



Original article

Is the positive response of seed germination to plant-derived smoke associated with plant traits?

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ARTICLE INFO

Article history:

Received 21 October 2014

Received in revised form

5 May 2015

Accepted 5 May 2015

Available online 16 May 2015

Keywords:

Ecological indicator values

Fire

Life form

Seed properties

Temperate species

Weeds

ABSTRACT

Relationships between seed germination response to plant-derived smoke and various plant traits (habitat requirements, life form, seed morphology, seed bank type) were analysed for 97 species of the Hungarian flora using published data. It was hypothesized that smoke-responsive species – those displaying enhanced germination in response to smoke – differ from non-responsive species – smoke having an indifferent or inhibitory effect on germination – in habitat requirements and/or certain life history traits. To our knowledge, no such comparison has previously been reported for a European flora. We found that species indicating disturbance and those preferring soils rich or moderately rich in nitrogen were more frequent in the smoke-responsive group (80% and 41%, respectively) than in the non-responsive group, while the non-responsive group contained a high percentage of natural species (i.e. species dominant or characteristic in natural plant communities; 47%) and species indicative of nutrient poor (38%) or (sub)mesotrophic (38%) soils. Annuals or biennials (67%) dominated the smoke-responsive group, whereas in the non-responsive group these short-lived species and perennial herbs were equally abundant (43% each). There was a tendency for higher frequency of long-term persistent seed bank among smoke-responsive species (78%) than in the non-responsive group (54%). These findings suggest that smoke-stimulated germination is associated with only a few specific plant traits for species from a semiarid temperate region of Europe, but highlight the frequent occurrence of smoke-enhanced germination among short-lived, nitrophilous or disturbance tolerant species. These results can contribute to a better understanding of post-fire regeneration of plant communities, and could also be considered during vegetation restoration or weed management.

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1. Introduction

Seed dormancy and germination characteristics of plant species may vary depending on habitats (Baskin and Baskin, 1988; Schütz, 2000; Thompson et al. 1977, 1998) and the species' life history strategies for regeneration (Keeley, 1991; Thompson et al. 1998). For example, in the genus *Carex*, Schütz (2000) reported that species growing in forests germinated earlier in spring and at lower temperatures than the species of open habitats. In the fire-prone California chaparral, Keeley (1991) classified two post-fire regeneration strategies differing markedly in seed characteristics

(seed bank type, dormancy, seed mass and dispersal mode) and the timing of germination. Most fire-resister shrubs with vegetative resprouting capacity recruit by heavy, non-refractory seeds dispersed by birds, and lack seed dormancy and a persistent soil seed bank. Their germination typically occurs in the first rainy season following dispersal, in the absence of fire-related cues, such as heat shock or chemicals leached from charred wood. In contrast, fire-recruiter species usually have locally dispersed, refractory seeds with lower seed weight, which persist in the soil seed bank until their dormancy is broken by fire-related stimuli, and germinate in late winter or early spring (Keeley, 1991).

In addition to heat and charred wood, smoke derived from burning vegetation is another product of fires that can provide a cue for triggering seed germination. Since the discovery of the phenomenon (De Lange and Boucher, 1990), plant-derived smoke and

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its aqueous solution (smoke-water) has been shown to stimulate germination for more than 1200 species from phylogenetically distant plant families and different continents (Dixon et al. 2009; Kulkarni et al. 2011). The phenomenon is particularly frequent in fire-prone Mediterranean ecosystems (Baskin and Baskin, 1998; Brown et al. 2003; Dixon et al. 1995; Keeley and Bond, 1997; Moreira et al. 2010), but it has also been recorded for several species of non-fire-prone semi-deserts (Merritt et al. 2006; Pierce et al. 1995), arable weeds (Adkins and Peters, 2001; Stevens et al. 2007) and cultivated plants (Kulkarni et al. 2011). The germination stimulating capacity is mainly attributed to karrikinolide (3-methyl-2H-furo[2,3-c]pyran-2-one), a butenolide compound identified in smoke (Flematti et al. 2009). In fire-prone ecosystems, the germination response to smoke appeared to be mostly independent of fire regeneration strategy, life form, seed mass and dispersal mode (Abella, 2009; Brown et al. 2003; Dixon et al. 1995). In a test of 221 fynbos species, Brown et al. (2003) found that smoke-enhanced germination showed only weak positive relationships with herbaceous perennial life form and wind seed dispersal mode, and suggested that the smoke response is evolutionarily neutral. Only few such extensive analyses investigating the association between germination response to smoke and life history traits has been published for species from temperate regions (e.g. Tsuyuzaki and Miyoshi, 2009), and – to the best of our knowledge – have not been reported for a European flora. Human-induced fire as a management tool has long been and still is an important factor forming the European landscape (Deák et al. 2014; Feurdean et al. 2012; Goldammer and Bruce, 2004; Niklasson et al. 2010). In addition, climate change is predicted to increase fire frequency in a large part of the world including most of Europe in the 21st century (Pechony and Shindell, 2010). Thus, assessing the germination response to smoke and its relationships with specific plant traits of the species might contribute to a better understanding and predicting of the regeneration processes of plant communities in this region.

In this study we examine whether the benefit of smoke-stimulated germination varies depending on the prevailing habitat conditions and the life history characteristics of species from a semiarid temperate region of Europe. We hypothesized that species displaying positive germination responses to smoke differ from those lacking smoke-enhanced germination in ecological attributes indicating their habitat requirements or preferences (H_1), and/or in certain life history traits associated with regeneration (seed properties and life form, H_2). Based on the literature and our own experiments, these two hypotheses were tested on 97 species of the Hungarian flora. As fire has frequently been linked to human land use in the Carpathian region over the last 1000 years (Deák et al. 2014; Feurdean et al. 2012), we expect that smoke-enhanced germination favours plant traits that are often associated with disturbances in general, e.g. short-lived life forms, preference for nitrogen and light, small seeds and a long-term persistent seed bank (Belsky, 1992; Ghermandi et al. 2004; Šoltés et al. 2010; Thompson et al. 1998; Török et al. 2008).

2. Materials and methods

An extensive literature search was conducted for laboratory and field studies published between 1998 and 2014 (up to 31 March) on the effect of smoke treatment on the germination or seedling establishment of species belonging to the Hungarian flora (native and naturalized alien species; Király, 2009). The collated database contains the germination response to smoke treatment for 97 species (Appendix A), which was collected from 33 studies (Appendix B) supplemented with our own unpublished results. The unpublished data were obtained by using the same experimental

methods as described in Mojzes and Kalapos (2014). Data were assessed at species level, even when in the original published study the smoke response was reported for a particular subspecies or variety of a species. In the case of nomenclatural synonyms, The International Plant Names Index (2012) was used for species identification. The smoke response of species, quantified in germination percentage or seedling density depending on the study, is expressed as binary data. Positive (+) response was attributed to a species if it significantly ($p < 0.05$) displayed inherent or inducible smoke-stimulated germination (*sensu* Long et al. 2011) at least under one particular experimental condition, even if under other circumstances smoke treatment had a neutral or inhibitory effect (e.g. due to high concentrations of smoke-water applied: Adkins and Peters, 2001; Light et al. 2002; or dormancy that should be alleviated so that seeds become sensitive to smoke: Baker et al. 2005; Long et al. 2011). Such species are referred to as 'smoke-responsive' hereafter in this study. In order to analyse the smoke response itself, data describing the effects of combined treatment (e.g. smoke and heat) compared to the untreated control, were excluded. Negative (–) response was assigned to a species if it has not displayed smoke-enhanced germination under any of the conditions tested, i.e. germination was not affected by smoke treatment (undetected response according to Long et al. 2011) or it decreased compared to the control. For such species, the term 'non-responsive to smoke' is used in this study. Different types of smoke treatment, such as aerosol smoke, smoke-water or karrikinolide applied to seeds directly or to the germination medium, were not distinguished (each referred to as 'smoke treatment' in this study). The reason for this was to assess more general associations between the smoke response and other (seed morphological and ecological) plant traits and ensure a sufficient sample size for the analysis.

The following plant traits were included in the analysis: thousand-seed mass (TSM; g), deviation of seed shape from sphericity measured by the variance of seed dimensions (length, width and thickness, after transforming each value so that width is unity, a method very similar to that described by Thompson et al. 1993), seed mass category (following the categorization of Hodgson et al. 1995), seed bank type (according to the definition of Thompson et al. 1997), Raunkiaer life form (categorized by Soó, 1964–1985), tolerance of habitat disturbance (Simon, 1988) and ecological indicator values *sensu* Ellenberg adjusted for the Hungarian situation by Borhidi (1995) reflecting the relative soil nitrogen (N), soil moisture (W), soil reaction (i.e. soil pH; R), temperature in accordance with the temperature regime of vegetation zones (T) and light (L) levels of the habitat (Appendix A). Seed size and shape data were extracted from published literature, mainly from the seed atlas of Schermann (1967), or were measured directly. In the latter case, mature seeds were harvested from wild populations growing in habitats typical for the species. Whenever possible, pooled seed samples from several mother plants of the same stand were collected to avoid bias caused by maternal effects. Seed samples were stored in paper bags at room temperature. Thousand-seed mass data were calculated from measurement of 3×100 fully ripened seeds, weighed to an accuracy of 0.1 mg. Seed shape data were calculated from measurement of 10 seeds per species. Seed length and width were measured under a binocular microscope equipped with a measuring lens to the accuracy of 0.1 mm, and seed thickness was measured with a precision of 0.05 mm by using a thickness metre (Mitutoyo, Japan). Seed bank type data were collected from published literature, mainly from the database of Thompson et al. (1997).

For seed mass and the deviation of seed shape from sphericity, statistical comparisons between the two groups of species characterized by positive or negative germination response to smoke

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