



Fire and seed maturity drive the viability, dormancy, and germination of two invasive species: *Acacia longifolia* (Andrews) Willd. and *Acacia mearnsii* De Wild

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Abstract

• **Key message** *Acacia longifolia* and *Acacia mearnsii* exhibit different reproductive behavior (viability, germination, and dormancy) in relation to fire and seed maturation. The potential of invasion of *A. longifolia* is stronger than that of *A. mearnsii*. *A. longifolia* germinates abundantly between fires and after fires, while *A. mearnsii* only germinates after fire and needs higher thermal thresholds to break dormancy.

• **Context** Fire affects environments through the modification of biological processes such as seed viability, dormancy, and germination. Seed maturation stage can modulate seed response to fire. Invasive alien species could be enhanced by forest fires.

• **Aims** To analyze the viability, germination, and dormancy of two invasive alien species (*Acacia longifolia* and *Acacia mearnsii*) in relation to fire and seed maturation.

• **Methods** Viability of seeds was obtained performing a tetrazolium test. Additionally, we obtained germination and dormancy in mature and fresh seeds simulating fire conditions through different levels of fire factors (smoke, ash, charcoal, and heat).

• **Results** Control viability of seeds was 100% in the two *Acacia* species and maturation stages and severe heat reduced it to zero. Germination of *A. longifolia* varied depending on the maturation stage, being higher in fresh seeds. In *A. mearnsii*, germination did not change with maturation. In both species, heat stimulated germination by breaking seed dormancy. Seed maturation stage and fire factors affect the germination speed of each species differently.

• **Conclusion** Fire reduces viability, stimulates germination, and breaks dormancy of the two species. Seed maturity exerts notable effects on *A. longifolia* reproductive behavior.

Keywords Invasive alien species · Seed maturation · Germination · Fire factors · Seed dormancy · *Acacia*

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1 Introduction

Forest fires are one of the main environmental factors affecting natural and seminatural populations worldwide. They occur around the world causing economic losses in forestry and endangering biodiversity. Furthermore, there are indications that climate change, with the increase of global temperature, will also increase fire frequency and magnitude (IPCC 2013).

Fire also plays an important role shaping plant communities in many ways, driving their diversity (He et al. 2019), shaping plant traits (Keeley et al. 2011), creating open gaps, and modifying the dormancy and germination of many species (Auld and O'Connell 1991; Reyes and Casal 2008). Fire and summer temperatures work together breaking seed dormancy (Luna 2020), opening the possibility for new species to establish in natural communities or even become dominant. Since germination is the most critical stage in the life cycle of many plants, the influence of fire on seed dormancy breaking and germination may be decisive for the establishment of native (Reyes et al. 2000) and invasive alien species (IAS) (Arán et al. 2017). The ecological advantage of the non-dormant phase is that seeds can germinate abundantly in favorable conditions and establish large populations quickly.

Another factor that affects viability (a viable seed is one which is capable of germination under suitable conditions; Bradbeer 1988), dormancy, and germination of some species is the seeds' maturation stage (El-Keblawy and Al-Ansari 2000). In this work, we understand maturation as the set of physiological processes that occur in post-dispersal seeds. In some species, seed maturation is a strategy related with dormancy so that the ecological sense of the maturation phase is to prevent seed germination immediately after dispersion and preserve them until environmental conditions are favorable to the establishment of seedlings. Viability and dormancy of some species either remain constant for many years or vary during the first year of maturation (Orscheg and Enright 2011). Seed maturation can interact with fire and/or with summer temperatures (Luna 2020) by modulating the dormancy and germination response to fire (Reyes and Casal 2001; Ooi 2010). Specifically, Arán et al. (2017) found that 2-year-old *Acacia melanoxylon* R. Br. seeds slightly increased germination compared with fresh seeds and that the seeds of the soil bank (many years of maturation) were mainly dormant seeds whose germination was stimulated by high fire temperatures, and García-Duro et al. (2019) found great modifications of the viability, dormancy, and germination of *Paraserianthes lophanta* (Willd.) I.C. Nielsen due to fire.

Fire and seed maturity are relevant for the expansion of IAS (García-Duro et al. 2019). Some of the more proliferous IAS in Europe belong to *Acacia* genus (Lorenzo et al. 2009). According to many studies, acacias endanger many natural

habitats (Sanz-Elorza et al. 2004; Adair 2008; Vicente et al. 2013). *Acacia* species have been reported to cause major structural changes in the areas they invade due to the accumulation of biomass and litter (Gaertner et al. 2011), which may increase the occurrence and intensity of forest fires. *Acacia* is a cosmopolitan genus native to Australia, which has been introduced in many areas around the world (Bennet 2014). Some of its species has become invasive, threatening native flora and ecosystems, particularly Mediterranean ones (Souza-Alonso et al. 2017).

Many IAS have their seed dormancy broken and are stimulated to germinate (Riveiro et al. 2019). Particularly, heat shocks generated during fires are reported to have an important role releasing seed dormancy of *Acacia* species (Arán et al. 2013; Ooi et al. 2014; Cruz et al. 2017). Seeds from Australian *Acacia* seed banks are generally 85% viable (Milton 1980; Arán et al. 2017) and may remain dormant for 50 years or more (Holmes 1989; Leino and Edqvist 2010). Since fire may eliminate native seeds from the surface layer, stimulation of germination of seeds from soil seed bank by fire could cause a massive germination event of acacias. Marchante et al. (2008) observed a large-scale invasion of *Acacia longifolia* (Andrews) Willd. after a fire occurrence in Portugal.

The first stages of invasion are critical in IAS, since the actions for control and/or eradication are more cost-effective. When a species becomes established, it is difficult and unlikely to eradicate (Genovesi 2005; Hulme 2012). We chose two invasive *Acacia* species in Europe: *A. longifolia* and *Acacia mearnsii* De Wild., (Sanz-Elorza et al. 2004) at initial stages of invasion (Reyes et al. 2018).

A. mearnsii has been recorded in 4 European countries (Portugal, Spain, France and Italy); and *A. longifolia* has been recorded in 5 European countries (Portugal, Spain, France, Italy, Greece), according to GBIF (GBIF Backbone Taxonomy 2020). In contrast, other invasive acacias (i.e., *Acacia dealbata* Link) have been recorded in many European countries, and the number of records is much higher. They are listed in "100 world's worst invasive alien species" and "100 of the most invasive alien species in Europe" (ISSG 2017; Nentwig et al. 2017; DAISIE 2008). They are possibly at risk of expanding to other European countries due to their invasive potential. Looking further into the reproductive behavior of these IAS will allow for the implementation of efficient control measures to properly manage them.

In order to obtain more information about the potential of expansion of the two wattles, we have set the following objectives: (i) to determine the viability of *A. longifolia* and *A. mearnsii* seeds before and after fire, (ii) to test fire factor effects on the dormancy and germination of seeds of *A. longifolia* and *A. mearnsii* (iii) to know the interaction between seed maturation and fire factors in seed dormancy and germination.

2 Material and methods

Seeds of both *Acacia* species were collected during the seed dispersal period from naturalized populations of approximately 7–8 years old in 2017 in Galicia (southwestern Europe) placed in forests in the municipality of Padrón (location provided by Mouriño, J. in personal communication). Seeds were collected in two consecutive years and stored in open paper bags under laboratory conditions until the beginning of the tests. Therefore, there were two seed lots from each species: fresh seeds (collected in 2017) and mature seeds (collected in 2016, hence 1 year of maturation in laboratory conditions).

Seed viability was determined conducting a tetrazolium viability test (Calvo et al. 2015) with untreated seeds from each species and maturation stage. At the end of the experiment, a posteriori viability test based on the consistency of the seeds was conducted; soft seeds were considered dead, and seeds which maintained their hardness were considered still viable.

A control test was performed to simulate unburnt conditions, and a scarification test was carried out to simulate the ideal germination conditions of species with physical dormancy. The scarification performed was mechanical, cutting the seed coat at the distal end of the seed.

In order to know if there was a difference between the germination response of *A. longifolia* and *A. mearnsii* to fire factors and to determine if the seed maturation affected this response, a series of germination tests was conducted. Different levels of the main fire factors (heat, charcoal, ash, and smoke) were tested.

In addition to the control and scarification treatment, 15 fire treatments were performed following previous studies (García-Duro et al. 2019; Riveiro et al. 2019): 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), three ash treatments (ash-low, 0.110 g/Petri dish \approx 74 kg/ha; ash-medium, 0.275 g/Petri dish \approx 435 kg/ha; ash-high, 0.550 g/Petri dish \approx 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 each *Acacia* species, since they tend to form single-species woodlands. 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). Seeds placed in Petri dishes were introduced into a smoke-saturated fabric chamber and were kept 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 2000; Thomas et al. 2009).

For each treatment, 5 replicates of 25 seeds were made. Each replicate was placed on a 9-cm diameter Petri dish, using cellulose filter paper as substrate. At the beginning of the test, 4 ml of distilled water was added to each replicate; subsequently, seeds were evaluated three times a week for 3 months. On those days, more water was added to keep seeds moist, and seeds which had germinated (visible radicle) were removed from the Petri dish.

Seed incubation was performed in a germination chamber, which allows control of light and temperature conditions. Following other studies (Reyes et al. 2015a; Cruz et al. 2019), the thermo-photoperiod was 16 h of light at 24 °C and 8 h of darkness at 16 °C, simulating favorable conditions for germination.

The data obtained were used to calculate the pre- and post-average viability percentage, the average germination percentage, the average dormancy percentage, the speed of germination as T_{50} (it measures germination speed as the time required by seeds to reach 50% of final germination) and the distribution of germination over time. Those seeds that at the end of the experiment were viable but had not germinated were considered dormant seeds.

General linear models (GLM) at a significance level of 0.05 were carried out to test the effects of fire factors and seed maturity on dormancy, germination percentage, and T_{50} . Only treatments with 3 replicates or more over 0% germination were used for the T_{50} analysis. A posteriori HSD Tukey tests were performed to compare each treatment with the control within each species and maturation stage. Those analyses were performed in IBM SPSS Statistics 24.

3 Results

3.1 Seed viability

The tetrazolium tests showed a viability of 100% in both maturity stages in the two *Acacia* species. The scarification performed to seeds from the two *Acacia* species and maturation stages showed a clear response, 100% of the seeds germinated (Table 1). These results were supported by the previous tetrazolium viability test performed to the seeds.

The posteriori viability test showed that despite the lower germination ratios in most of the treatments, seeds

Table 1 Average germination percentage ($\times \pm$ SD) and T_{50} ($\times \pm$ SD) for mature and fresh seeds of *A. longifolia* and *A. mearnsii* in scarification treatment. Different labels indicate significant differences in the HSD Tukey test performed between maturation stages for germination percentage and T_{50} (days)

Scarification		Germination %	T_{50}
<i>A. longifolia</i>	Mature	100 \pm 0 ^a	3.6 \pm 0.9 ^b
	Fresh	100 \pm 0 ^a	3.0 \pm 0 ^b
<i>A. mearnsii</i>	Mature	100 \pm 0 ^a	3.0 \pm 0 ^b
	Fresh	100 \pm 0 ^a	3.0 \pm 0 ^b

were still viable at the end of the experiment (Fig. 1). In *A. longifolia*, with moderate (80 °C, 5 min; 80 °C, 10 min) and intermediate (110 °C, 5 min; 110 °C, 10 min) heat treatments, almost all the viable seeds had germinated (Fig. 2); the seeds that did not germinate had lost their viability. Extreme heat shocks (150 °C, 5 min; 150 °C, 10 min; 200 °C, 5 min; 200 °C, 10 min) suppressed the viability of the seeds, making them incapable of germination.

In *A. mearnsii* mature seeds, a small decrease in viability was observed with 110 °C, 10 min (Fig. 1). Extreme heat shock (150 °C, 5 min; 150 °C, 10 min, 200 °C, 5 min; 200 °C, 10 min) reduced the seed viability of both maturation stages.

3.2 Germination percentage

Germination percentage varied depending on *Acacia* species, maturation stage of the seeds, and fire treatments performed.

Germination percentage in *A. longifolia* varied greatly depending on the maturation stage of the seeds, in addition to the fire treatments. For mature seeds, control germination was 0.4% (Fig. 1a), and most treatments did not differ from control (smoke, 5 min; smoke, 10 min; smoke, 15 min; ash-low, ash-medium, ash-high, charcoal, 150 °C, 5 min; 150 °C, 10 min; 200 °C, 5 min; 200 °C, 10 min). Four heat treatments showed significant differences from control (80 °C, 5 min; 80 °C, 10 min; 110 °C, 5 min; 110 °C-10 min). These fire treatments greatly enhanced germination, being 100 to 200 times greater than that of control. Heat treatment 80 °C, 10 min showed the highest stimulation, being significantly different from the other stimulating heat treatments.

Control germination for fresh seeds was 65.6% (Fig. 1b), and some treatments (smoke, 5 min; smoke, 10 min; smoke, 15 min; ash-low, ash-medium, ash-high, charcoal; 110 °C, 5 min) did not differ from control. Moderate heat treatments (80 °C, 5 min; 80 °C, 10 min) differed from that of the control, increasing the germination percentage of seeds (88.8% and 90.4% respectively). Higher heat treatments (110 °C, 10 min; 150 °C, 5 min; 150 °C, 10 min; 200 °C, 5 min; 200 °C, 10 min) greatly inhibited seed germination, 110 °C, 10 min was 3.2% and the remaining treatments were 0%.

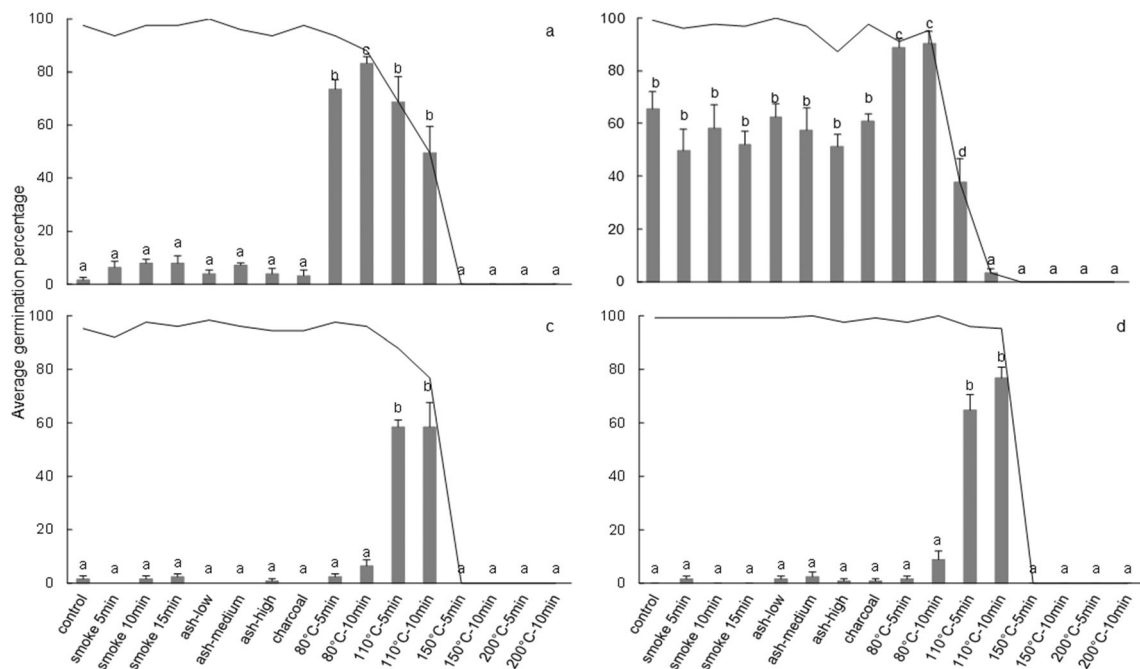


Fig. 1 Viability and germination after fire factors for mature and fresh seeds of *A. longifolia* and *A. mearnsii*. Average germination percentage ($\times \pm$ SD) in bars and average viability percentage in lines. Different labels over the bars for each species indicate significant differences in

germination between the control and fire treatments in the HSD Tukey test performed. **a** *A. longifolia* mature seeds. **b** *A. longifolia* fresh seeds. **c** *A. mearnsii* mature seeds. **d** *A. mearnsii* fresh seeds

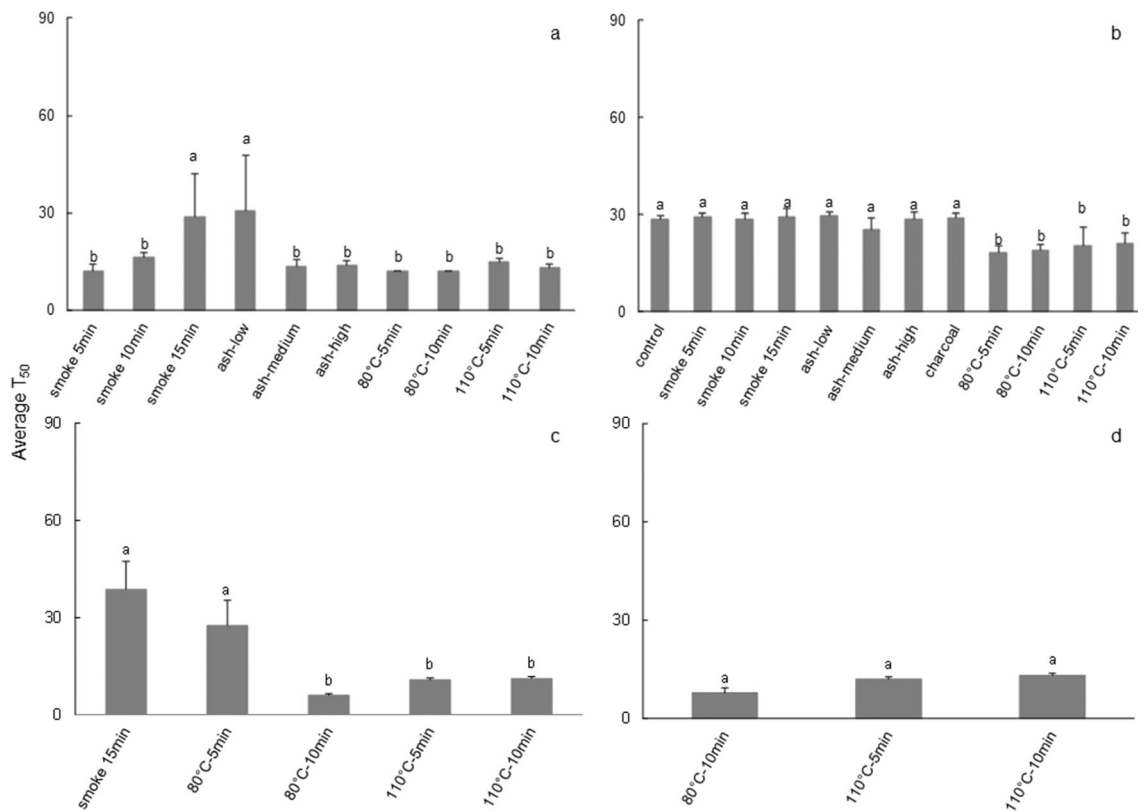


Fig. 2 Average T_{50} ($\times \pm$ SD) in days for mature and fresh seeds of *A. longifolia* and *A. mearnsii*. Different labels over the bars for each species indicate significant differences between fire treatments in the

HSD Tukey test performed. **a** *A. longifolia* mature seeds. **b** *A. longifolia* fresh seeds. **c** *A. mearnsii* mature seeds. **d** *A. mearnsii* fresh seeds

In *A. mearnsii*, the maturation of seeds had no effect. In both cases, mature seeds and fresh seeds followed the same germination pattern. Germination in control was low—0.4% in mature seeds and 0% in fresh seeds (Fig. 1c, d). Most treatments showed a similar germination percentage to control (smoke, 5 min; smoke, 10 min; smoke, 15 min; ash-low, ash-medium, ash-high; 80 °C, 5 min; 80 °C, 10 min; 150 °C, 5 min; 150 °C, 10 min; 200 °C, 5 min; 200 °C, 10 min). Only heat treatments 150 °C, 5 min and 150 °C, 10 min differed from control (Fig. 1c, d). For mature seeds, this germination was 58.4% in both cases; for fresh seeds, it was 64.8% and 76.8% respectively. These percentages imply a high stimulation of the germination by intermediate heat shocks.

3.3 Seed dormancy

In *A. longifolia*, the control dormancy of seeds varied greatly depending on the maturation stage of seeds (Table 2). In mature seeds, this dormancy was very high (96.0%), while in fresh seeds it was 33.6%. In *A. mearnsii*, dormancy was the same for both mature and fresh seeds (93.6% and 99.2% respectively). In both species, this control dormancy was not modified by most fire factors (smoke, ash, and charcoal). Instead, heat shocks modified the seed dormancy; in both species and maturation stages, seed dormancy was reduced

by some fire factors (Table 2). As heat shock severity increased, seed dormancy was reduced until it became zero with severe heat shocks (150 °C, 5 min; 150 °C, 10 min; 200 °C, 5 min; 200 °C, 10 min); in *A. longifolia*, the reduction began with 80 °C, 5 min, while in *A. mearnsii*, it began with 110 °C, 5 min.

In all species and seed maturation stages, scarification reduced the dormancy of seeds to zero (Table 2).

3.4 T_{50}

In *A. longifolia*, this measure was possible in almost all treatments (Fig. 2a, b). In mature seeds most treatments reached T_{50} at the same time, in 13.4 days on average. Two treatments (smoke-5 min and ash-low) were significantly different from the others (28.8 and 30.8 days). In fresh seeds there were differences in T_{50} between the control, smoke, ash and charcoal treatments (28.6 days) and heat treatments (80 °C-5 min, 80 °C-10 min, 110 °C-5 min, 110 °C-10 min; 19.8 days). Between mature and fresh seeds, the main difference was that control and smoke-10 min could not be measured in the former. Furthermore, T_{50} were higher on average in fresh seeds (25.7 days opposite 16.7 days).

In *A. mearnsii*, it was only possible to measure T_{50} in 5 treatments in mature seeds and in 3 treatments in fresh seeds

Table 2 Average dormancy percentage ($\times \pm$ SD) for mature and fresh seeds of *A. longifolia* and *A. mearnsii* after different levels of fire factors and after scarification. Different labels indicate significant differences in the HSD Tukey test performed between the control and treatments

	Seed dormancy			
	<i>A. longifolia</i>		<i>A. mearnsii</i>	
	Mature	Fresh	Mature	Fresh
Control	96.0 \pm 8.3 ^a	33.6 \pm 1.8 ^b	93.6 \pm 4.0 ^a	99.2 \pm 12.8 ^a
Smoke, 5 min	87.2 \pm 8.0 ^a	46.4 \pm 3.6 ^b	92.0 \pm 4.4 ^a	97.6 \pm 18.0 ^a
Smoke, 10 min	89.6 \pm 4.0 ^a	39.2 \pm 1.8 ^b	96.0 \pm 5.4 ^a	99.2 \pm 15.6 ^a
Smoke, 15 min	89.6 \pm 2.2 ^a	44.8 \pm 1.8 ^b	93.6 \pm 5.4 ^a	99.2 \pm 10.0 ^a
Ash-low	96.0 \pm 2.2 ^a	37.6 \pm 2.2 ^b	98.4 \pm 2.8 ^a	97.6 \pm 10.0 ^a
Ash-medium	88.8 \pm 4.9 ^a	39.2 \pm 3.6 ^b	96.0 \pm 3.3 ^a	97.6 \pm 16.3 ^a
Ash-high	89.6 \pm 4.6 ^a	36.0 \pm 4.4 ^b	93.6 \pm 6.1 ^a	96.8 \pm 11.3 ^a
Charcoal	94.4 \pm 2.2 ^a	36.8 \pm 2.2 ^b	94.4 \pm 6.1 ^a	98.4 \pm 6.6 ^a
80 °C, 5 min	20.0 \pm 3.3 ^b	2.4 \pm 2.8 ^{cd}	95.2 \pm 11.0 ^a	96.0 \pm 3.6 ^a
80 °C, 10 min	6.4 \pm 4.6 ^{cd}	4.8 \pm 6.6 ^{cd}	89.6 \pm 4.6 ^a	91.2 \pm 5.2 ^a
110 °C, 5 min	0.8 \pm 7.8 ^d	2.4 \pm 9.5 ^{cd}	30.4 \pm 1.8 ^b	31.2 \pm 2.2 ^b
110 °C, 10 min	0.8 \pm 12.5 ^d	1.6 \pm 10.4 ^d	19.2 \pm 1.8 ^c	18.4 \pm 2.2 ^c
150 °C, 5 min	0 \pm 0 ^d	0 \pm 0 ^d	0 \pm 0 ^d	0 \pm 0 ^d
150 °C, 10 min	0 \pm 0 ^d	0 \pm 0 ^d	0 \pm 0 ^d	0 \pm 0 ^d
200 °C, 5 min	0 \pm 0 ^d	0 \pm 0 ^d	0 \pm 0 ^d	0 \pm 0 ^d
200 °C, 10 min	0 \pm 0	0 \pm 0 ^d	0 \pm 0 ^d	0 \pm 0 ^d
Scarification	0 \pm 0 ^d	0 \pm 0 ^d	0 \pm 0 ^d	0 \pm 0 ^d

(Fig. 2c, d). The 3 treatments in fresh seeds (80 °C, 10 min; 110 °C, 5 min; 110 °C, 10 min) coincided with those of mature seeds. These 3 treatments did not differ and 50% of the seeds had germinated in 11 days and 9.3 days respectively. In *A. mearnsii* mature seeds, smoke, 5 min and 80 °C, 5 min had a delay in germination in contrast to the other treatments; they needed 38.7 and 27.6 days respectively to reach 50% of germinations.

The T_{50} of scarified seeds was much lower than in any other treatment: seeds reached half of total germinations in 3 days in all cases (Table 1).

3.5 Temporal distribution of germination

Distribution of germination over time is presented for control and treatments which have stimulated germination.

In mature seeds of *A. longifolia*, the vast majority of seeds germinated between the 7th and 28th day (Fig. 3a). In control seeds, germination took place on the 12th day. The temporal distribution of germination in fresh seeds of *A. longifolia* was quite different and more expanded over time. Germination started on day 7 and stopped on day 50 (Fig. 3b), with some single germinations occurring after that day.

In seeds of *A. mearnsii*, the time in which most germination occurred was shorter, between the 10th and 20th day. Mature (Fig. 3c) and fresh (Fig. 3d) seeds had the same distribution of germination. In mature seeds, control germination started on the 10th day, while fresh seeds did not germinate.

4 Discussion

The viability of the two *Acacia* species studied is very high under control conditions, regardless of seed maturation stage. This total viability was proven by the 100% germination of scarified seeds in both species and maturation stages. Milton and Hall (1981) reported 97% viability in *A. longifolia* seeds and Holmes (1989) reported 99% viability in *A. mearnsii* seeds in soil seed banks of South Africa. In Galicia (south-western Europe), Arán et al. (2017) found similar data in fresh seeds (aerial bank) and mature seeds (soil seed bank) of *A. melanoxylon*. In our species, this viability persisted after some fire treatments (smoke, ash, charcoal, and low and intermediate heat shocks) but totally declined with severe heat shocks. Comparing the two studied species, seeds of *A. mearnsii* better resisted severe effects of high temperatures. In *A. longifolia*, mature seeds resisted to more heat than fresh seeds, while in *A. mearnsii*, fresh seeds resisted slightly further. These high values of viability, before and after fire treatments, add a new point of view to seed behavior and help to explain the reasons that determine its high invasiveness (Richardson and Kluge 2008).

Conversely, the germination and dormancy results obtained showed great differences between the two *Acacia* species in relation to both seed maturity stage and fire factor response.

A. longifolia has seeds ready to germinate both in periods between fires and in periods immediately after fire, while the seeds of *A. mearnsii* are especially prepared to germinate after fire, and in addition, more severe thermal shocks are required to break their dormancy than to break the dormancy of the seeds of *A. longifolia*. Other authors noted that *A. longifolia* and *A. mearnsii* have physical dormancy and fire stimulation (Pieterse and Cairns 1986; Kulkarni et al. 2007; Marchante et al. 2010), but so far, these reproductive features in relation to fire have not been meticulously described in such a precise way. Regarding the effect of fire on dormancy, *A. longifolia* and *A. mearnsii* follow very different strategies. It could be said that *A. longifolia* has a dormant multi-response because newly ripened seeds have low dormancy, but after 1 year of maturation, their dormancy becomes very high. However, the dormancy of *A. mearnsii* seeds is very high at ripening and stays so after 1 year. Baeza and Vallejo (2006) also found multi-response strategy of dormancy in *Ulex parviflorus* Pourr. but in the opposite way to *A. longifolia*. Following the classification of Ooi et al. (2014), *A. longifolia* belongs to the facultative pyrogenic dormancy release class and

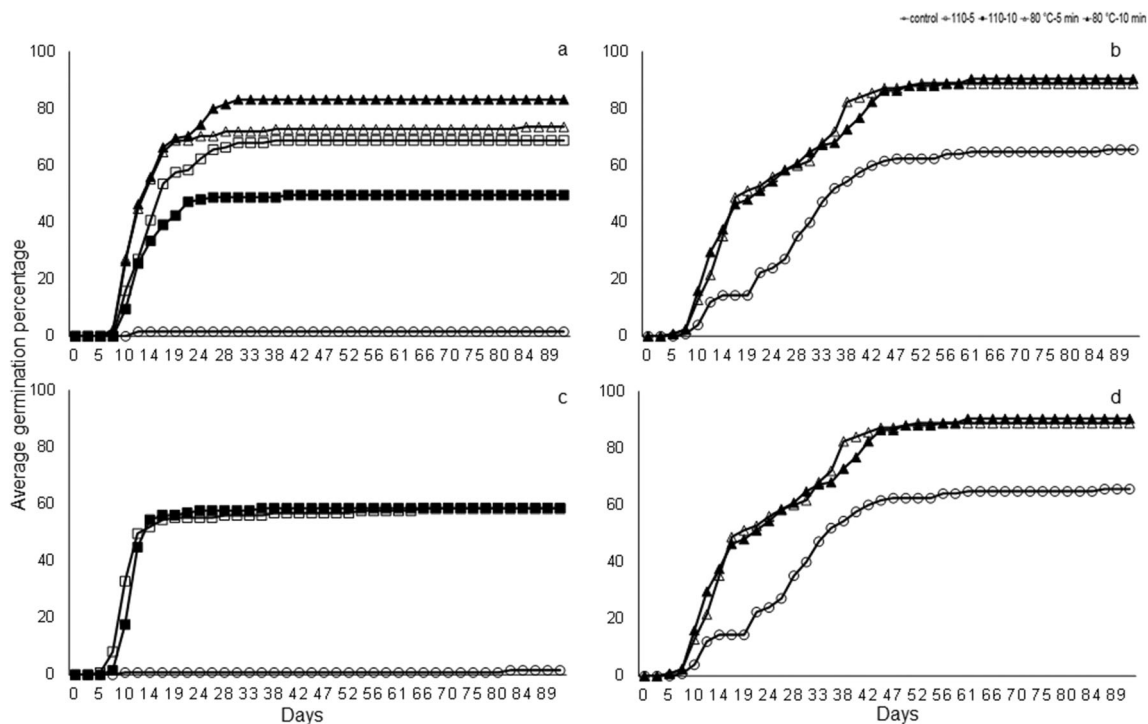


Fig. 3 Temporal distribution of germination for mature and fresh seeds of *A. longifolia* and *A. mearnsii* in control and treatments that stimulated seed germination. **a** *A. longifolia* mature seeds. **b** *A. longifolia* fresh seeds. **c** *A. mearnsii* mature seeds. **d** *A. mearnsii* fresh seeds

A. mearnsii to obligate pyrogenic dormancy release class. Another notable issue of this research is that of the 4 studied fire factors, only heat reduces dormancy in both species. Smoke rarely causes dormancy breaking (Clarke et al. 2000; Tieu 2001; Gómez-González et al. 2008) in other species of fire-prone environments. In addition, the scarification of seeds demonstrated that dormancy of *A. longifolia* and *A. mearnsii* seeds (Milton and Hall 1981; Holmes 1989) is only physical, so any factor able to break the hard coat without causing damage to the embryo will promote germination in a few days. This is a very common type of dormancy among *Leguminosae* species, but it is not present in all (Ooi et al. 2014; Galíndez et al. 2019). Arán et al. (2017) demonstrated in seeds of *A. melanoxylon* soil bank that not all seeds of soil bank respond to fire; there remains a part of dormant seeds that could break dormancy through other mechanisms, such as scarification by friction with soil particles or the expansion and contraction caused by summer temperatures. This loss of dormancy can be added to that caused by fire in some species (Santana et al. 2010, 2013; Luna 2020), generating extensive germination in mature seeds.

Also, heat was the only fire factor studied in this paper that produced significant effects on the germination of *A. longifolia* and *A. mearnsii*. In both species, moderate heat treatments stimulate germination, but in *A. longifolia*, stimulation starts at 80 °C, 5 min and does not decay until the heat exceeds 110 °C, 10 min. In *A. mearnsii*, germination

stimulation starts with 110 °C, 5 min. Moreover, mature seeds of *A. longifolia* reached maximum stimulation with 80 °C, 10 min and fresh seeds with 80 °C, 5 min, while seeds (fresh and mature) of *A. mearnsii* did so with 110 °C, 5 min and 110 °C, 10 min respectively. Arán et al. (2013) and Cruz et al. (2017) also found significant stimulations of the germination of *A. melanoxylon* with 80 °C, 5 min and 80 °C, 10 min. Other leguminous species of the Iberian Peninsula such as *Cytisus scoparius* (L.) Link, *Pterospartum tridentatum* Willk. (Rivas et al. 2006), *U. parviflorus* (Baeza and Roy 2008), and those from other Mediterranean areas, such as *Bituminaria bituminosa* (L.) C.H.Stirt. and *Spartium junceum* L. (Reyes and Trabaud 2009), also greatly increase their germination with 80 °C, 10 min and 110 °C, 5 min. *A. mearnsii* seeds are more resistant to heat shocks, reaching high values of germination even at 110 °C, 10 min. Fresh seeds of *A. longifolia* germinate well in periods between fires. Nevertheless, mature seeds of *A. longifolia* and the fresh and mature seeds of *A. mearnsii* need threshold temperatures that only occur during fire. Severe heat treatments (from 150 °C, 5 min) killed all the seeds. However, this combination of temperature and duration is not common in the soil of Galicia forests (Mataix-Solera et al. 2013; Reyes et al. 2015b). Furthermore, the soil seed bank of *Acacias* species is usually very abundant and at a depth of between 2- and 5-cm deep (Arán et al. 2017), where it is protected from severe thermal shocks. In both species, smoke, ash, and charcoal did not

stimulate germination, but did not reduce seed viability either. That means that many viable seeds of these two species increase the soil seed bank every year, and, after a forest fire, a large number of seeds germinate and many of the ones that do not are still viable to germinate after the occurrence of another fire.

The maturation stage of seeds can exert remarkable effects on percentage and speed of germination of some plant species (El-Keblawy and Al-Ansari 2000). We have detected different behavior depending on the species: in *A. longifolia*, the maturation stage influences the control germination percentage and the response to fire severity, whereas in *A. mearnsii*, it does not have an influence. Arán et al. (2017) found higher germination in fresh seeds of *A. melanoxylon* than in mature seeds from soil seed bank. Reyes and Casal (2001) also found different sensibility to fire factors in seeds of *Pinus radiata* D. Don and *Eucalyptus globulus* Labill., depending on the age of seeds.

The mature seeds of both Acacia species and fresh seeds of *A. mearnsii* slightly germinated in control, smoke, ash, and charcoal treatments, and instead, the fresh seeds of *A. longifolia* multiply the germination percentages with those same treatments by a factor of 6. On average, speed of germination was lower in fresh seeds of *A. longifolia* than in mature seeds, while in *A. mearnsii*, mature and fresh seeds presented low values of T_{50} and similar to those of mature seeds of *A. longifolia*. Cervantes et al. (1996) found different germination capacity and germination speed in seeds of *Acacia cochliacantha* Humb. & Bonpl. ex Willd., *Acacia farnesiana* (L.) Willd., and *Acacia pennatula* (Schltdl. & Cham.) Benth., with ages from 3 months to 5 years old. Times required for germination of *A. longifolia* and *A. mearnsii* are shorter than those registered for *A. melanoxylon* (Arán et al. 2017; Cruz et al. 2017), and this is another trait of their invading character. The temporal distribution of germination of both species is very similar and does not change with the maturation of seeds, coinciding with the results of Arán et al. (2017) and of Burrows et al. (2009) in *A. melanoxylon*.

5 Conclusion

The two studied species exhibit different reproductive behavior in relation to fire and seed maturation. The potential of invasion of *A. longifolia* is stronger than that of *A. mearnsii*, because *A. longifolia* can germinate abundantly in absence of fire and the seeds that do not germinate enter a dormant phase, becoming available in the soil seed bank to germinate after a forest fire. *A. longifolia* has the ability to germinate both after fires and in periods between fires.

In contrast, *A. mearnsii* barely germinates in periods between fires and needs higher temperatures to break dormancy and germinate, so its dependence on fire is greater.

The two Acacia species germinate abundantly after fires and thermal shocks over 100 °C are necessary to reduce their soil seed bank. In a more severe and recurring fire scenario, both species will have advantage over native species because both *Acacias* germinate rapidly, with high percentages, and produce seeds at early ages (2–3 years, personal observation). Other native species adapted to fire such as *Ulex europaeus* L., *C. scoparius*, or *P. tridentatum* (Reyes and Casal 2008; Cruz et al. 2020) are shrubs and therefore could not compete with invading trees that grow very fast in height. Among the native vegetation of Galicia, two fast-growing tree species could compete with the two studied species without fire, *Salix atrocinera* Brot. and *Betula pendula* Roth.; however, their germination is not stimulated by fire (Reyes and Trabaud 1997; Cruz et al. 2020), and its competitiveness would be compromised after fire.

The best weapon to fight these IAS in southwestern Europe is prevention, and for this, the native vegetation must be preserved. For this reason, after a forest fire, we recommend favoring native vegetation by sowing seeds and planting seedlings of indigenous species and removing the established *Acacia* seedlings.

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Data availability The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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