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Burial depth and temperature effects on the germination and viability of Giant ragweed (Ambrosia trifida L.) seeds

David A. Bohan³ | Göran Bergkvist⁴

Aleksandra Savić¹ | Björn Ringselle² | Didac Barroso-Bergadà³

¹Department of Weed Research, Institute for Plant Protection and Environment, Belgrade, Serbia

²Division of Bioeconomy and Health, Department of Agriculture and Food, Research Institutes of Sweden (RISE), Uppsala, Sweden

³INRAE, Université Bourgogne, Université Bourgogne Franche-Comté, Dijon, France

⁴Department of Crop Production Ecology, Swedish University of Agricultural Sciences, Uppsala, Sweden

Correspondence

Göran Bergkvist, Department of Crop Production Ecology, Swedish University of Agricultural Sciences, Uppsala, Sweden. Email: goran.bergkvist@slu.se

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Abstract

Ambrosia trifida is a problematic weed species in many annual crops, and its allergenic pollen can be harmful to human health. Understanding the latency and germination rates of this weed species is crucial for planning effective weed management strategies. The objective of this study was to investigate the interaction of burial depth (5, 10, 15, 25 and 40 cm) and temperature (5, 10, 15, 20, 25 and 30°C) on % germination, viability and latency in A. trifida using seeds from one population from Nebraska, North America, and two populations from Serbia, Europe. Nebraskan seeds were three times heavier than the Serbian seeds and had a higher seed viability and germination rate and lower germination latency. Despite this, burial depth and temperature affected the seeds from all populations in a similar way: the germination rate decreased and latency increased with increasing burial depth, while germination rate increased and latency decreased with increasing temperature. At shallow burial depths (5 cm), almost all seeds had very low levels of dormancy, while seeds buried deep (40 cm) did not germinate at any temperature treatment. We conclude that burial depth and temperature have opposite effects on A. trifida germinate rate and latency, but at very shallow or very deep soil depths, the seeds will germinate or will not germinate, respectively, regardless of the tested temperatures. The low dormancy at shallow soil depths means that A. trifida may be vulnerable to management strategies that focus on quickly emptying the seedbank without burying the seeds.

KEYWORDS

dormancy, integrated weed management, minimal tillage, seed bank, seed decay, survival analysis, Weibull distribution

INTRODUCTION 1

Weeds can cause great crop yield losses unless properly managed (Oerke, 2006). Weed management, especially direct weed control using herbicides and tillage, requires a lot of farm resources and can have a negative environmental impact both on the farm (e.g., soil degradation, reduced biodiversity) and downstream from the farm (e.g., eutrophication due to nutrient leaching, herbicide residues in drinking water and food) (Klik & Rosner, 2020). To be able to reduce the negative impacts of weed control, it is essential to have a thorough understanding of biology and traits so that preventive measures can be used instead of direct weed control and so that weed control

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efficacy can be maximised when direct control is used (Gaba et al., 2017). Detailed knowledge of germination and emergence of weed seeds provides insights into when weeds are most vulnerable so that resource-efficient weed management can be planned (Batlla & Benech-Arnold, 2014). If tillage or herbicides are applied too early, only a small percentage of weeds will emerge and thus be killed. If tillage or herbicides are applied too late, weed plants may already be too large to be controlled (Carey & Kells, 1995). Accordingly, if all weed seeds germinated at the same time, the population would also be extremely vulnerable to disturbance such as weed control measures.

The mean time to seed germination after being placed in the soil, termed the germination time or latency, depends on the intensity of dormancy (a failure of a viable seed to germinate under favourable conditions) release (Harre et al., 2019). Understanding the concept of seed dormancy is crucial as it explains why a dormant seed, despite favourable environmental conditions, does not germinate (Baskin & Baskin, 2004). Dormancy is divided into primary and secondary dormancy, which specifies when the dormancy is imposed; and into physiological, morphological or other types of dormancy, which specifies what conditions are needed to break the dormancy (Baskin & Baskin, 2004; Finch-Savage & Leubner-Metzger, 2006). For instance, a freshly maturated dormant seed has primary dormancy, which develops during seed maturation on the mother plant (Hilhorst, 1998), while secondary dormancy is acquired after maturation and dispersal from the mother plant, induced by unfavourable environmental factors (Egley & Duke, 1985). In morphological dormancy, the delay in germination is because the mature seed requires a period of embryo growth after it has been dispersed (Baskin & Baskin, 2004). In comparison, physiological dormancy means that specific chemical processes are necessary for the mature seed to germinate (Baskin & Baskin, 2004). In this case, the embryos are hindered by a hormonal imbalance or the inability to penetrate the hard endocarp (Finch-Savage & Leubner-Metzger, 2006). The main cause of physiological dormancy is the embryo's reduced metabolic activity, so the dormancy of the seed must be broken to achieve the appropriate level of enzymes, hormones, soluble metabolites and other components the embryo needs for germination (Baskin & Baskin, 2004).

Models have been developed that describe how seed germination and breaking of dormancy are influenced by various factors (e.g., temperature, light and soil microbial communities) (Benech-Arnold et al., 2000; Harre et al., 2019). Temperature has been identified as the most important factor determining the time it takes to break dormancy and to germinate (Alebrahim et al., 2011; Ruziev et al., 2020). For example, low winter temperatures lessen dormancy in Polygonum aviculare, while high summer temperatures reinforce it (Benech-Arnold et al., 2000; Kruk & Benech-Arnold, 1998). Moreover, the effect of temperature on dormancy release may interact with other factors such as soil moisture and nitrate concentration (Benech-Arnold et al., 2000). In addition to different types of dormancy, seeds also have differential persistence in the soil, with some seeds surviving just a few years, while seeds from some species can be viable for decades (Conn & Deck, 1995; Egley & Chandler, 2017; Thompson et al., 1997). To plan resource-efficient management of weeds it is

essential to know when seeds are likely to germinate, how long they can be expected to remain viable in the soil and from what soil depths they can emerge (Alexander & Schrag, 2003).

The Ambrosia multiple genus contains species (e.g., A. artemisiifolia L. [common ragweed], A. psilostachya DC. [perennial ragweed], A. tenuifolia Spreng. [slender ragweed], A. trifida L. [giant ragweed]) that have become problematic as invasive and weedy plants (Savić et al., 2024), largely due to their seed traits (Abul-Fatih & Bazzaz, 1979; Farooq et al., 2019). These plants have high seed production (Leskovšek et al., 2012) and longevity (Baskin & Baskin, 1977) and are readily dispersed. Moreover, Ambrosia pollen is highly allergenic and can cause great harm to human health (Lommen et al., 2018). Ambrosia trifida is a particularly important weed of this genus (Baysinger & Sims, 1991; Follak et al., 2013; Savić et al., 2021). It originates from North America (Bassett & Crompton, 1982; Bassett & Terasmae, 1962) and has invaded many parts of Europe (Follak et al., 2013; Obradov et al., 2021). The species was first recorded in Serbia on the Pannonian Plain: Voivodina province (Koljadžinski & Šajinović, 1982). It is on the A₂ List, indicating a high phytosanitary risk of A. trifida for the European and Mediterranean region (EPPO) with risks to agricultural production and human health. According to Gibson et al. (2005), A. trifida is one of the most problematic weeds in soybean and maize crops in the USA. Authors have also reported A. trifida derived yield losses of up to 90% in maize (Harrison et al., 2001), 50% in soybean (Baysinger & Sims, 1991) and 25% in sunflower (Vrbničanin et al., 2012). Compared to other Ambrosia species. A. trifida produces relatively few seeds per plant, from a few hundred to a few thousand (Abul-Fatih & Bazzaz, 1979; Goplen et al., 2016), with extreme exceptions up to 10 000 (Sickels & Simpson, 1985).

Ambrosia trifida often produces polymorphic seeds of different sizes and colours (Schutte et al., 2012; Schutte, Regnier, & Harrison, 2008). It is well known that North American populations of *A. trifida* are characterised by larger seeds and a more robust morphology than European A. *trifida* populations (Bassett & Crompton, 1982; Savić et al., 2021). Daws et al. (2007) suggested that the heavier seeds of North American A. *trifida* have contributed to their dominance in North America. Larger seeds are also more capable of emerging at greater soil depths than smaller seeds, and this confers an advantage in environments where seeds are buried to 5–10 cm, for example, by tillage. However, larger seed size does not confer an advantage to seeds left on the soil surface or that are buried so deep that even seedlings from larger seeds cannot emerge (Harrison et al., 2007).

Ambrosia trifida features physiological seed dormancy (Schutte et al., 2012) where temperature directly influences the level of dormancy and germination latency (Batlla & Benech-Arnold, 2015). Embryo-covering structures inhibit germination through different possible mechanisms, such as supplying chemical germination inhibitors, limiting the loss of germination inhibitors from the embryo, preventing embryo water uptake and also mechanically restricting embryo growth (Bewley & Black, 1994). Likewise, reducing embryo gas exchange may be essential for preserving dormancy because oxygen can be critical for metabolising inhibitory compounds within the embryo (Barthe et al., 2000). For A. *trifida*, physiological dormancy caused by the embryo and embryo-covering was reduced by burial in moist soil at 2° C (Schutte et al., 2012).

Previous studies on A. *trifida* have indicated that temperature is an important ecological trigger in seed germination and that the rate of germination increases with increasing temperatures when seeds have been incubated at 4°C before the test (Ruziev et al., 2020; Schutte et al., 2012), but that the rate of germination decreased when temperatures exceeded 25°C and decreasing down to the highest investigated temperature 40°C (Ruziev et al., 2020). Abul-Fatih and Bazzaz (1979) showed that A *trifida* seeds can germinate successfully up to 41°C. This opens a hypothesis that there is an interaction between temperature needed for germination and burial depth, which previous studies have not investigated for A. *trifida*.

Seedlings of A. trifida emerge from a depth of 2-5 cm, and the greatest seed burial depth from which A. trifida emerge is approximately 20 cm (Harrison et al., 2007). A large percentage of A. trifida seeds located in the top 10 cm of soil lost viability after 4 years (Harrison et al., 2001, 2007), while some seeds buried at 20 cm or deeper can remain viable for more than 9 years (Harrison et al., 2007). Through tillage, persistent A. trifida seeds at deep depths may be moved to depths more conducive to seedling emergence, although the likelihood and timing of seedling emergence from these seeds is influenced by both dormancy loss dynamics mainly determined by burial depth and germination latency mainly determined by temperature (Davis et al., 2013; Harrison et al., 2007). There are numerous studies on the effect of different factors such as temperature (Guillemin & Chauvel, 2011), light (Batlla & Benech-Arnold, 2014) and soil types (Benvenuti, 2003) on seed germination and growth (Guillemin & Chauvel, 2011: Socolowski et al., 2008), Although some have looked at the interaction between burial depth and temperatures for other species (e.g., Polygonum persicaria, Chenopodium album, Spergula arvensis. Rumex obtusifolius, Conyza canadensis in Benvenuti et al., 2001; Mennan & Zandstra, 2006; Ottavini et al., 2019; Vleeshouwers, 1997), this interaction has not yet been studied for A. trifida.

This study aims to increase our understanding of how burial depth, temperature and their interaction affect *A. trifida* seed germination and viability. Our hypotheses were that (1) increasing burial depth will reduce germination rate and increase germination latency; (2) increasing temperature when seeds are moved to a suitable environment will increase the germination rate and reduce germination latency and (3) with greater burial depth, higher temperatures are required to break seed dormancy.

2 | MATERIALS AND METHODS

2.1 | Seed collection

A germination experiment was conducted to determine the effect of burial depth and temperature on *A. trifida* emergence over time in three different populations from Serbia and Nebraska, USA. The seeds were collected at maturity (in autumn) from at least 100 different mother plants from agricultural fields cropped with soybean and maize. Branches with mature seeds were harvested by hand from every third plant found and dried for 7 days in a greenhouse (temperatures ranged from 25 to 30°C). The single-seeded fruit (the dispersal unit, referred to as 'seed' hereafter) were mechanically threshed, cleaned from the hardened enclosing and inspected individually. Seeds that were empty or had insect damage were discarded. The seed collection was done in October 2018 at two different localities in Serbia (Population Serbia II Central Bačka 45°30′ N, 19°31′ E and Population Serbia II Dobrić 44°41′ N, 19°34′ E) and from Nebraska, USA (42°23′ N 96°57′ W). The seeds were stored in paper bags at room temperature during 1 month, before use in the germination experiments.

2.2 | Germination study and viability test

The experiment was set up in an agricultural field in Serbia (Dobrić $\Box 44^{\circ}41'$ N, 19°34' E). Before the establishment of the experiment, the area had been fallow and undisturbed for the previous 2 years. Before the fallow period, it had been cultivated with maize and wheat in rotation for many years. The soil is a clay loam with pH (H₂O) 5.20; organic matter 2.31%, nitrogen (N) 0.11%, and with 20.5 and 5.41 mg per 100 g dried soil potassium (K) and phosphorus (P), respectively (Pantović et al., 1989).

In November 2018, the experiment was set up by burying packages made of nylon stockings, with each package containing 100 seeds. For each population, 720 packages were buried, divided into five burial depths (5, 10, 15, 25 and 40 cm), six temperatures for germination assessments (5, 10, 15, 20, 25 and 30°C), three replicates for eight assessment times (four times in 2019 and four in 2021). This gave 90 treatment combinations, 270 packages per assessment time and 2160 packages in total. The packages were buried in eight 2×1 m plots in the field, one plot for each assessment time, randomly selected.

The packages were carefully removed from each depth on each of the four sampling time points per year, 1 month apart from April to July, without disturbing the soil structure of other plots. The germination experiments were conducted during 15 days using the packaged seeds (Figure 1) in controlled thermostats, at the six temperatures of experimental assessment. Seeds buried at a depth of 5 cm all germinated between autumn 2018 and March 2019 and were therefore not included in the experiment, reducing the number of levels for burial depth from five to four. In 2021, seeds buried at 10 cm were demised. In 2019 and 2021, no seeds buried at a depth of 40 cm germinated successfully. These treatment levels by year combinations were therefore excluded from all subsequent analyses. It should be noted that these exclusions mean that the experiments conducted in 2019 and 2021 differ in size and therefore degrees of freedom.

Prior to burial, the average weight of the different seed populations was determined by weighing 50 seeds for each population in the WEED





FIGURE 1 Illustration of the experimental design. Three populations of A. *trifida* (Nebraska, Serbia I, Serbia II) were buried at different depths (5, 10, 15, 25 and 40 cm) in autumn 2018. In each of the 4 months (April, May, June and July) in 2019 and 2021, seeds from different depths were subjected to a germination test at different temperatures (5, 10, 15, 20, 25 and 30°C).

three replicates. Latency to germination and the rate of germination were experimentally evaluated by randomly selecting 50 seeds from each of the appropriate packages and placing them on filter papers in Petri dishes with distilled water. In 2019, packages from three populations, four burial depths, six temperatures, three replicates and four sampling occasions were evaluated. In 2021, three populations, three burial depths, six temperatures three replicates and four sampling occasions were evaluated. The number of seeds germinating in each dish was recorded daily for the next 15 days. Visible protrusion of the radicle was treated as the criterion for germination. Germination rate is defined as the percentage of seeds that have germinated after 15 days and the seed latency is defined as the mean time in days it takes for seeds to germinate. After the experiment was finished in 2021, from the remaining seeds, the percentage of viable seeds from burial depths 15 and 25 cm was evaluated using the Crush test (Karrer et al., 2016) (15 seeds \times 6 replications for burial depths 15 and 25 cm).

2.3 | Statistical analysis

The seed weight of the populations prior to experimentation was analysed using one-way ANOVA, with the seed population as a fixed factor. The effect of burial depth on the viability of the seeds was analysed using two-way ANOVA with the seed population and burial depth and their interaction as fixed factors. The rate of germination of the seeds was analysed using a three-way ANOVA with the three populations, burial depths, temperatures and their interactions treated as fixed factors. All ANOVA were subjected to post-hoc testing with the Bonferroni correction (Napierala, 2012) to verify the conclusions of the analyses.

The time to germination, or latency, was described using a Kaplan-Meier object. The Kaplan-Meier objects were formed from the number of seeds that had not germinated at each time point (Crawley, 2012), across burial depths and temperatures, separately for the 2019 and 2021 experiments. The data were not censored. The parametric survival analysis was done using the srvreg function from the R library survival. The full model considered each population as factor levels, while burial depth and temperatures were considered factors that could interact. Modelling was done with the Exponential and the Weibull error distributions, to respectively evaluate whether the hazard function for germination was constant or changed continuously over the experimental time course. Selection of the model terms was done by backwards selection using χ^2 values, with appropriate degrees of freedom, calculated from changes in model deviance. All data analyses were performed in R (version 4.3.0) (R Core Team, 2024).

3 | RESULTS

3.1 | The estimated Weibull scale for 2019 and 2021

The germination hazard function experienced by the seeds was not constant, with the estimated Weibull scale for 2019 (0.21) and 2021 (0.18) indicating that the per capita probability of germination declined over time. The Weibull model was a good fit in 2019 ($\chi_7^2 = 326.42$, p < 0.001) and 2021 ($\chi_7^2 = 109.31$, p < 0.001), with a significant improvement over the model with exponential errors in both experimental years (p < 0.001). No interaction terms between factors were significant in either of the experimental years.

3.2 | Population differences

The Nebraskan population had significantly heavier seeds, higher germination rate, shorter germination latency and higher seed viability than the two Serbian populations, which did not differ significantly from each other in any metric. The seeds of the Nebraskan A. *trifida* population were, on average, three times heavier than the two Serbian populations ($F_{2,147} = 1154$; p < 0.001; Figure 2A). The Crush test conducted on the seeds at the end of the experiment showed that the seeds from Nebraskan population had 75% higher viability than the Serbian populations ($F_{2,30} = 16.8$; p < 0.001) (Figure 2B). There were no significant interactions between populations and burial depth ($F_{2,30} = 1.6$; p = 0.217).

The Nebraskan seeds had a higher germination rate than the Serbian populations in both 2019 ($F_{2,594} = 57.6$, p < 0.001) (Figure 3A) and 2021 ($F_{2,396} = 85.7$, p < 0.001) (Figure 3B). The germination latency was shorter for Nebraskan seeds than Serbian seeds. In 2019, the mean latency time to germination was 7.6 (s.e. = 0.03) and 8.1 (s.e. = 0.03) days for Serbian I and Serbian II seeds, respectively,

compared to 5.2 (s.e. = 0.02) days for Nebraskan seeds (χ_2^2 = 243.6, p < 0.001) (Figure 4A). In 2021, the mean latency time to germination was 11.8 (s.e. = 0.04) days for Serbian I seeds and 9.7 (s.e. = 0.03) days for Serbian II seeds compared to 7.9 (s.e. = 0.04) days for Nebraskan seeds (χ_2^2 = 90.62, p < 0.001) (Figure 4B).

3.3 | Burial depth effects

Greater burial depth had no significant effect on seed viability ($F_{2,30} = 0.6$; p = 0.81), but resulted in a lower germination rate in both 2019 ($F_{2,594} = 76.1$, p < 0.001) (Figure 3C) and 2021 ($F_{1,396} = 47.1$, p < 0.001) (Figure 3D) and increased germination latency (Figure 4). In 2019, the mean latency time to germination was 6.6 (s.e. = 0.07) days at a burial depth of 10 cm, 7.1 (s.e. = 0.08) days at a burial depth of 15 cm and 7.5 (s.e. = 0.08) days at a burial depth of 25 cm ($\chi_2^2 = 32.5$, p < 0.001) (Figure 4C). In 2021, the mean latency time to germination was 9.4 (s.e. = 0.08) and 9.9 (s.e. = 0.09) days for a burial depth of 15 and 25, respectively ($\chi_1^2 = 4.5$, p < 0.001) (Figure 4D).





FIGURE 3 Germination rate of A. *trifida* depending on population and temperature (A, B) and burial depth and temperature (C, D) in 2019 (A, C) and 2021 (B, D). Box plots show average germination rates for each population and burial depth.



FIGURE 4 Proportion of germinated seeds (latency curves) predicted from a parametric model with corresponding Kaplan–Meier estimates (with 95% confidence intervals) for seed of *A. trifida* depending on population (A, B), burial depth (C, D) and temperature (E, F) in 2019 (A, C, E) and 2021 (B, D, F).

3.4 | Temperature effects depending on burial depth

On average, increasing temperature resulted in higher germination rates in both 2019 (F_{5.594} = 50.1, *p* <0.001) (Figure 3A,C) and 2021 $(F_{5,396} = 7.7, p < 0.001)$ (Figure 3B,D), and shorter germination latency (Figure 4). In 2019, the germination rate of the Serbia II population was less affected by temperature than the other populations, causing a significant interaction between temperature and population $(F_{10.594} = 2.3, p < 0.005)$ (Figure 3A), while there was no such interaction in 2021 ($F_{10,396} = 1.1, p = 0.4$) (Figure 3B). The effect of temperature on germination decreased with burial depth in 2019 $(F_{10.594} = 1.9, p < 0.005)$ (Figure 3C), but not in 2021 $(F_{5.396} = 0.3, p < 0.005)$ p = 0.9) (Figure 3D). The mean latency time decreased with increasing temperature, with seeds germinating after 7.83 (s.e. = 0.13) days in 5°C and after 6.9 (s.e. = 0.11) days at 30°C ($\chi_5^2 = 50.3$, p < 0.001) in 2019 (Figure 4E); and after 10.3 (s.e. = 0.16) days in 5°C and after 9.4 (s.e. = 0.13) days at 30°C ($\chi_1^2 = 14.54$, p < 0.001) in 2021 (Figure 4F). There were no significant interactions between population and temperature in 2019 and 2021 ($\chi_5^2 = 7.5$, p = 0.6; $\chi_1^2 = 14.54$, p = 0.9) (Figure 4E,F).

4 | DISCUSSION

4.1 | Population and seed weight differences

The fact that the Nebraskan population had heavier seeds than the Serbian populations is a likely explanation for their observed greater seed viability and germination rate as well as shorter latency. Harrison et al. (2007) found that larger seeds in A. trifida had a higher germination rate, though they did not find that larger seeds had a higher seed viability as they had in our study. Other studies have also found that populations with larger seeds have higher viability, and a better ability to emerge from deeper soil depths (e.g., Chauhan & Johnson, 2010). A major limitation to our results is that we did not study the effect of seed weight within populations, so it is possible that other population traits could have affected differences between populations in seed viability, germination rate and latency. However, seed weight is likely to be a major contributing factor, since it has been correlated to germination and latency (Chauhan & Johnson, 2010; Harrison et al., 2007). Further studies with the inclusion of a larger number of populations and seeds of different sizes within the same populations would be needed to generalise the effect of seed size and to separate the effect of seed size from the effect of population.

4.2 | Burial depth effects

The first hypothesis, which stated that increasing burial depth would reduce the germination rate and increase germination latency, was corroborated by our results. Except for a small number of Nebraskan seeds, all the seeds buried at 5-cm depth germinated within a few months, suggesting a general lack of dormancy. This can be contrasted with the study of Harrison et al. (2007), where seeds from 5-cm depth continued to germinate even after years of burial. The difference in results may be because Harrison et al. (2007) conducted their experiments in a colder climate compared to the relatively mild winter in

Serbia, where the current study was conducted, and higher temperatures can have a great impact on seed germination and reduction of dormancy as seen in this study, as well as in Schutte et al. (2012). From 5-cm depth, the germination rate decreased and germination latency increased with increasing depth to 40 cm, where no seeds germinated at any of the temperatures tested. Moreover, the estimated Weibull germination hazard function declines with time, suggesting that the probability of germination per seed declines over time. This suggests that the longer time that passes without germination, the less likely a seed is to germinate in deeper soil layers. These results are consistent with several previous studies who found increasing dormancy or decreased emergence in A. trifida seeds with increasing soil depth (Harrison et al., 2007; Norsworthy & Oliveira, 2005; Thomas et al., 2006). This also seems to be the case for some other species. For example, Benvenuti and Mazzoncini (2018) observed that germination decreases at increasing seeding depths for Abutilon theophrasti, Polygonum convolvulus and Portulaca oleraceae, and Guillemin and Chauvel (2011) found the same for A. artemisiifolia seeds. The loss of seed viability that occurred at 10 cm in 2021 could potentially be due to mortality caused by pathogenic fungi (Van Mourik et al., 2005) or the impact of temperature variations in the upper layers of the soil (Zhang et al., 2021).

4.3 | Temperature effects

The second hypothesis, which stated that the seed germination rate would increase and germination latency decreases with increasing temperature, was supported by the results. Increasing temperatures up to 30°C increased the germination rate and reduced germination latency for seeds of all three populations and at all burial depths except at 40-cm depth where no seeds germinated regardless of temperature. These results are consistent with results from some other weed species such as P. aviculare and Acroptilon repens (Alebrahim et al., 2011; Batlla & Benech-Arnold, 2015). Ruziev et al. (2020) found that the germination rate of A. trifida decreased when temperatures exceeded 25°C. Most likely, the small difference in results is because Ruziev et al. (2020) performed the germination test after simulated stratification, where they stored the seeds at low temperature (4°C) for 3 months. In our study, the A. trifida seeds were exposed to variable temperatures during several months up to 3 years after burial in the natural conditions of the soil, where the temperature decreases with increasing soil depth, and where the soil in deeper layers is denser and less aerated than in the upper layers (Tsilingiridis & Papakostas, 2014) which could make them more dormant than seeds stratified a short time at low temperatures (Ruziev et al., 2020). Seeds that are more dormant generally require higher temperatures to break the dormancy than less dormant seeds (Kępczyński & Sznigir, 2013), which could explain why the germination rate and latency did not decrease up to the investigated 30°C in our study while it did so in the study by Ruziev et al. (2020). Weed seeds that are subjected to a long period of stratification germinate slowly at low temperatures (Allen & Meyer, 1998). During a stay in longer time at different depths in the soil, the seeds entered the phase dormancy

and higher temperatures were needed to break this phase. Similarly to our study, Kępczyński and Sznigir (2013) used seeds that had been stratified for a long time and they showed for *Amaranthus retroflexus* that the rate of germination at 35°C was higher than at 25°C.

The fact that the seeds in the current study were stratified in a natural soil with relatively poor aeration could also play a role. Poor oxygen exchange acts to preserve dormancy since oxygen deficiency deactivates metabolic processes that leads to the production of the germination stimulators (Barthe et al., 2000). Cytokinin is responsible for the regulation of abscisic acid (ABA) that promote dormancy and inhibit or slows down germination (Barthe et al., 2000;Kermode, 2005; Stikić & Jovanović, 2015). When the conditions for germination are unfavourable, ABA increases the concentration and keeps the seeds in a latent state. When conditions become more favourable, the concentration of ABA decreases, which allows the activation of other hormones that promote germination (Kermode, 2005; Stikić & Jovanović, 2015).

The third hypothesis, which stated that the deeper the burial depth, the higher the temperatures needed to break seed dormancy, was supported by our results. A. trifida seeds are exposed to different temperatures depending on burial depth. The soil temperature during summer in an agricultural field 7 km away from the experiment area was lower at 30 cm than 5 cm soil depth, while the opposite was true during winter (Figure S1). Both summer temperatures and the temperature fluctuation between summer and winter may result in greater seed dormancy and a longer mean latency time (Tsilingiridis & Papakostas, 2014). One limitation of the current study is that soil temperatures were measured in a different soil than where the experiment was conducted and soil temperature can be affected by soil type, moisture content and slope direction. It is also a limitation that the different soil layers could have other differences than the temperature that were not considered, such as microbial activity (Barthe et al., 2000; Schafer et al., 2014; Schutte, Regnier, Harrison, Schmoll, et al., 2008). Since environmental factors are important for breaking of dormancy and germination time, we suggest that more data concerning the microenvironment are collected and included in analyses and interpretations in future research.

The age of the seeds and other factors are also likely to influence this relationship (Alebrahim et al., 2011; Andersson & Milberg, 1998; Benech-Arnold et al., 2000; Harre et al., 2019; Harrison et al., 2007; Liyanage & Ooi, 2017). There was a significant interaction between temperature and burial depth on the germination rate of seeds extracted 1 year after burial in 2019, but not for seeds extracted 3 years after burial in 2021. In general, there was a lower germination rate in 2021, and comparatively little difference between burial depths, compared to 2019 (Figure 3). This may be explained by the fact that older seeds tend to have increased dormancy (Andersson & Milberg, 1998). Thus, in 2019, there was a clear relationship between burial depth and the temperature necessary to break dormancy, while in 2021, temperature was not sufficient on its own to influence the germination rate. Our finding that higher temperatures are needed to break dormancy at higher burial depths is supported by studies on other species. For example, Benvenuti et al. (2001) found that the germination rate in Rumex obtusifolius dropped and latency increased as

burial depth and temperature dropped. Vleeshouwers (1997) found similar behaviour in *Polygonum persicaria, Chenopodium album* and *Spergula arvensis* though under comparatively shallow burial depths (0.5, 1, 2 cm) and temperatures (5, 10, 15, 20, 25°C). In agreement with the trend noted here, the germination rate for *Conyza canadensis* reached its maximum value at the lowest burial depth and decreased dramatically with increasing depth, for all temperatures (Ottavini et al., 2019).

4.4 | Implications for weed management

Accurately predicting weed emergence timing is crucial for planning weed management strategies (Page & Nurse, 2015), and optimising control efficacy of direct control efforts (Davis et al., 2013) can significantly reduce yield loss. Investigating the ecology of germination latency is essential for exploring management suitable for suppressing the germination of weed seeds when the possibility of conventional weed control is low (Alexander & Schrag, 2003). Our research shows that the latency and germination behaviours of seeds at different depths in the soil can provide important information about seed dormancy and the temperatures necessary to break dormancy. In general, the results of this study show that as the age of the seeds increases, dormancy becomes more pronounced, and it takes more time for the seeds to germinate. At the same time, the germination rate was the highest when seeds were from shallow burial depths. While previous papers have built predictive models for weed germination based on the effect of various factors (Benech-Arnold et al., 2000; Harrison et al., 2007), the results of our research emphasise the importance of understanding dormancy and latency to establish timely weed management.

The results of this study support earlier findings that the viable A. *trifida* seed bank is relatively short-lived at shallower burial depths (Harrison et al., 2007). Here, all populations displayed very low levels of dormancy at shallow soil depths (5 cm), and much greater levels of dormancy deep in the soil (40 cm), with a relatively linear relationship between germination rate/latency and both burial depth and temperature. Arguably, this could mean that ploughing could be employed to place *A. trifida* seeds deeper into the soil where they might remain dormant for up to a decade (Harrison et al., 2007). Subsequent ploughing might then return the viable seeds back to the surface. Tillage exposes seeds to a light before reburial and changes the temperature of the soil by exposing soils from lower depths to surface temperatures, thereby increasing the amplitude of temperature fluctuations, impacting seed dormancy and potentially promoting germination (Mohler, 1993).

A no-till or shallow-till strategy may be effective for retaining most of the *A. trifida* seeds at a shallow soil depth, where intensive weed control over a 1- or 2-year period would effectively empty the soil seed bank and prevent germinated plants from setting new seed. This strategy would be most effective if aided by management to increase the abundance of seed predators of *A. trifida* seeds (Harrison et al., 2003). Such seed predators are most effective against seeds that are not deeply buried (Sarabi, 2019). Seeds at intermediate soil depths (8-16 cm) still present a challenge for effective control. A. trifida seeds can emerge from this depth (Harrison et al., 2007), with ranges of dormancy that could lead to emergence over several years. Populations with larger seeds and seed viability would also have higher likelihood of emerging at these depths (Leishman et al., 2000). Thus, it would be valuable to experimentally test whether deep ploughing, prior to the initiation of such a no-till or shallow-till strategy, might be used to place the existing seedbank a depth (>35 cm) sufficient to prevent germination and emergence. Deep ploughing should then not be repeated until all surface and most deep seeds are likely to be dead. Our results also suggest that mixing seeds that have previously been at different depths through soil tillage would produce populations with variable dormancies. The management of these mixed populations would require control over extended periods, compared to a situation with only very shallow tillage, due to the more varying times necessary to break dormancy. However, experiments to test and validate these different control strategies are needed to confirm their effectiveness for A. trifida control.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Information about the data presented in this study is available from Aleksandra Savić (aleksandra.m.savic@gmail.com).

ORCID

Aleksandra Savić D https://orcid.org/0000-0003-0741-8453 Björn Ringselle D https://orcid.org/0000-0002-7081-1277 Didac Barroso-Bergadà D https://orcid.org/0000-0002-4887-9814 David A. Bohan D https://orcid.org/0000-0001-5656-775X Göran Bergkvist D https://orcid.org/0000-0001-9287-0510

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SUPPORTING INFORMATION

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