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Fire effects on germination response of the native species *Daucus carota* and the invasive alien species *Helichrysum foetidum* and *Oenothera glazioviana*

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A B S T R A C T

Fire is an ecological factor that affects ecosystem structure and functioning and determines later recovery of the ecosystem through the modification of biological processes, such as seed germination and seedling establishment. Another factor that modifies ecosystems is the presence of invasive alien species, which easily colonize new habitats after disturbances such as forest fires. Within this research, we analysed the germination response to fire of three species that share a habitat, one native species (*Daucus carota* L.) and two invasive alien species (*Helichrysum foetidum* (L.) Moench and *Oenothera glazioviana* Micheli) to identify and compare the effects of fire on the germination of these three species. For this purpose, germination tests were performed by using seeds treated with heat, smoke, charcoal and ash, simulating conditions of forest fires.

The three species showed slightly different responses to fire factors. At high levels, heat and ash prevented the germination of the three species. In contrast, intermediate heat shocks and some smoke treatments stimulated *O. glazioviana* germination, while the other species remained unaffected. *H. foetidum* presented high germination success for most treatments. The difference in the germination response of the three species can change the current balance among three species in natural fire-prone ecosystems, contributing to the spread of *O. glazioviana* and *H. foetidum* to new areas and potentially reducing native *D. carota* populations.

1. Introduction

Fires and alien species invasion are two of the main environmental factors affecting both natural and managed ecosystems (Mack and D'Antonio, 1998; Keeley, 2006; Baeza et al., 2007), particularly in the recent decades. Fire has played an important role in ecosystems due to its influence on species' evolution processes (Trabaud, 1992) and has been present in many ecosystems on Earth for millennia (Pausas, 2004; Keeley et al., 2011). Because of climate change, fire recurrence and intensity are increasing, burning millions of hectares every year, affecting ecosystems and human populations (Pausas, 2004).

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Fires are increasing in savanna and grassland, primarily in the tropics but also in temperate regions (Flanningan et al., 2009). In southern Europe, the area burned has increased as a result of changes in agricultural policy causing rural exodus and the establishment of forest and shrubland on abandoned land (Mouillot and Field, 2005). In Europe, the northwest of the Iberian Peninsula is the region with the highest forest fire activity (San-Miguel-Ayanz et al., 2012). In Galicia (northwest of the Iberian Peninsula), during the decade 2001–2010, forest fires burned 288,732.10 ha of shrublands and forests (Cubo et al., 2012), which is more than 25% of the total forest area of the region. In addition, both intensity and recurrence of fires are expected to increase due to climate change and land-use change (IPCC. 2014), which will also favour the colonization of non-native plants (Thuiller et al., 2008; Wang et al., 2017).

In fire-prone ecosystems, fire has shaped plant traits, and some species present adaptations to fire, such as resprouting, serotinity or heat-shock triggered germination (Keeley et al., 2011). Fire modifies plant communities by reducing or completely removing aboveground vegetation, leaving open gaps where the same or new species can establish. Fires often affect seed germination and determine establishment of seedlings (Guthrie et al., 2016). Some invasive species are able to establish themselves in ecosystems affected by fire (Hulme et al., 2007; García-Duro et al., 2019), usually due to their quick germination (Arán et al., 2013) and/or to the stimulation of their seeds by fire factors (Arán et al., 2017; Cruz et al., 2017).

Invasive alien species affect the recovery of native species after fire because the invasive species are usually strong competitors (Levine et al., 2003; Hager, 2004), driving reductions of the area occupied by native species. In fact, 80% of threatened species around the world are at risk due to competition caused by invasive species (Pimentel et al., 2005). On the global scale, the presence of non-native invasive species in local ecosystems has substantial negative economic and environmental impacts (Pimentel et al., 2005).

A high proportion of coastal areas in Galicia are protected under the Natura 2000 Network and include several natural ecosystems and priority habitats included in the EU Habitats Directive (Council Directive 92/43/EEC, 1992). In these habitats, together with other similar endemic species, we find *Daucus carota* L. (Apiaceae), a widespread species of wild carrot present throughout the Galician territory (Castroviejo, 1986–2015) and native to Europe, temperate Asia and northern Africa. In exotic environments, such as the western Oregon Upland Prairies, burning favours the establishment of this species (Maret and Wilson, 2005). *D. carota* is of importance due to the possibility of this species harbouring genes for carrot improvement, which is why *D. carota* has been included in Annex I of the International Treaty on Plant Genetic Resources for Food and Agriculture (Collett et al., 2011).

Commonly sharing habitat with this native species are *Helichrysum foetidum* (L) Moench (Asteraceae) and *Oenothera glazioviana* Micheli (Onagraceae), two alien species that have invaded forest and agricultural lands (Fagúndez and Barrada, 2007).

H. foetidum is native to South Africa, was introduced in Galicia as an ornamental species and is naturalized in littoral areas (Guitián et al., 1988). In fynbos, this species is a fire ephemeral and presents low germination, but it can be enhanced by fire (Brown et al., 2003).

The *Oenothera* genus is native to America, but *O. glazioviana* arose in central Europe by hybridization (Castroviejo, 1986–2015). Currently, this species is present all over the world due to its high potential for invasion (Mihulka and Pyšek, 2001). *O. glazioviana* also has a coastal distribution in Galicia (Castroviejo, 1986–2015), but it is even more generalist than *H. foetidum* and tends to establish in altered environments. The three species are biennial forbs, have dormant seeds and form soil seeds banks (Baskin and Baskin, 1994; Teketay, 1997; Brown et el., 2003; Clark and Wilson, 2003; Maret and Wilson, 2005). *O. glazioviana* is the only one of the three species studied that has seeds with hard coats. Indeed, the habitats that the three species occupy are often affected by fire, which might provide the suitable environment for these species to establish and maintain their populations (Thuiller et al., 2008; Wang et al., 2017). Furthermore, associated with a high recurrence of fire, there is a risk that the invasive species outcompete native ones. Heat, ash, charcoal and smoke produced during forest fires exert notable effects on the germination of many species. Moderate heat may stimulate germination of some species, and high heat may inhibit germination in many species (Keeley, 1987; Rivas et al., 2006; Herrero et al., 2007). Ash produced during forest fires modifies germination of many species, and in some cases, large concentrations of ash inhibit germination (Reyes and Casal, 2004; Kemball et al., 2010). Charcoal can have stimulating or neutral effects (Keeley and Fotheringham, 2000; Reyes et al., 2015b) on seeds germination. In species from the Mediterranean basin, smoke stimulate germination (Çatav et al., 2014) not modify it (Reyes and Trabaud, 2009; Reyes et al., 2015a) or even inhibit it (Ne'eman et al., 2012). These four fire factors can enhance or reduce the germination of some plant species, leading to a very different colonization of the space after the occurrence of a fire.

Understanding the germination response to fire invasive alien species is important to manage them properly because these species currently share habitat with native species, such as *D. carota*, that could be displaced from their natural habitat. For these reasons, this study has been carried out with the following objective: to analyse the effects of fire through its main factors (heat, smoke, ash and charcoal) on *D. carota, H. foetidum* and *O. glazioviana*.

2. Material and methods

To identify differences in the germination response of *D. carota, H. foetidum* and *O. glazioviana* to fire factors and to determine whether their germination response is related to being or not an invasive species, we conducted a series of germination tests consisting of 18 treatments. Different levels of the main fire factors (heat, charcoal, ash and smoke) were tested.

Seeds of the three different species were collected during the seed dispersal season, in summer 2015, from natural populations in an area close to the Natura 2000 site Carnota-Monte Pindo (42°53′15″N 9°08′06″W), in W Galicia. The seeds were taken from at least 30 individuals of each species in order to cover the environmental and genetic diversity of the population, and the seeds were stored in open paper bags under laboratory conditions (21 °C and <70% RH) until the beginning of the germination tests (2 months later). The microclimate of Carnota-Monte Pindo does not present frosts, and therefore, the seeds were not vernalized.

In addition to the control, seventeen fire treatments were performed following previous studies (Cruz et al., 2017): eight heat treatments (80°C-5 min, 80°C-10 min, 110°C-5 min, 110°C-10 min, 150°C-5 min, 150°C-10 min, 200°C-5 min, 200°C-10 min), one charcoal treatment (0.26 g/Petri dish, the equivalent of 411 kg/ha), five ash treatments (Ash1: 0.027 g/Petri dish ≈ 43.5 kg/ha, Ash2: 0.055 g/Petri dish ≈ 87 kg/ha, Ash3: 0.110 g/Petri dish ≈ 174 kg/ha, Ash4: 0.275 g/Petri dish ≈ 435 kg/ha, Ash5: 0.550 g/Petri dish ≈ 870 kg/ha) and three smoke treatments (Smoke-5 min, Smoke-10 min, Smoke-15 min).

A forced-air oven was used to apply the heat shocks; the selected temperatures corresponded with the most likely temperatures and time in the soil surface layer (0–5 cm depth) in forest fires (Salgado et al., 1995).

Charcoal, ash and smoke were obtained from burning twigs and branches of *Ulex europaeus* L., which is one of the predominant species in Galician ecosystems. The amount of ash used was based on the quantities of ash per hectare measured by Soto et al. (1997) in fires of moderate intensity in Galicia. The amount of charcoal was selected based on the quantity recorded in experimental forest fires in Scandinavia (Ohlson and Tryterud, 2000). Ashes were separated with a 0.4 mm sieve and charcoal with a 2.4 mm sieve. Smoke treatments were performed by direct exposure of the seeds to aerosol smoke-saturation conditions using the "Fume 2000" smoke applicator (Reyes and Trabaud, 2009; Reyes et al., 2015b) based on the methodology proposed by de Lange and Boucher (1990). Smoke was generated by burning aerial parts of *Ulex europaeus* L., a shrub species often associated with the 3 studied species in the northwest of the Iberian Peninsula. Seeds placed in Petri dishes were introduced into a smoke-saturated fabric chamber and were maintained in these conditions for 5, 10 or 15 min. These treatments coincide with those tested by other authors in fire-prone areas (Keeley and Fotheringham, 1998; Thomas et al., 2010).

For each treatment, 5 replicates of 25 seeds were made. Each replicate was placed in a 9 cm diameter Petri dish, using cellulose filter paper as substrate. At the beginning of the experiment, 4 mL of distilled water was added to each replicate; subsequently, seeds were evaluated three times a week, and on those days, more water was added to keep seeds moist.

Seed incubation was performed in a germination chamber. Following other studies (Reyes et al., 2015a; Cruz et al., 2017), the thermo-photoperiod was 16 h of light at 24 °C and 8 h of darkness at 16 °C, simulating the favourable conditions during the germination period for these species (spring). Germination was checked three times every week for 35 days. A seed was considered to have germinated when it showed a visible radicle. The data obtained were used to calculate the average germination percentage and the distribution of germination over time.

The differences in germination percentage were tested using linear mixed models because they are an extension of simple linear models for data that involve random effects, such as non-independent, multilevel/hierarchical, longitudinal, or correlated data. The model tested here accounts for the intensity level, nested within the corresponding fire factors. A posteriori HSD Tukey tests were performed to compare each treatment to the control within each species. Also, treatments were compared across species. Those analyses were performed in R, with the lme4 (Bates et al., 2015) and multcomp (Hothorn et al., 2008) packages.

3. Results

3.1. Germination percentage

The germination percentage varied depending on the species and treatment (Fig. 1). Statistical analysis detected highly significant differences ($p < 0.001$) between the control and some fire factors in the three species. The value of control germination reached by the native species, *D. carota,* was 34.4% (Fig. 1a), and the values reached by the invasive species were 77.6% in *H. foetidum* (Fig. 1b) and 12.0% in *O. glazioviana* (Fig. 1c), being significatively different ($p < 0.005$).

Moderate heat treatments (80ºC-5 min and 80ºC-10 min) significantly stimulated the germination of *O. glazioviana* reaching 35.2% and 31.2% (Fig. 1c), respectively, while they did not modify the germination of *D. carota* and *H. foetidum* (Fig. 1a and b). With intermediate heat treatments (110ºC-5 min and 110ºC-10 min), *D. carota* experienced significant reductions in germination (12.8% and 9.6%, Fig. 1a), *H. foetidum* was not modified (Fig. 1b), and *O. glazioviana* increased its germination (79.2% and 73.2%, Fig. 1c) 6-fold higher than its control germination. High-intensity heat (150ºC-5 min, 150ºC-10 min, 200ºC-5 min, 200ºC-10 min) completely inhibited germination (Fig. 1a, b, c).

Charcoal treatment did not modify the germination percentage in any of the three species studied. Ash treatments tended to reduce the germination of the three species as the ash concentration increased, to the point that Ash4 and Ash5 completely inhibited germination for all species (Fig. 1a, b, c). In addition, Ash2 significantly reduced the germination of *H. foetidum* (40.8%, Fig. 1b), and Ash3 reduced the germination of *D. carota* to 11.2% and *H. foetidum* to 8.8% (Fig. 1a and b). Smoke treatments did not alter the germination of *D. carota* and *H. foetidum*; however, low- and high-exposure treatments (Smoke-5 min and Smoke-15 min) strongly stimulated the germination of *O. glazioviana*, in contrast to the intermediate exposure treatment (Smoke-10 min), which maintained germination values close to the control (Fig. 1c).

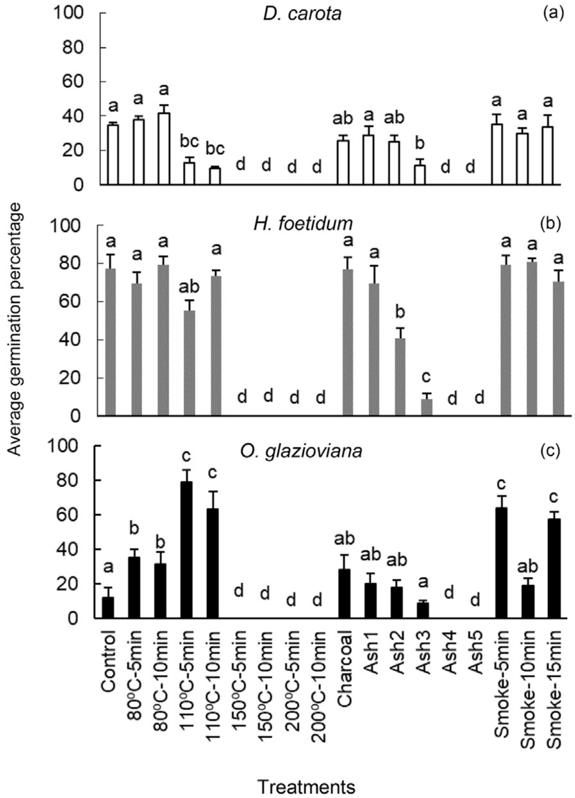

Fig. 1. Average germination percentage ($\overline{x}$±SEM) for seeds of *D. carota* (a), *O. glazioviana* (b) and *H. foetidum* (c). Different labels over the bars for each species indicate significant differences in the HSD Tukey test performed between the control and fire treatments.

In summary, none of the fire treatments stimulated *D. carot*a and *H. foetidum* seed germination, but heat (moderate and intermediate levels) and smoke enhanced the germination of *O. glazioviana*. Charcoal did not modify the germination of the three species, and ash produced significant reductions in germination as the ash concentration increased. The seed germination of the three species was inhibited at high levels of heat and ash.

3.2. Temporal distribution of germination

D. carota showed a regular pattern of germination over time, with high percentage of germination after the eighth day after sowing (Fig. 2a). Control germination started on the third day and progressed gradually until the twentieth day; afterwards, germination declined and became sporadic. In the charcoal and ash treatments, germination was slower and remained low until the end of the experiment. The smoke and moderate heat treatments followed a similar pattern to the control.

In *H. foetidum* the seed control germination was markedly high and early, concentrated between the third and tenth post-sowing day, after which almost all the seeds had germinated (Fig. 2 b). A delay of germination was observed in seeds treated with 110ºC-5 min, 110ºC-10 min, Ash2 and Ash3, whose germination did not begin until the sixth day. The moderate heat, charcoal, Ash1 and smoke treatments were similar to the control.

The vast majority of seeds from *O. glazioviana* germinated during a short period of time. Most of the treatments started germination on the sixth day after sowing and ended before 15 days. Some late sporadic germination occurred in seeds treated with charcoal and ash, whose germination was lower but extended over time.

4. Discussion

Fire affects the germination response of the native species *D. carota* and invasive alien species *H. foetidum* and *O. glazioviana* in different ways. Heat treatments under 110ºC-10 min stimulated *O. glazioviana* germination. This stimulation is a common effect of fire on species with hard-coated seeds (Keeley and Fotheringham, 2000; Herrero et al., 2007; Reyes and Trabaud, 2009), such as those of *O. glazioviana*. The stimulation of seed germination by heat is usually due to the seed coat melting or cracking caused by high temperatures (Kamal and Behere, 2002) that make the seed coats permeable to both water and oxygen, breaking the exogenous dormancy (Keeley, 1987; Keeley and Fotheringham, 2000). However, after cracking

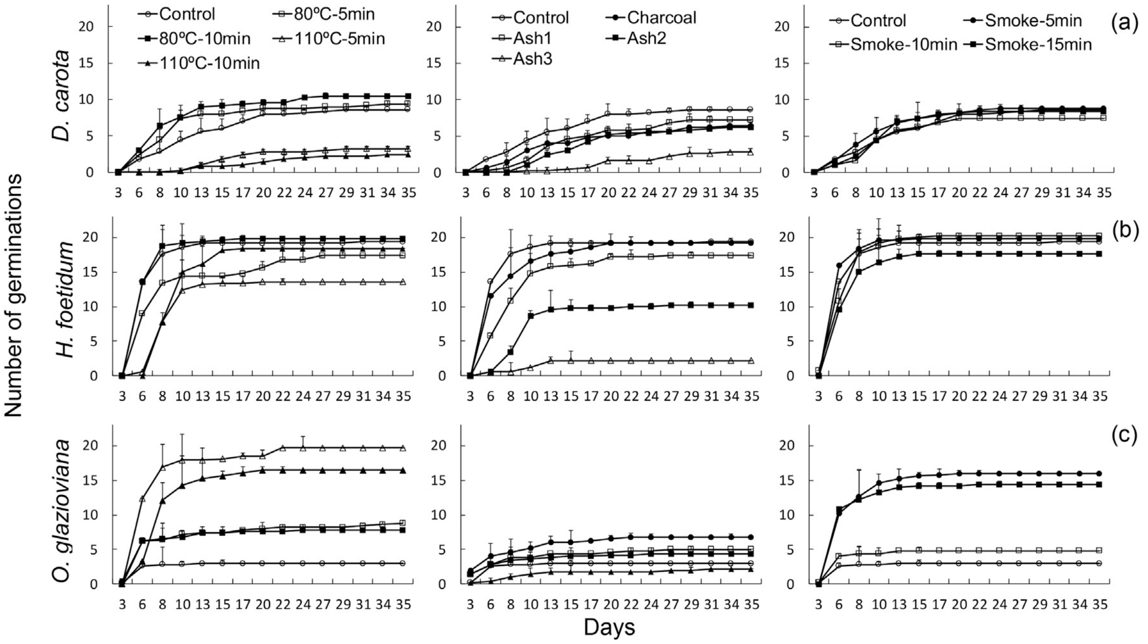

Fig. 2. Temporal distribution of germination + SD of *D. carota* (a), *H. foetidum* (b) and *O. glazioviana* (c) in treatments without total suppression of germination.

the seed coats, high temperatures can damage the embryo, making germination impossible. Previous works demonstrate that the balance among both processes can trigger a massive post-fire germination in different species (Herrero et al., 2007; Arán et al., 2017; García-Duro et al., 2019). Regarding our three species, the relatively low germination of the native species *D. carota* under low and intermediate heat shocks contrasts with the high *H. foetidum* germination and the stimulation of *O. glazioviana* germination, making both invasive alien species more likely to succeed in fire-prone environments under these specific conditions. High temperatures above 110ºC-10 min totally prevent germination of three species.

Other studies link charcoal addition to increased germination (Keeley and Fotheringham, 2000). We did not find any effect on the germination response of native or invasive alien species; perhaps the effects of charcoal depend on the type of the burned material and hence are strongly related to the target species' native or alien status (Reyes et al., 2015b; García-Duro et al., 2019).

In contrast to charcoal, ash had a significantly negative impact on the germination of the three species, *H. foetidum* being the most sensitive one. The decreased germination associated with ash addition has already been found in other species (Reyes and Casal, 2004; Kemball et al., 2010; Cruz et al., 2017), and it is likely caused by the increase of the osmotic pressure induced by ashes, according to González-Rabanal and Casal (1995). Although large quantities of ash prevented any germination in all three studied species, *H. foetidum* also showed a strong decrease in germination under low-intermediate ash quantities. However, despite those negative effects, *H. foetidum* overall germination success remained higher than *D. carota* germination. Hence, alien species are supposed to be strong competitors to *D. carota* and other native species in post-fire burned environments.

The influence of smoke components on seed germination has been widely studied, and the majority of the identified smoke-stimulated species are native to the Mediterranean ecosystems across the world (Keeley and Pausas, 2018). *H. foetidum* in South African fynbos presents low germination in control treatments and reacts positively to smoke (Brown et al., 2003). However, those stimulating effects were not displayed by *H. foetidum* in southwest Europe, probably due to its high germination in our control tests. The other alien species, *O. glazioviana*, showed a positive response to smoke exposure, similar to other species of cosmopolitan distribution (Keeley and Fotheringham, 2000). *O. glazioviana* germination was almost 6-fold greater than the control in some treatments. According to Baskin and Baskin (1994), species of the genus *Oenothera* usually have physiological dormancy, so the stimulation of germination by smoke is likely due to active compounds of the smoke, such as 3-methyl-2H-furo[2,3-c]pyran-2-one (Flematti et al., 2004; van Staden et al., 2004), which might act in the same way as other chemical stimuli that break the seed dormancy (Gardner et al., 2001). In contrast, smoke did not change the germination response of the native species *D. carota*. Similar results were found in studies conducted by Rivas et al. (2006) in native species of the Euro Siberian flora, and these findings suggest that the native or alien origin might have an influence on seed germination, contributing to the success of invasive alien species.

The time required for germination of the three species is short. A short germination period can be a very important ecological advantage when colonizing an empty space (Grime, 2006; Arán et al., 2013); however, the germination time is similar for the three species, and the small differences are not expected to have a strong influence on their recruitment and the success of their populations in the study area. Severe heat and ash treatments tend to slightly increase the time required for germination, and the length of this period seems to grow proportionally to the intensity of the treatment.

In the absence of fire, the native species *D. carota* and the invasive alien species *H. foetidum* and *O. glazioviana* had substantially different germination percentage, characteristic acquired throughout evolution in very different environments (Castroviejo, 1986–2015; Guitián et al., 1988). In addition, these species also showed slightly different germination responses after fire that can be related to the characteristics of their native ecosystems; thus, their native or alien origin might have strong consequences on their success in burned environments. In any case, the three species germinate quickly, a common trait of opportunistic or ruderal species (Grime, 2006), and the main differences are not associated with the length of the germination period but to the amount of seeds that germinate.

From the analysis of the germination response, it can be concluded that *H. foetidum* will quickly colonize burned environments due to its early germination, high germination success, and the relatively small effect of fire factors on its germination. This conclusion is also valid for *O. glazioviana*, which in addition to having a large seed bank, is stimulated by some fire factors such as smoke and heat, contributing to the spreading and maintenance of their populations in fire-prone ecosystems and burned environments in general. In contrast, the overall germination response of *D. carota* is affected more negatively by fire than these two invasive alien species, showing a lower post-fire germination response due to inhibition by several factors. More work is needed to analyse the establishment of the seedlings and the competition between them in fire-prone environments to know with certainty the post-fire success of the populations of these three species; however, these results suggest that the invasive alien species would occupy the empty space created after fire faster than *D. carota*, and as a collateral consequence, fires would contribute directly or indirectly to endangering the native populations of *D. carota* and its gene bank.

Declarations of interest

None.

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