 2007; Ruprecht et al., 2013). However, little is known about the factors that might explain this variability.

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Most of our knowledge about the response of seeds to fire is based on studies performed in ecosystems regularly experiencing natural fires. In such fire-prone ecosystems, plants have developed numerous anatomical, morphological and physiological adaptations to fire that help diaspores maintain their capacity for germination and promote survival following fire (Keeley et al., 2011, 2012). Anatomical adaptations most frequently associated with seed persistence in fire-prone habitats are hard, thick and water-impermeable seed coats (Keeley and Fotheringham, 2000; Keeley et al., 2012). These specialized seed coats allow seeds of fire-dependent species to break dormancy after exposure to high temperatures. It is well documented that fire-induced germination is concentrated in a few families, e.g. Fabaceae, Rhamnaceae, Ericaceae, Geraniaceae, Malvaceae, Sterculiaceae, Cistaceae and Convolvulaceae (Keeley and Fotheringham, 2000; Baskin and Baskin, 2001). Thus, heat-stimulated germination in seeds is considered to be evolutionarily conserved (Verdu and Pausas, 2007), most probably because closely related species share the same seed anatomy, e.g. seed coat structures (Martin, 1946; Keeley and Bond, 1997 and references therein). In other species, seeds may resist the high temperatures during a fire, but germination is not specifically stimulated by heat (Buhk and Hensen, 2006; Luna et al., 2007; Paula and Pausas, 2008). In these species, a thick seed coat might protect seeds from fire, e.g. by providing insulation around the embryo (e.g. Williams and Bell, 1998; Gómez-González et al., 2011). Such traits that increase survival of seeds exposed to fire could have resulted through natural selection mediated by fire (Gómez-González et al., 2011) or as an evolutionary response to other factors, such as endozoochory or drought (Bradshaw et al., 2011). In line with this, fire tolerance of seeds may also appear in ecosystems where fire is not a natural and predictable selective pressure (Granström and Schimmel, 1993; Ruprecht et al., 2013).

Apart from the role of the seed coat in mediating germination responses to fire, our understanding of seed–fire interactions in relation to seed traits as well as of the mechanisms behind is still relatively poor. There are only a few studies of seed morphological traits (e.g. seed size) potentially responsible for the reaction of seeds to fire. Moreover, in these studies there is little consistency about the relationship between seed size and heat stimulation or tolerance (Gonzalez-Rabanal and Casal, 1995; Gashaw and Michelsen, 2002; Hanley et al., 2003). The role of seed shape in the fire tolerance of diaspores has so far not been studied in detail (but see Gómez-González et al., 2011). In this latter evolutionary study, Gómez-González and colleagues (2011) found that anthropogenic fire selected for more rounded seeds in a species from the Asteraceae in Chile. According to their findings, seeds from populations with a longer fire history and greater fire frequency were more rounded, more pubescent and thicker-coated.

We studied germination responses of temperate European species to experimental fire and related these responses to anatomical and morphological seed traits and heat tolerance. In our study, we expect that traits that have been shown or hypothesized to influence the response of seeds to fire in species of fire-prone ecosystems also contribute to fire tolerance of diaspores in non-fire-prone ecosystems. Most previous studies did not take into account phylogenetic relationships among species, which can result in spurious results due to non-independence caused by their shared ancestry (Felsenstein, 1985). Closely related species are more likely to be similar to each other than expected by chance simply because many of their traits are inherited from their ancestor without change; therefore, a basic assumption of linear statistical models (non-independence of data points) is violated when comparing species. This can lead to elevated type I error rates and biased inferences of trait evolution (for instance, differences in the number of species within lineages can result in statistically significant relationships when in fact there are none). Our aim in this

comparative study is to identify seed traits that affect the response to fire in diaspores not historically subjected to recurrent fires, taking into account the phylogenetic relationships of the studied species. We hypothesize that the thickness, complexity (number of cell layers and tissue types) and strength (lignification) of the seed coat will influence the fire resistance of seeds in species of non-fire-prone ecosystems. In addition, we hypothesize that morphological traits, like seed size and shape, may also be influential. Specifically, we aimed to (1) study seed traits that may be involved in fire tolerance in ecosystems that are not prone to fire, and to (2) reassess the role of anatomical and morphological traits responsible for seed performance after fire in a non-fire-prone ecosystem. We analyzed the germination responses of seeds or one-seeded fruits of 37 temperate European herbaceous species to experimental fire, and related these responses to heat tolerance and anatomical and morphological seed traits.

## 2. Materials and methods

### 2.1. Species selection and seed collection

We selected 37 herbaceous plant species, which are typical constituents of grassland and ruderal habitats of Transylvania, Romania. The species belonged to the most common plant families of the region's open habitats (see Appendix A, Table A1). Diaspores (seeds or one-seeded, indehiscent fruits) were collected in bulk from native populations in 2011 and 2012. Collections included at least 30 different plant individuals from one to three sites each. Seeds or one-seeded fruits cleaned of appendages (mostly pappus or thin awns) were subsequently dry-stored in darkness at room temperature (c. 20 °C) until they were subjected to cold-wet stratification at 3 °C for three months prior to the experiments.

### 2.2. Experiments on fire tolerance of seeds

In order to find out how fire influences the germination of seeds, we conducted the same experiment separately on two sets of species. Fire tolerance of the first set of species was tested in 2012 (the results of this experiment are treated in detail in Ruprecht et al., 2013; this paper discusses solely the response of seeds to experimental fire and heat treatments, without involving seed traits), while the second set of species was tested in 2013. In both cases we used seeds collected in the previous year. Stratified seeds were subjected to an experimental fire at the end of March (2012 or 2013), when seeds were put directly on the soil surface in 1-L pots (c. 10 cm × 10 cm × 10 cm) filled with 2:1 mixture by weight of commercial potting soil and sand. For the experimental fire, seed containing pots were arranged randomly one beside the other, covered by dry litter (365 g m<sup>-2</sup>), and then the litter was burned. By this treatment we wanted to simulate the effect of a grassland fire on seeds on the soil surface. Fuel load was determined based on field measurements in grassland sites of Transylvania, Romania in early spring. Each species × fire treatment group had six replicates, and each pot contained 40 seeds. In the case of one species (*Origanum vulgare*) we used 60 seeds, because of the low seed viability, and in the case of another species (*Anthriscus sylvestris*) we used 35 seeds, because we did not have enough seeds. As a control for fire treatment, we installed pots (generally 40 seeds each) in six replicates per species with properly stratified but untreated seeds, and these seeds were not covered by litter.

The pots from both experimental series (192 in 2012 and 444 in 2013) were placed in the University Botanical Garden at Cluj-Napoca, covered with a transparent polyethylene sheet on the top of a wooden frame, and watered regularly. The experimental setup was the same for both species sets (2012 and 2013), i.e. the quantity

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