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Title page

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

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Abstract

Relationships between seed germination response to plant-derived smoke and various plant traits (habitat requirements, life form, seed morphology, seed bank type) were analyzed 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.

Keywords: ecological indicator values, fire, life form, seed properties, temperate species, weeds

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 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-2*H*-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 from, 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 analyze 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 meter (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 were made by two-sample t-tests (Quinn and Keough 2002). Data were log-transformed to meet the normality and homoscedasticity assumptions of the test. For categorical variables, the frequency distributions of species were compared between the two groups by using a Chi-square test of homogeneity. For each variable, categories were pooled in such a way as to meet the assumption that no more than 20% of the expected frequencies were less than 5 (Quinn and Keough 2002). In each comparison, differences were considered significant at $p < 0.05$. For the analyses, the GraphPad InStat 3.05 (GraphPad Software, San Diego, California, USA) package was used.

3. Results

Among the ecological attributes reflecting habitat conditions, the level of disturbance of the species' typical habitat and the relative nitrogen requirement (N) displayed significantly and markedly different frequency distributions between the two species groups (Fig. 1). In the smoke-responsive group, the proportion of species indicative of habitat disturbance exceeded four times the proportion of natural species (i.e. species dominant or characteristic in natural plant communities; Fig. 1a). Eighty four percent of species associated with habitat disturbance are weeds (i.e. constituents of segetal or ruderal weed communities associated with anthropogenic disturbance). In contrast, in the group of species non-responsive to smoke, species associated with natural or disturbed habitats were represented similarly (47% and 53%, respectively; Fig. 1a). Furthermore, in the non-responsive group, the proportion of weeds was much less (48% of species characteristic in disturbed habitats) in favour of disturbance tolerant native species (37%). In the smoke-responsive group, a substantial proportion (41%) of species preferred soils rich or moderately rich in nitrogen (N = 6-7), while in the species group non-responsive to smoke, about three quarters of the species were characteristic of nutrient poor (N = 1-3) or (sub)mesotrophic (N = 4-5) habitats (38% each; Fig. 1b). No significant differences were found between the two species groups in the distribution of relative soil moisture (W), soil reaction (R), habitat temperature (T) and light (L) requirements (Figs. 1c-f).

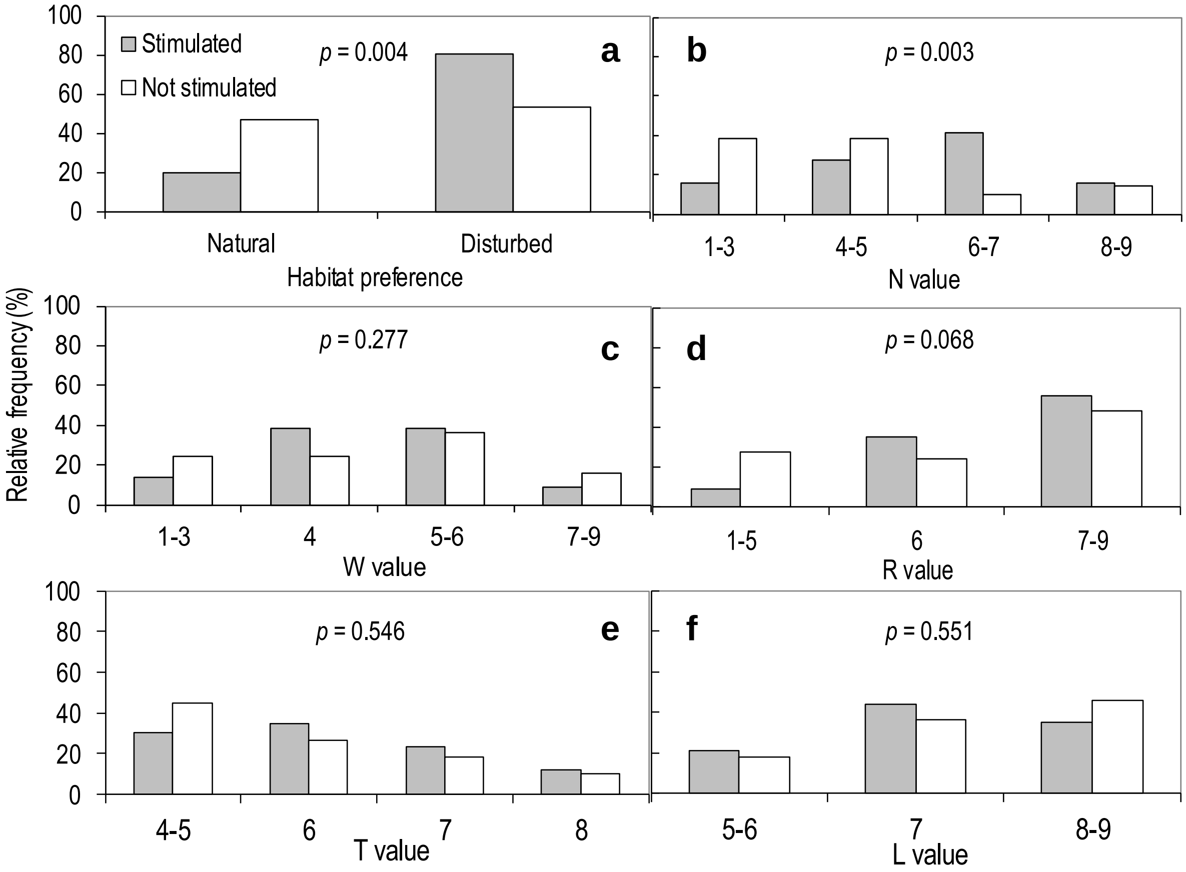

Figure 1. Frequency distributions of smoke-responsive (Stimulated) and non-responsive (Not stimulated) species in the Hungarian flora according to **a.** habitat preferences (n = 97), and relative requirements for **b.** soil nitrogen (N, n = 94), **c.** soil moisture (W, n = 94), **d.** soil reaction (R, n = 93), **e.** habitat temperature regime (T, n = 92) and **f.** light (L, n = 93). Species preferring natural habitats are unique or rare, strictly protected, protected, dominant native, accessorial native or natural pioneer species of natural plant communities; species associated with disturbed habitats include disturbance tolerant native, adventive, cultivated or weed species. N values range from 1 (plants on soils extremely poor in mineral nitrogen) to 9 (plants on over-fertilized soils, extremely rich in nitrogen on a range of N contents typical for European soils). W values range from 1 (plants of extreme arid habitats) to 12 (submersed aquatic plants). R values range from 1 (extremely acidophilic, calcifuge plants) to 9 (calcicole plants, basophilic specialists). T values range from 1 (plants of subnival or supraboreal zone) to 9 (plants of the Eumediterranean evergreen zone). L values range from 1 (full shade plants)

to 9 (full-sun plants of open habitats). The *p* values show the results of Chi-square tests of homogeneity.

Among the life history traits analyzed in this study (life form and seed properties) the distribution of Raunkiaer life forms was most varied between the two species groups differing in germination response to smoke. The majority (67%) of smoke-responsive species were annuals or biennials, whereas the proportion of species lacking germination enhancement in response to smoke of these life forms and that of perennial herbs were the same (43% each; Fig. 2a).

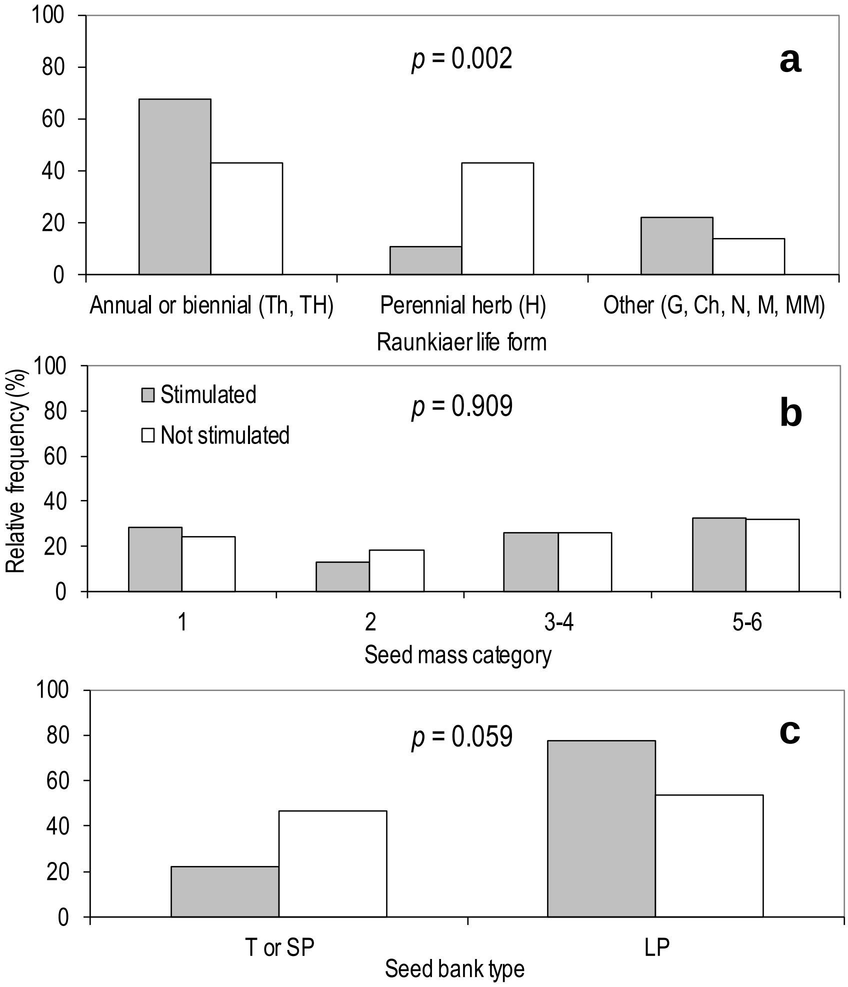

Figure 2. Frequency distributions of smoke-responsive (Stimulated) and non-responsive (Not stimulated) species in the Hungarian flora according to **a.** Raunkiaer life forms (n = 97), **b.**

seed mass categories (n = 96) and **c.** seed bank types (n = 55). Life forms: therophytes (Th); hemitherophytes (TH); hemicryptophytes (H); geophytes (G); chamaephytes (Ch); nanophanerophytes (N); microphanerophytes (M); mega-mesophanerophytes (MM). Seed mass categories: 1: ≤ 0.2 g; 2: 0.21-0.50 g; 3: 0.51-1 g; 4: 1.01-2 g; 5: 2.01-10 g; 6: ≥ 10.01 g). Seed bank types: transient (T); short-term persistent (SP); long-term persistent (LP). The *p* values show the results of Chi-square tests of homogeneity.

Mean thousand-seed mass and seed shape (expressed as the extent to which shape differs from sphericity) did not differ significantly between the two types of germination, despite the 2.5-fold greater variance of seed dimensions for species non-responsive to smoke (Table 1). Consistent with this, no significant difference was found in the distribution of species according to seed mass categories between the two species groups (Fig. 2b). However, long-term persistence tended to be more frequent (78%) than the transient and short-term persistent seed bank types together (22%) for species with smoke-stimulated germination, while for species non-responsive to smoke, the proportions of the two seed bank categories were similar (54% and 46%, respectively; Fig. 2c). Most of the species with long-term persistent seed bank were characteristic of disturbed habitats (weeds, disturbance tolerant natives or adventive species) in both the smoke-responsive group (86%) and the group non-responsive to smoke (80%; Appendix A).

Seed trait	**Stimulated**	**Not stimulated**	***p* value**
TSM	3.09 ± 0.85 (44)	2.04 ± 0.57 (49)	0.524
Variance of seed dimensions	0.97 ± 0.25 (38)	2.43 ± 0.85 (46)	0.222

Table 1. Thousand-seed mass (TSM; g) and the variance of three seed dimensions (transformed so that width is unity) for species in the Hungarian flora that are smoke-

responsive (Stimulated) or non-responsive (Not stimulated). Mean values ±1 SE. The numbers of species are indicated in parentheses. The *p* values show the results of two-sample t-tests. *Quercus robur* with its extremely high value was excluded from TSM.

4. Discussion

Among the eleven plant traits studied, only one life history and two habitat characteristics showed significant differences between the species group that displayed a positive germination response to smoke and the group which did not. These results suggest that smoke-stimulated germination is associated with only a small number of distinctive plant traits for species from a semiarid temperate region of Europe, and in concert with previous findings, support the widespread occurrence of positive germination response to smoke across a variety of life history traits (Brown *et al*. 2003; Dixon *et al*. 1995) and habitats (Crosti *et al*. 2006; Dixon *et al*. 2009).

The different distribution patterns of the degree of disturbance and the relative nitrogen level of the habitat for the two germination response groups are consistent with our hypothesis (H_1) that habitat conditions favouring smoke-stimulated germination should be different from those preferred by the species not displaying a positive germination response to smoke. As expected, species indicating habitat disturbance, including a large number of weeds, were prevalent in the species group which showed improved germination in response to smoke. A possible explanation for this is that rather than being a natural disturbance factor (i.e. wildfires), fires have frequently been associated with human activities (particularly with land use) in the Hungarian vegetation (Deák *et al*. 2014; Feurdean *et al*. 2012). Similar to other disturbances (such as livestock grazing or ploughing), fire also eliminates aboveground vegetation, reduces competition, increases temperature and light at the soil surface, reduces soil moisture and can elevate soil nitrate levels (Baskin and Baskin 1998). In such circumstances, species which can tolerate and utilize the altered, post-fire environment are most likely to be weeds responding to human disturbances. Smoke may function as a signal for these weedy species indicating that conditions are suitable for seedling establishment. An increased abundance of weeds was observed in several grasslands of Hungary after fire (Deák *et al*. 2014). In Australia, weeds appeared to be highly responsive to the application of smoke-water in a disturbed forest (Ruthrof *et al*. 2011) and to that of karrikinolide in agroecosystems (Stevens *et al*. 2007). In our study, the high proportion of species associated with soils rich or moderately rich in nitrogen among the smoke-responsive species is in accordance with the predominance of weeds in this species group. Fire can increase the level of soil ammonium or nitrate (Baskin and Baskin 1998; Certini 2005), which might be conducive to the establishment of nitrophilous weeds. Weed species favouring high nitrogen availability invaded the burnt area during early succession following a large wildfire in a *Picea abies* forest of the Tatra Mountains (Šoltés *et al*. 2010). In contrast, numerous smoke-responsive species are characteristic to nutrient poor habitats in South Africa (Brown *et al*. 2003) and Australia (Dixon *et al*. 1995).

Among the life history traits studied, life form appeared to be a reliable predictor of the germination response to smoke for species belonging to the Hungarian flora. Predominantly annual or biennial species displayed smoke-enhanced germination and this is in line with our predictions based on the frequently reported positive response of short-lived species to disturbance (Belsky 1992; Ghermandi *et al*. 2004; Török *et al*. 2008). At the same time, our result may suggest that smoke is a more important germination signal for species regenerating mainly or exclusively from seeds, than for perennials, most of which are capable of maintaining their populations by resprouting from vegetative organs after fire. In fire-prone Mediterranean ecosystems, the life forms that appeared to be the most responsive to smoke were annuals (Keeley and Bond 1997; Tormo *et al*. 2014) or herbaceous perennials (Brown *et al*. 2003). However, the lack of significant differences in seed properties between the species groups which displayed or did not display enhanced germination in response to smoke does not support the hypothesis (H_2) that smoke-stimulated germination should be associated with specific regeneration-related life history traits. Similar seed shape in the two species groups may possibly be explained by the dual (stimulatory vs. inhibitory) effect of smoke on germination depending on the exposure time and the concentration of smoke solution (Light *et al*. 2002). At low concentration, species having larger seed surface area (i.e. more slender or flatter seeds) may benefit from more contact with smoke-water, but a higher concentration of smoke solution or prolonged exposure to smoke(-water) might cause greater reduction in the germination of such species. Tsuyuzaki and Miyoshi (2009) tested 40 species in a cool temperate zone of northern Japan, and found that the germination of slender seeds diminished more than that of round seeds after exposure to aerosol smoke. In line with our results, in other studies on 18-61 species from fire-prone or fire-free environments there was no relationship between seed mass and the effect of smoke on seed germination percentage (Abella 2009; Daws *et al*. 2007; Tsuyuzaki and Miyoshi 2009). It is possible that other seed traits, such as seed coat thickness (Adkins and Peters 2001) and/or seed dormancy status (for species that require dormancy alleviation before becoming smoke-responsive: e.g. Baker *et al*. 2005) may play more important role in determining the germination response to smoke than seed mass and shape. In our study, a possible explanation for the lack of significant difference in seed bank types between the two germination response groups can be that smoke-responsive species in the Hungarian flora are not typical fire-recruiters with persistent soil-stored seed banks (in contrast to certain fire-prone regions (e.g. Californian chaparral: Keeley 1991; Keeley and Bond 1997), where fire-recruiters are abundant). Irrespective of germination response to smoke, at least 80% of the species with long-term persistent seed banks were weedy, disturbance tolerant native or adventive species. Thus, the tendency for higher frequency of long-term persistence among the smoke-responsive species may be due to the greater proportion of species associated with disturbed habitats in this group (see Figs. 1a and 2c). Consistent with this pattern, Thompson *et al*. (1998) reported higher seed persistence with increasing habitat disturbance for a large set of the north-west European flora.

In conclusion, in this examination of a subset of the Hungarian flora, a few but marked differences in life history and habitat traits between the two species groups differing in germination response to smoke indicate a frequent occurrence of smoke-stimulated germination among annual or biennial, nitrophilous or disturbance tolerant species, which often maintain long-term persistent seed banks. This knowledge can potentially assist in more efficient vegetation restoration (Read *et al*. 2000; Ruthrof *et al*. 2011) or weed control (Adkins and Peters 2001; Dixon *et al*. 2009; Kulkarni *et al*. 2011). Our study also highlights the need for further research involving a greater number of species to confirm our results and make generalizations about the relationships between the germination response to smoke and specific plant traits for the European semiarid temperate flora.

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Appendix A. Germination response to smoke treatment, seed properties, life form and habitat requirements for the species involved in the analysis. Abbreviations: Smoke – seed germination is stimulated (+) or not stimulated (–) by aerosol smoke, smoke-water or karrikinolide treatment; Ref. – literature sources of the species' smoke response data (0 indicates Mojzes and Kalapos unpublished results assessed by the same protocol as described in Mojzes and Kalapos (2014); Var. – the variance of three seed dimensions (length, width and thickness, transformed so that width is unity); TSM (g) – thousand-seed mass expressed in grams; Mass categ. – seed mass category (1: ≤ 0.2 g; 2: 0.21-0.50 g; 3: 0.51-1 g; 4: 1.01-2 g; 5: 2.01-10 g; 6: ≥ 10.01 g); Bank – seed bank type (T: transient; SP: short-term persistent; LP: long-term persistent); Life form – Raunkiaer life form (Th: therophyte; TH: hemitherophyte; H: hemicryptophyte; G: geophyte; Ch: chamaephyte; N: nanophanerophyte; M: microphanerophyte; MM: mega-mesophanerophyte); Habitat – habitat preference (Species preferring natural habitats are unique or rare (U), strictly protected (SP), protected (P), dominant native (DN), accessorial native (AN) and natural pioneer (NP) species. Species associated with disturbed habitats include disturbance tolerant native (DT), adventive (A), cultivated (C) and weed (W) species.); N – nitrogen requirement from 1 (plants on soils extremely poor in mineral nitrogen) to 9 (plants on over-fertilized soils, extremely rich in nitrogen); W – soil moisture requirement from 1 (plants of extreme arid habitats) to 12 (submersed aquatic plants); R – soil reaction requirement from 1 (extremely acidophilic, calcifuge plants) to 9 (calcicole plants, basophilic specialists); T – temperature requirement from 1 (plants of subnival or supraboreal zone) to 9 (plants of the Eumediterranean evergreen zone) and L – light requirement from 1 (full shade plants) to 9 (full-sun plants of open habitats). Nomenclature follows the source published papers. Asterisks indicate species that are not native to Hungary (Király 2009).

Species	Family	Smoke	Ref.	Var.	TSM	Mass categ.	Bank	Life form	Habitat	N	W	R	T	L
Achillea millefolium	Asteraceae	–	12	1.38	0.12	1	T	H	DT	5	6	5	5	8
Alnus glutinosa	Betulaceae	+	8	0.36	1.00	3	SP	MM-M	DN	7	9	6	5	5
*Alopecurus myosuroides**	Poaceae	+	3	1.27	2.05	5		Th	W	7	6	7	6	7
Anagallis arvensis	Primulaceae	+	25	0.15	0.55	3	LP	Th	W	6	4	7	6	6
Angelica sylvestris	Apiaceae	–	3	0.27	1.50	4	LP	H	AN	6	8	6	6	7
Anthriscus caucalis	Apiaceae	+	12	2.17	0.95	3		Th	W	8	5	6	7	7
Anthyllis vulneraria	Fabaceae	–	28	0.22	2.33	5	SP	H	AN	4	4	7	6	8
Aphanes arvensis	Rosaceae	–	12, 13	0.30	0.18	1	LP	Th	W	5	6	5	6	6
Arabidopsis thaliana	Brassicaceae	+	22	0.46	0.02	1	LP	Th-TH	NP	4	4	7	6	6
*Asclepias syriaca**	Apocynaceae	+	0	0.49	5.53	5	LP	H	W	4	4	6	7	7
Astragalus cicer	Fabaceae	–	2	0.20	2.55	5		H	AN	3	4	7	6	7
*Avena barbata**	Poaceae	+	12		11.70	6		Th	W					
Avena fatua	Poaceae	+	3, 9, 11, 19, 30	5.54	30.00	6		Th	W	4	5	7	7	7
*Avena sterilis**	Poaceae	+	3		16.74	6		Th	W					
Briza media	Poaceae	–	29	0.25	0.54	3	T	H	AN	3	6	5	5	8
*Bromus diandrus**	Poaceae	+	19		10.66	6		Th	A	3	2	8	8	8
Bromus sterilis	Poaceae	–	9	27.93	7.80	5	T	Th	W	5	4	6	7	7
Bromus tectorum	Poaceae	–	9	10.93	3.05	5		Th	NP	4	3	8	6	8
Calluna vulgaris	Ericaceae	+	20	4.29	0.04	1	LP	Ch(N)	AN	1	5	1	3	8
Camelina microcarpa	Brassicaceae	+	21	0.12	0.29	2	T	Th	W	4	4	8	6	7
Capsella bursa-pastoris	Brassicaceae	+	9, 21	0.72	0.13	1	LP	Th-TH	W	7	5		6	8
Cardamine hirsuta	Brassicaceae	–	12		0.09	1	LP	Th-TH	DT	7	5	5	6	6
Centaurium erythraea	Gentianaceae	–	23	0.09	0.01	1	SP	Th	AN	5	5	6	6	8
Chamerion angustifolium	Onagraceae	–	1, 32	1.56	0.08	1		H	DT	9	5	5	4	8
Chenopodium album	Amaranthaceae	+	9	0.10	0.90	3	LP	Th	W	7	4	6	6	7

Species	Family	Smoke	Ref.	Var.	TSM	Mass categ.	Bank	Life form	Habitat	N	W	R	T	L
Clematis vitalba	Ranunculaceae	+	8	0.25	1.35	4	SP	N-E	AN	7	5	6	7	7
*Conyza canadensis**	Asteraceae	+	4	1.40	0.05	1	SP	Th-TH	W	4	4	6	6	8
Cynodon dactylon	Poaceae	−	15	0.62	0.34	2		G(H)	DT	5	3	7	7	8
Dactylis glomerata	Poaceae	+	24	6.75	0.88	3	SP	H	DT	6	6	4	5	7
Danthonia decumbens	Poaceae	−	29	1.05	0.87	3		H	AN	2	5	5	5	8
Daucus carota	Apiaceae	+	11	0.40	2.20	5	LP	Th-TH	DT	4	4	7	6	8
Descurainia sophia	Brassicaceae	+	21	0.56	0.12	1		Th	W	6	4	7	6	8
Digitaria ciliaris	Poaceae	−	6		0.59	3		Th	W					
Drosera rotundifolia	Droseraceae	−	32		0.01	1		H	SP	1	9	1	4	8
Echinochloa crus-galli	Poaceae	+	17	0.39	2.00	4		Th	W	8	7	7	7	8
Echium vulgare	Boraginaceae	−	31	0.21	2.95	5		TH	NP	4	3	6	7	9
Epilobium glandulosum	Onagraceae	−	16	0.34	0.07	1		H	AN	5	9	5	7	7
Eragrostis cilianensis	Poaceae	+	25	0.01	0.14	1		Th	W	3	3	6	7	7
Erodium cicutarium	Geraniaceae	−	12, 13	2.52	2.71	5	LP	Th	W	4	4	7	6	8
Euphorbia exigua	Euphorbiaceae	−	31	0.21	0.51	3		Th	W	4	4	8	6	6
Fallopia convolvulus	Polygonaceae	+	3	0.16	4.00	5	LP	Th	W	3	5	5	5	7
Festuca idahoensis	Poaceae	−	5					H	P	2	3	9	3	6
Fraxinus ornus	Oleaceae	−	8	3.75	17.86	6		MM	DN	3	3	8	8	5
Galium aparine	Rubiaceae	+	3	0.02	6.70	5	T	Th	W	9	7	6	5	7
Heracleum sphondylium	Apiaceae	−	3	0.32	6.15	5	T	H	AN	5	5	6	5	5
Holcus lanatus	Poaceae	−	24, 29	1.02	0.34	2	LP	H(Ch)	AN	4	6	6	5	7
Hypericum perforatum	Hypericaceae	−	31	1.02	0.13	1	LP	H	DT	3	3	6	5	7
Hypochoeris radicata	Asteraceae	−	7	22.02	0.55	3	SP	H	AN	3	4	4	5	8
Juncus bufonius	Juncaceae	−	13	0.21	0.03	1	LP	Th	W	6	7	5	5	7
Juncus effusus	Juncaceae	−	32	0.75	0.01	1	LP	H	DT	3	9	6	5	8

Species	Family	Smoke	Ref.	Var.	TSM	Mass categ.	Bank	Life form	Habitat	N	W	R	T	L
Lamium purpureum	Lamiaceae	−	3	0.39	0.75	3	LP	Th(H)	W	6	5	7	5	7
Lathraea squamaria	Orobanchaceae	+	10	0.03	0.64	3		G	AN	6	6	6	5	3
Leontodon saxatilis	Asteraceae	−	12, 13		0.44	2		TH-H	A	5	7	6	7	8
Lepidium campestre	Brassicaceae	+	0	0.33	2.35	5	LP	Th	W	6	4	8	6	9
Linum trigynum	Linaceae	−	31	0.41	0.15	1		Th	NP	1	5	4	7	8
Lotus corniculatus	Fabaceae	−	32	0.06	1.10	4	LP	H	DT	2	4	7	5	7
Malva neglecta	Malvaceae	+	3, 9	0.17	2.30	5	LP	Th-TH	W	9	4	6	6	7
*Matricaria matricarioides**	Asteraceae	−	9	1.02	0.15	1	LP	Th	A	8	4	7	5	8
Melica ciliata	Poaceae	+	28	1.48	0.46	2		H	AN	2	1	7	7	9
Mercurialis annua	Euphorbiaceae	−	3	0.12	2.20	5		Th	W	8	4	7	7	7
*Oenothera biennis**	Onagraceae	−	32	0.30	0.45	2		TH	W	4	3	8	7	9
Orobanche caryophyllacea	Orobanchaceae	+	10			1		G	AN	2	3	9	6	8
Orobanche cernua	Orobanchaceae	+	10		0.15	1		Th-G	W	5	4	7	6	7
Orobanche minor	Orobanchaceae	+	10			1		G	W	6	6	6	8	7
Orobanche purpurea	Orobanchaceae	+	10		0.01	1		G	AN	2	3	8	7	8
Orobanche ramosa	Orobanchaceae	+	10	0.14	0.02	1		Th-G	W	6	4	7	8	7
Papaver rhoeas	Papaveraceae	+	9	0.27	0.09	1	LP	Th	W	4	4	7	7	6
*Pinus nigra**	Pinaceae	−	26	0.46	20.60	6		MM	C	2	4	9	8	7
Pinus sylvestris	Pinaceae	−	26	0.89	5.50	5		MM	AN(C)	2	4	5	4	7
Plantago lanceolata	Plantaginaceae	+	21	0.50	1.25	4	LP	H	DT(AN)	5	4	6	5	7
Plantago media	Plantaginaceae	−	21	0.49	0.26	2		H	DT	3	5	7	5	7
Poa annua	Poaceae	+	13	2.16	0.27	2	LP	Th-TH	W	8	6	6	5	7
Polygonum aviculare	Polygonaceae	+	3		1.70	4	LP	Th	W	5	4	6	5	9
Polygonum persicaria	Polygonaceae	+	3	0.24	1.60	4	LP	Th	W	7	7	6	5	6
Potentilla recta	Rosaceae	−	0	0.21	0.40	2	SP	H	AN	1	3	7	8	9

Species	Family	Smoke	Ref.	Var.	TSM	Mass categ.	Bank	Life form	Habitat	N	W	R	T	L
Quercus robur	Fagaceae	−	27	0.33	2500.00	6	T	MM-M	DN	4	6	6	6	6
Raphanus raphanistrum	Brassicaceae	+	18, 30	0.09	13.60	6	LP	Th	W	5	5	5	5	6
Rubus caesius	Rosaceae	−	33	0.55	3.40	5	SP	H-N	DT	9	7	7	5	7
*Rudbeckia hirta**	Asteraceae	−	16	2.26	0.39	2		Th-TH	C	5	8	8	7	8
Rumex acetosella	Polygonaceae	−	14, 32	0.02	0.35	2	LP	H(G)	AN	2	2	4	5	8
Rumex obtusifolius	Polygonaceae	−	9	0.08	2.20	5	LP	H	DT	9	6	7	5	7
Senecio jacobaea	Asteraceae	+	9, 24	1.56	0.22	2	LP	H	AN	5	3	7	5	8
Sherardia arvensis	Rubiaceae	−	31	0.44	1.95	4	SP	Th	W	5	5	8	6	6
*Sinapis alba**	Brassicaceae	+	9	0.01	3.95	5		Th	W	6	4	8	7	8
Sinapis arvensis	Brassicaceae	–	3	0.00	2.10	5	LP	Th	W	6	4	8	5	7
Sisymbrium orientale	Brassicaceae	+	18, 30, 0	0.68	0.12	1		Th-TH	W	6	5	7	8	8
Solanum nigrum	Solanaceae	−	25	0.36	0.90	3		Th	W	8	6	7	6	7
Solidago virgaurea	Asteraceae	−	32	2.86	0.61	3	T	H	AN	5	5	6	5	5
Sonchus oleraceus	Asteraceae	+	7	1.91	0.25	2	LP	Th	W	8	5	8	5	7
*Sorghum halepense**	Poaceae	+	3, 9	1.40	4.50	5		G(H)	C	7	6	7	8	7
Stellaria media	Caryophyllaceae	+	9	0.04	0.45	2	LP	Th-TH	W	8	5	7	5	6
Taeniatherum caput-medusae	Poaceae	−	5	5.75	2.96	5		Th	NP	2	2	8	8	9
Thlaspi montanum	Brassicaceae	–	1	0.20	0.65	3		Ch	U	2	2	9	5	8
Urtica urens	Urticaceae	−	12	0.36	0.50	2	LP	Th	W	8	5	6	6	7
Veronica hederifolia	Plantaginaceae	+	3	0.13	3.55	5	LP	Th	DT	7	4	7	6	6
*Veronica persica**	Plantaginaceae	+	3	0.18	0.69	3	LP	Th	W	7	5	7	6	6
Vulpia bromoides	Poaceae	−	7, 12, 13	17.21	0.80	3	T	Th	NP	2	2	3	8	9

Appendix B. List of studies cited in Appendix A.

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