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# Exploring germination thresholds and seed properties of *Ambrosia artemisiifolia* populations from different European regions for improving control strategies

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**Introduction:** *Ambrosia artemisiifolia*, a highly invasive weed species, poses significant challenges to agriculture and human health. This study investigated the germination thresholds and physical properties of *A. artemisiifolia* populations from diverse regions in Europe, encompassing Serbia, Croatia, Italy, and France.

**Results:** Results revealed intriguing variations in germination thresholds among the populations. The Italian population exhibited the lowest base temperature ( $T_b$ ) of 0.58°C, closely followed by the Croatian population (1.49°C), statistically similar to the Serbian (1.46°C) and French (2.74°C) populations. In contrast, the Serbian population displayed the lowest base water potential ( $\Psi_b$ ) of -1.44 MPa, followed by the French population (-1.23 MPa), with no significant differences observed between the Italian (-0.78 MPa) and Croatian (-0.80 MPa) populations. Analysis of physical seed properties unveiled notable disparities in size, weight, and shape. The Italian population boasted the smallest, lightest, and most spherical seeds, while the French population harbored the largest and most elongated seeds. Interestingly, the seeds of the Croatian population were the heaviest.

**Conclusions:** This study underscores the adaptability of *A. artemisiifolia* populations to diverse climatic conditions, showcasing varied responses across regions. These findings elucidate the intricate interplay between environmental factors and seed traits, offering valuable insights for the development of effective weed management strategies.

## KEYWORDS

invasive species, germination thresholds, seed properties, climate adaptation, weed management strategies

## 1 Introduction

Among the vast array of plant species within the *Ambrosia* genus, *Ambrosia artemisiifolia* L. emerges as a particularly troublesome species (Goeden and Andrès, 1999; Taylor, 2019). Originating in North America, this invasive plant from the Asteraceae family has rapidly expanded its reach, becoming a ubiquitous presence in diverse ecosystems around the world (Smith et al., 2013; Montagnani et al., 2017). Characterized by its robust vigor, superior adaptability, high seed yields, and rapid dispersal, *A. artemisiifolia* presents an important menace capable of significantly altering the dynamics of native flora and fauna (Essl et al., 2015). Over the last two centuries, *A. artemisiifolia* has spread in 80 countries, disrupting ecological balances, diminishing biodiversity, and threatening the production of valuable farmland, thereby reducing crop yields (Dong et al., 2020). The adaptability potential of *A. artemisiifolia* takes various forms, including genetic diversity and phenological variations. Studies have consistently highlighted the high genetic variability of this species, pointing to its capacity to adapt to diverse environments (Genton et al., 2005; Li et al., 2019; Sun et al., 2020). Beyond genetic diversity, also the phenological variations are further accentuating the species' ability to thrive across varied ecological niches (Buttenschön et al., 2009; Leskovšek et al., 2012; Scalone et al., 2016). This adaptability assumes even greater significance considering predictions of *A. artemisiifolia*'s continued expansion fueled by global warming (Cunze et al., 2013; Skálová et al., 2017; Sun et al., 2020). In addition to its disruptive impact on natural ecosystems, *A. artemisiifolia* has proven to be a significant agricultural weed. Changes in agricultural practices, especially the shift towards more intensive farming systems, have provided a suitable environment for the accelerated expansion of this invasive species (Kiss and Béres, 2006). Studies indicate that high populations of *A. artemisiifolia* can result in substantial yield losses, reaching up to 75% in soybean and 80% in maize, compared to estimated weed-free yields (Weaver, 2001; Cowbrough et al., 2003). Various control measures including chemical, physical and biological techniques have been explored to mitigate the impact of *A. artemisiifolia* (Buttenschön et al., 2009; Milakovic et al., 2014; Milakovic and Karrer, 2016). However, eradication of this species has proven to be a formidable challenge. Notably, *A. artemisiifolia* exhibits resistance to air and soil pollution (Pichtel et al., 2000; Ziska, 2002), and in some cases it remarkably retains the ability to reproduce even after damage from defoliation and mowing (Brandes and Nitzsche, 2006; Gard et al., 2013). Presently, control of this invasive weed species is feasible in major crops through chemical, mechanical, or combined measures (Scruggs et al., 2019; Máčajová et al., 2022; Wang et al., 2022). However, there is a concern over the potential development of herbicide resistance over time (Saint-Louis et al., 2005). Understanding the distribution and spread of this species is challenging. Its introduction to Europe was tied to trade, resulting in different introduction points at different times and contributing to genetic variations. Populations already present in Europe further propagated in a similar manner, fostering hybridization and population variations (Csontos et al., 2010; Chapman et al., 2016;

van Boheemen et al., 2017; Afonin et al., 2018). Despite existing studies on the introduction and distribution of *A. artemisiifolia* in the origin areas of the studied populations (Chauvel et al., 2006; Csontos et al., 2010; Galzina et al., 2010; Gentili et al., 2017), pinpointing the exact introduction pathway and population evolution remains a difficult, if not impossible, task. Given the species' great adaptability potential and diversification (Battlay et al., 2023), it might be more meaningful to explore the responses of different populations to climatic conditions.

To address this critical issue and improve the control of *A. artemisiifolia*, an in-depth study of its behavior and physiology is essential, particularly during crucial stages such as germination. Germination and subsequently the emergence are the most critical periods in weed species life cycle, as they can largely influence the future competition with the crops and damage to the yield (Forcella et al., 2000). These critical periods mostly depend on the temperature and water availability needed for germination processes. In this regard it was discovered that seeds have temperature and water thresholds below which germination is not possible, these thresholds are defined as base temperature ( $T_b$ ) and base water potential ( $\Psi_b$ ) respectfully (Arnold, 1959; Dahal and Bradford, 1994). This knowledge can inform the development of emergence models, aiding in predicting growth dynamics and suggesting optimal timing for control operations, thereby reducing herbicide use and airborne pollen levels (Masin et al., 2005, 2010, 2014; Colbach et al., 2007). Given the high variability of *A. artemisiifolia*, that reflects in both a wide range of temperatures and water availability needed for germination (Leiblein and Lösch, 2011; Dinelli et al., 2013; Knolmayer et al., 2024), it is crucial to determine if populations from different regions exhibit similar behavior. Considering that there are only a few articles found in the literature that examined these parameters (Guillemin et al., 2013), in this study, we compared four *A. artemisiifolia* populations, examining seed parameters and determining base temperature ( $T_b$ ) and base water potential ( $\Psi_b$ ) essential for germination, as well as different seed physical properties. By discovering the germination dynamics of diverse populations, our research aims to contribute to a broader understanding of *A. artemisiifolia* behavior. Insights gained can potentially inform the development of effective control strategies that are appropriate to specific populations, ultimately mitigating the ecological, agricultural, and health impacts of this invasive species.

## 2 Materials and methods

### 2.1 Seed collection

Experiments were conducted in 2018 at the University of Padova, Department of Agronomy, Food, Natural Resources, Animals and Environment (DAFNAE). The mature, ripe seeds (achenes) of *A. artemisiifolia* were hand collected in 2017 from four different locations: Dijon in eastern France  $-47^{\circ}20'43''N$   $5^{\circ}06'05''E$  (FR), Turin in northwestern Italy  $-45^{\circ}07'27''N$   $7^{\circ}31'04''E$  (IT), Zagreb in central Croatia  $-45^{\circ}44'02''N$   $15^{\circ}54'23''E$  (CRO) and

Šabac in northwestern Serbia  $-44^{\circ}45'49''\text{N}$   $19^{\circ}36'12''\text{E}$  (SRB); in each case the seeds were collected from an agricultural environment (Figure 1). The decision to collect seeds from these sites, very far apart from one another was based on previous studies (Scalone et al., 2016; Song et al., 2023; Putra et al., 2024), which determined the absence or very low variability between the close populations, even when separated by several kilometers from one another. In addition, this species shows niche-filling tendencies, meaning that there are little to no statistically significant differences between the populations that occupy a single niche, for example in a study conducted in Australia the expansion of the range of *A. artemisiifolia* was seen only in the case of introduction of this species populations from different continents (Song et al., 2023; Putra et al., 2024). After harvesting, all seeds underwent a two-step cleaning procedure. The seeds were firstly manually cleaned by rubbing them against a wooden tablet laced with rubber to avoid damaging the seeds. In this way, different impurities present were ground reducing their weight. After this initial step, a seed blower was used to separate the seeds from impurities blowing them away as they were lighter than the seeds. Once the cleaning was completed the seeds were stored in a dry environment at  $4^{\circ}\text{C}$  until utilized. In all the trials the original seeds collected at different sites were used.

## 2.2 Meteorological data

Since the geographical distribution of the examined populations is quite diverse it is reasonable to assume that certain parameters are influenced by the climate. To account for this, temperature and precipitation data were sourced from [Climate-Data.org](https://climate-data.org), a platform with confirmed reliability, that has been widely used in previous studies (Rodriguez and D'Alessandro, 2019; Stradford et al., 2021; Gardin et al., 2023). According to the Köppen-Geiger classification, Zagreb, Šabac and Turin are categorized as Cfa with warm

temperatures, humid and hot summers (Kottek et al., 2006). Dijon is classified as Cfb, which indicates a warm summer, high humidity and warm temperature. The average annual temperature in Zagreb is  $11^{\circ}\text{C}$ . July is the warmest month with a maximum temperature of  $27.4^{\circ}\text{C}$ , while January is the coldest at  $-2.8^{\circ}\text{C}$ . The average annual precipitation is 930 mm. Dijon has a similar average annual temperature of  $11^{\circ}\text{C}$ . July has the highest temperatures at  $24.7^{\circ}\text{C}$ , while February is the lowest at  $-0.3^{\circ}\text{C}$ . The average annual precipitation is 982 mm. In Turin, the average temperature rises slightly to  $12^{\circ}\text{C}$ . July remains the warmest month with a maximum temperature of  $27.3^{\circ}\text{C}$ , and the lowest average temperature is  $-1.7^{\circ}\text{C}$  in January. The city records an average annual precipitation of 1002 mm. In Šabac, the average annual temperature rises to  $12.9^{\circ}\text{C}$ . August is the warmest month with a maximum temperature of  $29.1^{\circ}\text{C}$ , while January has the lowest temperature at  $-2.6^{\circ}\text{C}$ . The average annual precipitation is 714 mm.

The data presented is the average on a monthly basis, spanning a 30-year period from 1991 to 2021 (Figure 2).

## 2.3 Temperature threshold

To determine the temperature thresholds for germination, climate chambers were set at the following temperatures: 1, 3, 6, 9, 12, 15, 18, 21, 24, 27 and  $30^{\circ}\text{C}$ . Four replicates of 50 seeds each were tested for each temperature and for each population of *A. artemisiifolia*, following an already established protocol in different similar works (Puteh et al., 2010; Loddo et al., 2013, 2018). The seeds were sown on filter paper (Whatman No. 1, Whatman, Maidstone, UK) in 9 cm-diameter Petri dishes with 4 ml of distilled water. After sowing, the Petri dishes were sealed with parafilm and placed inside the climate chambers (W87R, KW Apparacchi Scientifici SRL, via della Resistenza 119, 53035 Monteriggioni, Italy) set to the predetermined temperature, and



FIGURE 1

The overview map (top-right) shows the European continent, with a yellow box marking the region where the seed populations originated. The main map provides a detailed view of this region, highlighting the specific locations where seeds were collected.

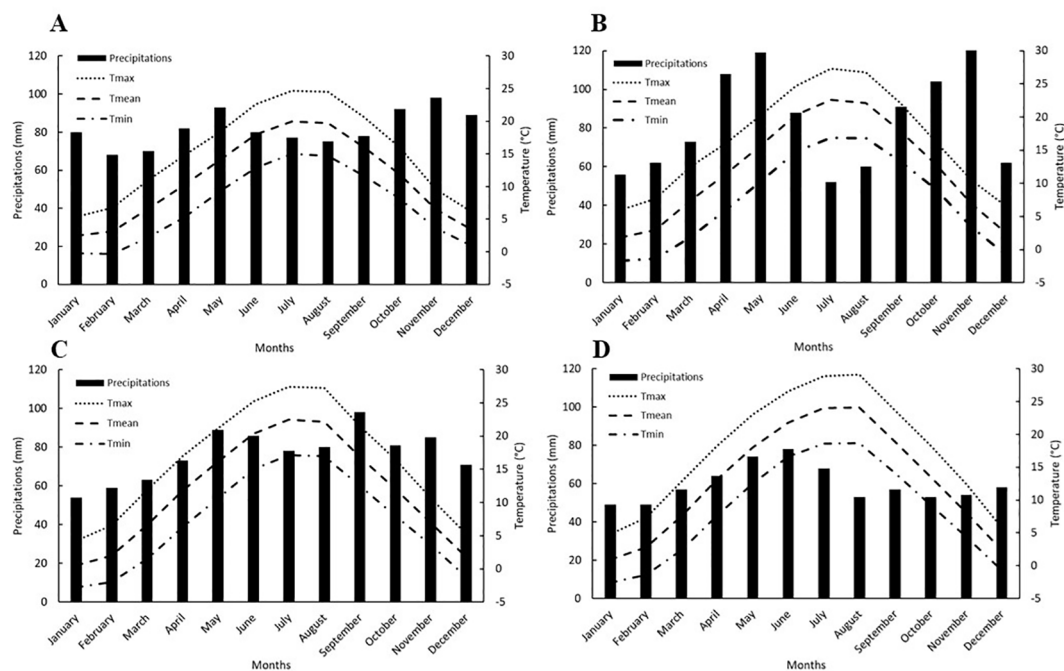


FIGURE 2

Average monthly precipitations, minimum, mean and maximum temperatures in Dijon (A), Turin (B), Zagreb (C) and Šabac (D) for a 30-year period from 1991 to 2021 (source: [Climate-Data.org](https://climate-data.org)). Tmax, maximum temperature; Tmean, mean temperature; Tmin, minimum temperature.

with a photoperiod of 12 h light and 12 h dark; water was added if needed. Germination was monitored every 2–3 days, and was considered concluded once all seeds had germinated or after 10 days had elapsed without further germination, as proposed by (Onofri et al., 2010; Baskin and Baskin, 2014b). All germinated seeds were counted and removed.

## 2.4 Water potential threshold

The water potential threshold was determined using the same seed of the populations previously described. Polyethylene glycol (PEG) 6000 (Sigma-Aldrich Chemie GmbH 25322-68-3, St. Louis, MO, USA) was used to simulate different conditions of water availability. Following the formula proposed by Kaufmann and Michel (1973), specific quantities of PEG-6000 were added to distilled water to obtain solutions of  $-0.05$ ,  $-0.10$ ,  $-0.30$ ,  $-0.50$ ,  $-0.70$ ,  $-1.00$ ,  $-1.50$ ,  $-2.00$  MPa; controls consisted in distilled water (0.00 MPa) alone. The seeds were sown on filter paper and placed in plastic containers with diameter and height of 10 cm and 7 cm, respectively, as described by Šoštarčić et al. (2021a) with the specific PEG-6000 solution; the liquid level was kept below the seeds to prevent them from being immersed in the solution. The experiment consisted of four replicates of 50 seeds each, for each population of *A. artemisiifolia*. After sowing, the plastic containers were closed and placed in climate chambers at 24°C with a photoperiod of 12 h light and 12 h dark. Germination was monitored every 2–3 days and was considered concluded after 10 days had elapsed without further germination (Onofri et al., 2010; Baskin and Baskin, 2014b). All germinated seeds were counted and removed.

## 2.5 Physical seed properties

Considering the diverse origins of the tested populations and in order to characterize them, the seed physical properties were also analyzed. Seed physical properties, such as size, weight, and shape, are critical traits that can significantly influence germination processes and plant performance under varying environmental conditions (Leishman, 2001; Norden et al., 2009). For example, variations in seed size and mass have been shown to affect germination metrics such as germination time (Murali, 1997) and germination percentage (Van Mólken et al., 2005). These characteristics indirectly impact plant distribution and abundance, contributing to the ability of species to establish across different habitats (Silveira et al., 2012). Importantly, seed size can vary both within and between plant species, sometimes by several orders of magnitude (Leishman et al., 1995; Silvertown and Bullock, 2003; Moles and Westoby, 2006). Such variability in seed traits is often correlated with differences in germination parameters, which may enhance a species capacity to colonize diverse habitats and expand its geographic range (Ranieri et al., 2012). Understanding these variations is therefore essential for interpreting inter-population differences and predicting weed emergence dynamics. For this, various metrics, including total area, perimeter, circularity, and weight, were measured and compared. To obtain high-resolution images, 100 seeds were randomly selected from each population and scanned using an Expression 1100 XL scanner (EPSON, Suwa, Nagano, Japan). An object with known dimensions was included during scanning for subsequent analysis. The obtained images were processed using the ImageJ open-source software (<https://imagej.net/ij/index.html>)

chosen for its established reliability, precision, and user-friendliness in previous studies (Schneider et al., 2012; Schroeder et al., 2021). Prior to measurements, the images were converted into black and white 8-byte images, assigning values exclusively to the seeds while excluding any extraneous elements. Calibration of the software was performed using the object with known dimensions scanned alongside the seeds, converting values from pixels to millimeters. To determine seed weight, four groups of 100 seeds from each population were measured using a Mettler PM100 laboratory precision balance (Mettler Toledo, Columbus, Ohio, USA).

## 2.6 Statistical analysis

All statistical analyses were performed in the R environment (version 4.3.2) (RStudio Team, 2023).

$T_b$  and  $\Psi_b$  were assessed with the `drc` and `drcSeedGerm` packages using the methods proposed by Mesgaran (2019).

A thermal time model with sub-optimal temperatures was used to determine the base temperature, as in the work of Nikolić and Masin (2024) and Oveisi et al. (2024). The model first fits a sigmoid nonlinear regression to the cumulative data from each temperature:

$$G(t) = \frac{G_{max}}{1 + \exp(b(\log(t) - \log(t_{50})))}$$

Where:

$G(t)$  = cumulative germination over time,  $t$ .

$G_{max}$  = maximum germination as  $t$  approaches infinity.

$b$  = slope around the inflection point.

$t_{50}$  = time at which germination is half  $G_{max}$ .

It then calculates the time to germination:

$$t(g) = t_{50} \left( \frac{G_{max}}{g} - 1 \right)^{\frac{1}{b}}$$

Where:

$t(g)$  = time to a given germination percentage.

$g$  = germination percentage.

The model then calculates the germination rate (rapidity), GR, which is simply the reciprocal of the time to a given germination percentile:

$$GR = \frac{1}{t_g}$$

And finally, it investigates the relationship between GR and temperature,  $T$ , for each  $g$  using a linear regression model of the form:

$$GR = b(T - T_b)$$

Where:

$T_b$  = the base temperature ( $^{\circ}\text{C}$ ).

$b$  = the slope.

A similar procedure was used to calculate the base water potential ( $\Psi_b$ ), substituting the different temperatures with the different levels of water potential (from 0 to  $-2$  MPa), while the temperature was a constant  $24^{\circ}\text{C}$ .

To determine whether there were significant differences in seed dimensions and weight, a one-way ANOVA was performed followed by Tukey's HSD test ( $p < 0.05$ ) for *post hoc* analysis. Differences between different base temperatures ( $T_b$ ) and base water potentials ( $\Psi_b$ ), were analyzed using Students T test.

## 3 Results

Base temperatures and base water potentials of the studied populations of *A. artemisiifolia* are shown in Table 1.

The analysis showed distinct trends in  $T_b$  across the tested populations (Table 1). Notably, the Italian population exhibited the lowest  $T_b$  and was significantly different from the Serbian and French populations. Differently, the French population displayed the highest  $T_b$ , but was not statistically different from the Serbian and Croatian populations. The Croatian population had noteworthy variability, as evident from the standard error values.

The base water potentials ( $\Psi_b$ ) among *A. artemisiifolia* populations exhibited more pronounced variations than the observed differences in  $T_b$  (Table 1). The  $\Psi_b$  of the Italian and Croatian populations were the highest, with no significant difference between them. Conversely, the Serbian and French populations displayed considerably lower  $\Psi_b$  values, with the lowest being the one of the Serbian population.

The results of the one-way ANOVA on the physical properties are presented in Table 2.

There were significant differences between the populations for every physical property tested (Figure 3). The seeds belonging to the French population were the largest, followed by the Croatian population and then by the Serbian and Italian, with seeds of a similar size. It can also be seen that the results concerning seed perimeter confirm the size comparison. However, although similar in area, it can be observed that the perimeter is different between the seeds of Serbian and Italian population of this weed species.

Seed circularity is an insightful parameter offering information about seed shape. A value closer to 1 indicates a shape more akin to a perfect circle, while a value closer to 0 signifies a more elongated form. It is noteworthy that none of the tested populations exhibits perfectly round seeds. Among them, the Italian population comes closest to a circular shape, while the French population showcases the most elongated seeds.

TABLE 1 Estimated base temperature and base water potential for different populations of *A. artemisiifolia*, the letters indicate a significant difference  $p$ -value  $< 0.05$ .

Population	$T_b$ ( $^{\circ}\text{C}$ )	SE ( $\pm$ )	$\Psi_b$ (MPa)	SE ( $\pm$ )
Dijon (FR)	2.74 c	0.48	-1.23 c	0.04
Turin (IT)	0.58 a	0.12	-0.78 a	0.07
Zagreb (CRO)	1.49 abc	0.69	-0.80 a	0.05
Šabac (SRB)	1.46 bc	0.35	-1.44 b	0.12

IT, Italy; CRO, Croatia; SRB, Serbia; FR, France.

TABLE 2 Results of the one-way ANOVA for different properties of the four *A. artemisiifolia* populations tested.

Source of variation	n - 1	Physical properties of seeds							
		Area		Perimeter		Circularity		Weight	
		F value	p-value	F value	p-value	F value	p-value	F value	p-value
Population	3	74.4	2.2x10 <sup>-16</sup> ***	87.1	2.2x10 <sup>-16</sup> ***	59.5	2.2x10 <sup>-16</sup> ***	39.8	1.63x10 <sup>-6</sup> ***
Residuals									

\*\*\*P &lt; 0.001.

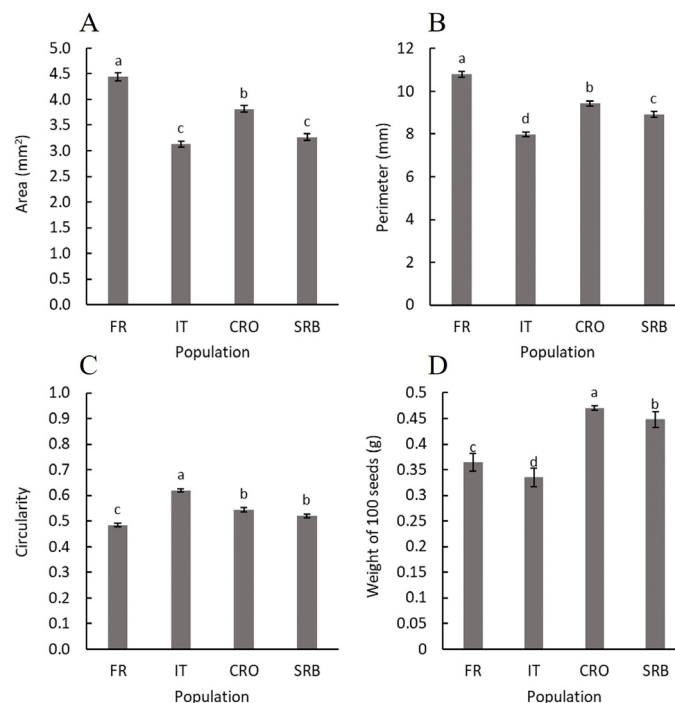


FIGURE 3

Seed area (A), seed perimeter (B), seed circularity (C), and the weight of 100 seeds (D) of different ecotypes of *A. artemisiifolia*. The letters indicate a significant difference p-value < 0.05. FR, France; IT, Italy; CRO, Croatia; SRB, Serbia.

Finally, the results show a distinctive seed weight for each population. Surprisingly, the seeds of the Croatian population, despite not being the largest, emerge as the heaviest among the populations. In contrast, the seeds of the French population, which are the largest in size, rank third in terms of weight. Remarkably, the lightest seeds are from the Italian population, aligning with the smaller size characteristic of this population's seeds.

## 4 Discussion

The results revealed disparities in both germination thresholds and physical properties among various populations of *A. artemisiifolia*. This aligns with prior studies highlighting the weed species considerable genetic and phenotypic variability (Leiblein-Wild and Tackenberg, 2014; Martin et al., 2016; Li et al., 2019). Rapid adaptation to new environments is a common trait among invasive weed species (Prentis et al., 2008; Clements and Jones,

2021; Gong et al., 2022). The introduction of *A. artemisiifolia* to Europe from its native habitat employed an adaptation strategy, establishing it as a formidable invasive species globally. Studies on *A. artemisiifolia* adaptation underscore its exceptionally high potential, with adaptations occurring rapidly, contributing significantly to its invasiveness (Battlay et al., 2023). These findings are in accordance with the results obtained in this study, revealing interesting differences and similarities among the studied populations.

The influence of climate and climate change on the behavior of *A. artemisiifolia* is well-documented (Hamaoui-Laguel et al., 2015; Case and Stinson, 2018; Gentili et al., 2019; Xian et al., 2023), consistent with the results obtained in this study. Analyzing meteorological data on minimum, maximum, and mean temperatures in the four areas (Figure 2) reveals that Turin and Zagreb experience similar temperatures. Conversely, Šabac tends to have higher temperatures in the spring-autumn period, while Dijon tends to have lower temperatures during the same period compared

to Turin and Zagreb. This may explain the similarities in  $T_b$  for the Turin and Zagreb populations, although the Croatian population shows significant variability, indicating a more diverse response. Notably, the spring temperatures for Zagreb intersect with those of other places, potentially explaining its wide germination range.

For the Serbian and French populations, Šabac experiences very low winter temperatures that rise rapidly in spring, remaining high until autumn. While the temperatures in Dijon are consistently lower than in other areas, the consistently high minimum temperatures may explain why this population has the highest  $T_b$ . This is in accordance with different studies conducted on this matter, explaining how  $T_b$  is closely linked with the temperature of the habitat, indicating that the plants, even of the same species growing under different temperature regimes will have different  $T_b$ , ergo plants growing in colder climates will have lower  $T_b$  compared with those growing in warmer climates (Trudgill et al., 2000; Bao et al., 2019). This finding highlights important considerations for effective weed control strategies. For instance, in Dijon, the combination of consistently high and steady minimum temperatures during the early months corresponds to a population with a higher  $T_b$ . This likely delays seedling emergence compared to populations from warmer regions, as emergence depends on the accumulation of sufficient thermal time above  $T_b$  (Grundy, 2003; Baraibar et al., 2018). Such delayed emergence may help *A. artemisiifolia* in Dijon avoid frost damage or other unfavorable early-season conditions, allowing optimal emergence and development during warmer months. This pattern aligns with adaptive strategies observed in other weed species (Ramesh et al., 2017). However, this delayed emergence has practical implications for weed management, necessitating adjustments in the timing of control measures to coincide with peak seedling emergence. Emergence predictive models can play a crucial role in this regard. In contrast, populations with lower  $T_b$  might emerge earlier, leading to differences in developmental stages across regions, further emphasizing the need for region-specific management strategies. Examining the  $\Psi_b$  of the studied species and observing precipitation data in Figure 2, it is evident that Turin receives the most precipitation in April and May, aligning with June precipitation in Zagreb. This explains the high  $\Psi_b$  of the Italian population and its similarity to the Croatian one. In contrast, Šabac receives significantly less precipitation during the same period, establishing it as the driest area compared to others. This likely accounts for the low  $\Psi_b$  of the Serbian *A. artemisiifolia* population, indicating adaptation to drought conditions. As for  $T_b$ , similar studies were conducted on the relationship between the  $\Psi_b$  of plants and water availability in different habitats. These studies also concluded that the seeds developing in more arid conditions will have a more negative  $\Psi_b$  compared to those, even of the same species, growing in more humid conditions (Ceri and Etherington, 1991; Baskin and Baskin, 2014a; Bao et al., 2022). Interestingly, despite high precipitation in the Dijon area, its  $\Psi_b$  is the second lowest. This discrepancy may be attributed to lower temperatures in this region compared to others, emphasizing the crucial interaction between temperature and precipitation for germination thresholds. A similar finding can also be observed in the work by Dürr et al. (2015), who observed that species growing in cool conditions were

more able to germinate in dry conditions than those growing in warmer conditions.

It is important to emphasize that the seeds used in these trials were the original seeds collected from their native sites and were not reproduced in a common garden or uniform environment. This approach was chosen to capture the seeds local responses, reflecting the base temperature ( $T_b$ ) and base water potential ( $\Psi_b$ ) specific to their place of origin. By including both external (climatic) and internal (genetic/maternal) effects influencing these parameters, this work aimed to provide results that are representative of real-world conditions. This is particularly critical given that emergence predictive models are designed for specific areas and require calibration to ensure their accuracy and efficiency in those environments (Masin et al., 2010, 2012, 2014; Šoštarčić et al., 2021b).

The results regarding the physical properties of the seeds are consistent with studies on invasive weed species, demonstrating high variability among different populations (Fenollosa et al., 2021). These findings parallel the results of germination thresholds and can be interpreted as an adaptation to different climatic conditions. Qiu et al. (2010) found a positive correlation between high precipitation and low temperatures, influencing seed size. This aligns with our results, as French seeds turned out to be the largest. The same authors also noted that larger seeds typically have lower temperature requirements for germination, contradicting our findings. However, our results align with those of Ge et al. (2020), who discovered that some larger seeds might have higher thermal requirements for germination.

Several studies investigating the influence of the origin of *A. artemisiifolia* have highlighted temperature as a major driver of seed variability between different populations. Typically, seeds from higher latitudes and lower temperatures produce larger seeds with lower germination potential compared to populations from lower latitudes and higher temperatures (Li et al., 2015; Zhou et al., 2021), consistent with the results obtained in this study.

In discussing the generalizability of our findings across different populations of *A. artemisiifolia*, it is important to consider the reasons behind the selection of the four populations used in this study. Previous research has shown that populations of *A. artemisiifolia* exhibit very low variability when situated within the same geographic niche, even when separated by several kilometers (Scalone et al., 2016; Song et al., 2023; Putra et al., 2024). A similar niche effect was also found by Farooq et al. (2019), according to the authors, this effect is a consequence of ecological adaptations to prevailing climatic conditions in the area. This consistency in population characteristics supports our decision to focus on populations from distinctly different regions across Europe. Additionally, the niche-filling tendencies of this species imply that significant variations are more likely to arise from populations that are very far apart or exposed to very different conditions, differences and similarities between the populations uncovered in this work are clear evidence in support of this claim. This context is crucial as it not only underpins the reliability of our data, suggesting that the observed differences in germination thresholds and seed properties are likely attributable to regional climatic conditions rather than mere geographic proximity. But it also highlights one of the main limitations of emergence predictive models—'one model cannot fit

all—emphasizing the need to develop specific models tailored to different areas.

The results presented here broaden our understanding of the behavior of this important invasive species, but can also be considered as an important contribution to effective control strategies. As it was mentioned previously, different control strategies for *A. artemisiifolia* are present, including chemical, mechanical and biological methods, that can also be combined, with varying degrees of effectiveness (Buttenschön et al., 2009; Gerber et al., 2011; Essl et al., 2015). Considering that the chemical weed control methods are often the most effective ones, it is no surprise that they are the most used ones, also for the control of this species. However, the need to control *A. artemisiifolia* also outside of the strictly agricultural context, both effective and environmentally friendly control becomes particularly challenging (Essl et al., 2015; Wang et al., 2022).

Using the temperature and water potential thresholds determined in this work, it could be possible to create emergence prediction models for the tested areas, to assist the farmers and authorities in choosing the best timing for control operations, thus maximizing the effectiveness and reducing the excessive use of herbicides (Masin et al., 2010, 2012). Moreover, the same principle could also be applied for mechanical control methods and integrated weed management (IWM) strategies, providing the species emergence percentage in time. An example of the usefulness of choosing the right time for weed control operations can be observed in the work of Beam et al. (2021), who found that the effectiveness of *A. artemisiifolia* control using IWM strategies strongly depends on the time of their application. Having in mind that today the timing of control operations against this weed species is decided arbitrarily, an emergence predictive model based on the data obtained in this study could significantly improve this weed management strategy.

## 5 Conclusion

This study sheds light on the germination thresholds and diversity among different European populations of *A. artemisiifolia*, offering crucial insights into the variability of this invasive species. The results demonstrated significant differences in germination thresholds, with the Italian population exhibiting the lowest base temperature (0.58°C), while the French population demonstrated the highest (2.74°C), and the Serbian population showing the lowest base water potential (−1.44 MPa), while the Italian one exhibited the highest (−0.78). Additionally, substantial disparities were also observed in seed physical properties, where the Italian population had the smallest and lightest seeds, while the French population had the largest and most elongated seeds. Given its high adaptability and the associated threats to human and animal health, as well as agricultural production, the findings presented in this research carry substantial importance.

By addressing the gap in knowledge regarding the differentiation of *A. artemisiifolia* at a European level, considering diverse climatic conditions and geographic origins, this study contributes valuable

information for the effective management of this weed species. The germination thresholds obtained can serve as foundational data for constructing emergence predictive models or enhancing existing ones, which are vital for timely control measures against this agricultural and health hazard in Europe.

Moreover, understanding the levels of seed variability provides a basis for refining control strategies and mitigating the spread of this invasive species. While this study offers valuable insights, further research is needed, including more populations from various European countries. Future studies, particularly those simulating the effects of climate change, will contribute to a more comprehensive understanding of *A. artemisiifolia*'s adaptability. Such insights are crucial for anticipating the species' impact on agricultural production and the overall well-being of European communities.

## Data availability statement

The original contributions presented in the study are included in the article/supplementary material. Further inquiries can be directed to the corresponding author.

## Author contributions

NN: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Resources, Software, Validation, Writing – original draft. VŠ: Conceptualization, Data curation, Investigation, Methodology, Resources, Validation, Writing – review & editing. MŠ: Conceptualization, Resources, Supervision, Visualization, Writing – review & editing. RM: Conceptualization, Formal analysis, Project administration, Resources, Supervision, Visualization, Writing – review & editing.

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## Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.



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## References

- Afonin, A. N., Luneva, N. N., Fedorova, Y. A., Kletchkovskiy, Y. E., and Chebanovskaya, A. F. (2018). History of introduction and distribution of common ragweed (*Ambrosia artemisiifolia* L.) in the European part of the Russian Federation and in the Ukraine. *EPPO. Bull.* 48, 266–273. doi: 10.1111/epp.12484
- Arnold, C. Y. (1959). The determination and significance of the base temperature in a linear heat unit system. *Proc. Am. Soc. Hortic. Sci.* 74, 430–445.
- Bao, G., Song, M., Wang, Y., Saikkonen, K., and Wang, H. (2019). Interactive effects of Epichloë fungal and host origins on the seed germination of *Achnatherum inebrians*. *Symbiosis* 79, 49–58. doi: 10.1007/s13199-019-00636-0
- Bao, G., Zhang, P., Wei, X. X., Zhang, Y., and Liu, W. (2022). Comparison of the effect of temperature and water potential on the seed germination of five *Pedicularis kansuensis* populations from the Qinghai–Tibet plateau. *Front. Plant Sci.* 13. doi: 10.3389/fpls.2022.1052954
- Baraibar, B., Mortensen, D. A., Hunter, M. C., Barbercheck, M. E., Kaye, J. P., Finney, D. M., et al. (2018). Growing degree days and cover crop type explain weed biomass in winter cover crops. *Agron. Sustain. Dev.* 38. doi: 10.1007/s13593-018-0543-1
- Baskin, C. C., and Baskin, J. M. (2014a). Biogeographical and evolutionary aspects of seed dormancy. *Seeds*. 1005–1073. doi: 10.1016/B978-0-12-416677-6.00012-3
- Baskin, C. C., and Baskin, J. M. (2014b). “Ecologically meaningful germination studies,” in *Seeds* (Elsevier, Amsterdam, The Netherlands), 5–35. doi: 10.1016/B978-0-12-416677-6.00002-0
- Battlay, P., Wilson, J., Bieker, V. C., Lee, C., Prapas, D., Petersen, B., et al. (2023). Large haploblocks underlie rapid adaptation in the invasive weed *Ambrosia artemisiifolia*. *Nat. Commun.* 14. doi: 10.1038/s41467-023-37303-4
- Beam, S. C., Cahoon, C. W., Haak, D. C., Holshouser, D. L., Mirsky, S. B., and Flessner, M. L. (2021). Integrated weed management systems to control common ragweed (*Ambrosia artemisiifolia* L.) in soybean. *Front. Agron.* 2. doi: 10.3389/fagro.2020.598426
- Brandes, D., and Nitzsche, J. (2006). Biology, introduction, dispersal, and distribution of common ragweed (*Ambrosia artemisiifolia* L.) with special regard to. *Nachrichtenbl. Deut. Pflanzenschutzd.* 58, 286–291.
- Buttenschön, R. M., Waldspühl, S., and Bohren, C. (2009). *Guidelines for management of common ragweed, Ambrosia artemisiifolia*, 27\_SMS. Available at: <http://www.EUPHRESKO.org>.
- Case, M. J., and Stinson, K. A. (2018). Climate change impacts on the distribution of the allergenic plant, common ragweed (*Ambrosia artemisiifolia*) in the eastern United States. *PLoS One* 13, 1–12. doi: 10.1371/journal.pone.0205677
- Ceri, E., and Etherington, J. (1991). The effect of soil water potential on seedling growth of some British plants. *New Phytol.* 118, 571–579. doi: 10.1111/j.1469-8137.1991.tb00998.x
- Chapman, D. S., Makra, L., Albertini, R., Bonini, M., Páldy, A., Rodinkova, V., et al. (2016). Modelling the introduction and spread of non-native species: international trade and climate change drive ragweed invasion. *Glob. Change Biol.* 22, 3067–3079. doi: 10.1111/gcb.13220
- Chauvel, B., Dessaint, F., Cardinal-Legrand, C., and Bretagnolle, F. (2006). The historical spread of *Ambrosia artemisiifolia* L. @ in France from herbarium records. *J. Biogeogr.* 33, 665–673. doi: 10.1111/j.1365-2699.2005.01401.x
- Clements, D. R., and Jones, V. L. (2021). Rapid evolution of invasive weeds under climate change: present evidence and future research needs. *Front. Agron.* 3. doi: 10.3389/fagro.2021.664034
- Colbach, N., Chauvel, B., Gauvrit, C., and Munier-Jolain, N. M. (2007). Construction and evaluation of ALOMYSYS modelling the effects of cropping systems on the blackgrass life-cycle: From seedling to seed production. *Ecol. Modell.* 201, 283–300. doi: 10.1016/j.ecolmodel.2006.09.018
- Cowbrough, M. J., Brown, R. B., and Tardif, F. J. (2003). Impact of common ragweed (*Ambrosia artemisiifolia*) aggregation on economic thresholds in soybean. *Weed. Sci.* 51, 947–954. doi: 10.1614/02-036
- Csontos, P., Vitalos, M., Barina, Z., and Kiss, L. (2010). Early distribution and spread of *Ambrosia artemisiifolia* in Central and Eastern Europe. *Bot. Helv.* 120, 75–78. doi: 10.1007/s00035-010-0072-2
- Cunze, S., Leiblein, M. C., and Tackenberg, O. (2013). Range expansion of *Ambrosia artemisiifolia* in Europe is promoted by climate change. *ISRN. Ecol.* 2013, 1–9. doi: 10.1155/2013/610126
- Dahal, P., and Bradford, K. J. (1994). Hydrothermal time analysis of tomato seed germination at suboptimal temperature and reduced water potential. *Seed. Sci. Res.* 4, 71–80. doi: 10.1017/S096025850000204X
- Dinelli, G., Marotti, I., Catizone, P., Bosi, S., Tanveer, A., Abbas, R., et al. (2013). Germination ecology of *Ambrosia artemisiifolia* L. and *Ambrosia trifida* L. biotypes suspected of glyphosate resistance. *Open Life Sci.* 8. doi: 10.2478/s11535-013-0135-z
- Dong, H., Song, Z., Liu, T., Liu, Z., Liu, Y., Chen, B., et al. (2020). Causes of differences in the distribution of the invasive plants *Ambrosia artemisiifolia* and *Ambrosia trifida* in the Yili Valley, China. *Ecol. Evol.* 10, 13122–13133. doi: 10.1002/ece3.6902
- Dürr, C., Dickie, J. B., Yang, X. Y., and Pritchard, H. W. (2015). Ranges of critical temperature and water potential values for the germination of species worldwide: Contribution to a seed trait database. *Agric. For. Meteorol.* 200, 222–232. doi: 10.1016/j.jagromet.2014.09.024
- Essl, F., Biró, K., Brandes, D., Broennimann, O., Bullock, J. M., Chapman, D. S., et al. (2015). Biological flora of the British Isles: *Ambrosia artemisiifolia*. *J. Ecol.* 103, 1069–1098. doi: 10.1111/1365-2745.12424
- Farooq, S., Onen, H., Ozaslan, C., Baskin, C. C., and Gunal, H. (2019). Seed germination niche for common ragweed (*Ambrosia artemisiifolia* L.) populations naturalized in Turkey. *South Afr. J. Bot.* 123, 361–371. doi: 10.1016/j.sajb.2019.03.031
- Fenolosa, E., Jené, L., and Munné-Bosch, S. (2021). Geographic patterns of seed trait variation in an invasive species: how much can close populations differ? *Oecologia* 196, 747–761. doi: 10.1007/s00442-021-04971-2
- Forcella, F., Benec Arnold, R. L., Sanchez, R., and Ghersa, C. M. (2000). Modeling seedling emergence. *F. Crop Res.* 67, 123–139. doi: 10.1016/S0378-4290(00)00088-5
- Galzina, N., Baric, K., Šćepanovic, M., Goršic, M., and Ostojic, Z. (2010). Distribution of invasive weed *Ambrosia artemisiifolia* L. @ in Croatia. *Agric. Conspec. Sci.* 75, 75–81.
- Gard, B., Bretagnolle, F., Dessaint, F., and Laitung, B. (2013). Invasive and native populations of common ragweed exhibit strong tolerance to foliar damage. *Basic. Appl. Ecol.* 14, 28–35. doi: 10.1016/j.BAAE.2012.10.007
- Gardin, A., Otero, O., Réveillac, E., Lafitte, A., Valentin, X., Lapalus, F., et al. (2023). Seasonality and growth in tropical freshwater ectotherm vertebrates: Results from 1-year experimentation in the African gray bichir, giraffe catfish, and the West African mud turtle. *Ecol. Evol.* 13, 1–17. doi: 10.1002/ece3.9936
- Ge, W., Bu, H., Wang, X., Martinez, S. A., and Du, G. (2020). Inter- and intra-specific difference in the effect of elevation and seed mass on germinability of eight *Allium* species. *Glob. Ecol. Conserv.* 22, e01016. doi: 10.1016/j.gecco.2020.e01016
- Gentili, R., Asero, R., Caronni, S., Guarino, M., Montagnani, C., Mistrello, G., et al. (2019). *Ambrosia artemisiifolia* L. temperature-responsive traits influencing the prevalence and severity of pollinosis: A study in controlled conditions. *BMC Plant Biol.* 19, 1–9. doi: 10.1186/s12870-019-1762-6
- Gentili, R., Gilardelli, F., Bona, E., Prosser, F., Selvaggi, A., Alessandrini, A., et al. (2017). Distribution map of *Ambrosia artemisiifolia* L. (Asteraceae) in Italy. *Plant Biosyst.* 151, 381–386. doi: 10.1080/11263504.2016.1176966
- Genton, B. J., Shykoff, J. A., and Giraud, T. (2005). High genetic diversity in French invasive populations of common ragweed, *Ambrosia artemisiifolia*, as a result of multiple sources of introduction. *Mol. Ecol.* 14, 4275–4285. doi: 10.1111/j.1365-294X.2005.02750.X
- Gerber, E., Schaffner, U., Gassmann, A., Hinz, H. L., Seier, M., and Müller-Schärer, H. (2011). Prospects for biological control of *Ambrosia artemisiifolia* in Europe: Learning from the past. *Weed. Res.* 51, 559–573. doi: 10.1111/j.1365-3180.2011.00879.x
- Goeden, R. D., and André, L. A. (1999). Biological control of weeds in terrestrial and aquatic environments. *Handb. Biol. Control.* 6, 871–890. doi: 10.1016/b978-012257305-7/50081-3
- Gong, W., Wang, Y., Chen, C., Xiong, Y., Zhou, Y., Xiao, F., et al. (2022). The rapid evolution of an invasive plant due to increased selection pressures throughout its invasive history. *Ecotoxicol. Environ. Saf.* 233. doi: 10.1016/j.ecoenv.2022.113322
- Grundy, A. C. (2003). Predicting weed emergence: a review of approaches and future challenges. *Weed. Res.* 43, 1–11. doi: 10.1046/j.1365-3180.2003.00317.x
- Guillemain, J.-P., Gardarin, A., Granger, S., Reibel, C., Munier-Jolain, N. M., and Colbach, N. (2013). Assessing potential germination period of weeds with base temperatures and base water potentials. *Weed. Res.* 53, 76–87. doi: 10.1111/wre.12000
- Hamaoui-Laguel, L., Vautard, R., Liu, L., Solmon, F., Viovy, N., Khvorostyanov, D., et al. (2015). Effects of climate change and seed dispersal on airborne ragweed pollen loads in Europe. *Nat. Clim. Chang.* 5, 766–771. doi: 10.1038/nclimate2652

- Kaufmann, M., and Michel, B. (1973). The osmotic potential of polyethylene glycol 6000. *Plant Physiol.* 51, 914–916. doi: 10.1104/pp.51.5.914
- Kiss, L., and Béres, I. (2006). Anthropogenic factors behind the recent population expansion of common ragweed (*Ambrosia artemisiifolia* L.) in Eastern Europe: Is there a correlation with political transitions? [*J. Biogeogr.* 33, 2156–2157. doi: 10.1111/j.1365-2699.2006.01633.x
- Knolmajer, B., Jócsák, I., Taller, J., Keszthelyi, S., and Kazinczi, G. (2024). Common ragweed—*Ambrosia artemisiifolia* L.: A review with special regards to the latest results in biology and ecology. *Agronomy* 14. doi: 10.3390/agronomy14030497
- Kottek, M., Grieser, J., Beck, C., Rudolf, B., and Rubel, F. (2006). World map of the Köppen-Geiger climate classification updated. *Meteorol. Z.* 15, 259–263. doi: 10.1127/0941-2948/2006/0130
- Leiblein, M. C., and Lösch, R. (2011). Biomass development and CO<sub>2</sub> gas exchange of *Ambrosia artemisiifolia* L. under different soil moisture conditions. *Flora. Morphol. Distrib. Funct. Ecol. Plants* 206, 511–516. doi: 10.1016/j.flora.2010.09.011
- Leiblein-Wild, M. C., and Tackenberg, O. (2014). Phenotypic variation of 38 European *Ambrosia artemisiifolia* populations measured in a common garden experiment. *Biol. Invasions* 16, 2003–2015. doi: 10.1007/s10530-014-0644-y
- Leishman, M. R. (2001). Oikos - 2003 - Leishman - Does the seed size number trade-off model determine plant community structure An assessment of.pdf. *OIKOS* 93, 294–302. doi: 10.1034/j.1600-0706.2001.930212.x
- Leishman, M. R., Westoby, M., and Jurado, E. (1995). Correlates of seed size variation: A comparison among five temperate floras. *J. Ecol.* 83, 517. doi: 10.2307/2261604
- Leskovešek, R., Datta, A., Knezevic, S. Z., and Simončič, A. (2012). Common ragweed (*Ambrosia artemisiifolia*) dry matter allocation and partitioning under different nitrogen and density levels. *Weed. Biol. Manage.* 12, 98–108. doi: 10.1111/J.1445-6664.2012.00439.X
- Li, X. M., She, D. Y., Zhang, D. Y., and Liao, W. J. (2015). Life history trait differentiation and local adaptation in invasive populations of *Ambrosia artemisiifolia* in China. *Oecologia* 177, 669–677. doi: 10.1007/s00442-014-3127-z
- Li, F., van Kleunen, M., Li, J., Liu, X., Gao, K., Zhu, J., et al. (2019). Patterns of genetic variation reflect multiple introductions and pre-admixture sources of common ragweed (*Ambrosia artemisiifolia*) in China. *Biol. Invasions* 21, 2191–2209. doi: 10.1007/s10530-019-01966-2
- Loddo, D., Ghaderi-Far, F., Rastegar, Z., and Masin, R. (2018). Base temperatures for germination of selected weed species in Iran. *Plant Prot. Sci.* 54, 60–66. doi: 10.17221/92/2016-PPS
- Loddo, D., Sousa, E., Masin, R., Calha, I., Zanin, G., Fernández-Quintanilla, C., et al. (2013). Estimation and Comparison of Base Temperatures for Germination of European Populations of Velvetleaf (*Abutilon theophrasti*) and Jimsonweed (*Datura stramonium*). *Weed. Sci.* 61, 443–451. doi: 10.1614/WS-D-12-00162.1
- Máčajová, P., Tóthová, M., Krchňavá, V., Týr, Š., and Tóth, P. (2022). Herbicide control of *Ambrosia artemisiifolia* in sunflower, soybean and maize. *Agric.* 68, 110–118. doi: 10.2478/agri-2022-0010
- Martin, M. D., Olsen, M. T., Samaniego, J. A., Zimmer, E. A., and Gilbert, M. T. P. (2016). The population genomic basis of geographic differentiation in North American common ragweed (*Ambrosia artemisiifolia* L.). *Ecol. Evol.* 6, 3760–3771. doi: 10.1002/ece3.2143
- Masin, R., Cacciatori, G., Zuin, M. C., and Zanin, G. (2010). AlertInf: Emergence predictive model for weed control in maize in Veneto. *Ital. J. Agrometeorol.* 5.
- Masin, R., Loddo, D., Benvenuti, S., Otto, S., and Zanin, G. (2012). Modeling weed emergence in Italian maize fields. *Weed. Sci.* 60, 254–259. doi: 10.1614/WS-D-11-00124.1
- Masin, R., Loddo, D., Gasparini, V., Otto, S., and Zanin, G. (2014). Evaluation of weed emergence model alertInf for maize in soybean. *Weed. Sci.* 62, 360–369. doi: 10.1614/WS-D-13-00112.1
- Masin, R., Zuin, M. C., Archer, D. W., Forcella, F., and Zanin, G. (2005). WeedTurf: a predictive model to aid control of annual summer weeds in turf. *Weed. Sci.* 53, 193–201. doi: 10.1614/WS-04-066R1
- Mesgaran, M. (2019). Modeling weed seed germination and seedling emergence. In: *RPlugs - Seed Germination Emerg.* Available online at: <https://rpubs.com/mbmesgaran/495385> (Accessed February 10, 2021).
- Milakovic, I., Fiedler, K., and Karrer, G. (2014). Management of roadside populations of invasive *Ambrosia artemisiifolia* by mowing. *Weed. Res.* 54, 256–264. doi: 10.1111/wre.12074
- Milakovic, I., and Karrer, G. (2016). The influence of mowing regime on the soil seed bank of the invasive plant *Ambrosia artemisiifolia* L. *NeoBiota* 28, 39–49. doi: 10.3897/neobiota.28.6838
- Moles, A. T., and Westoby, M. (2006). Seed size and plant strategy across the whole life cycle. *Oikos* 113, 91–105. doi: 10.1111/j.0030-1299.2006.14194.x
- Montagnani, C., Gentili, R., Smith, M., Guarino, M. F., and Citterio, S. (2017). The worldwide spread, success, and impact of ragweed (*Ambrosia* spp.). *CRC. Crit. Rev. Plant Sci.* 36, 139–178. doi: 10.1080/07352689.2017.1360112
- Murali, K. S. (1997). Patterns of seed size, germination and seed viability of tropical tree species in Southern India. *Biotropica* 29, 271–279. doi: 10.1111/j.1744-7429.1997.tb00428.x
- Nikolić, N., and Masin, R. (2024). Exploring germination requirements of *Iva xanthiifolia*: Implications for potential spread in Europe. *Plant Stress* 11, 100312. doi: 10.1016/j.plstress.2023.100312
- Norden, N., Daws, M. I., Antoine, C., Gonzalez, M. A., Garwood, N. C., and Chave, J. (2009). The relationship between seed mass and mean time to germination for 1037 tree species across five tropical forests. *Funct. Ecol.* 23, 203–210. doi: 10.1111/j.1365-2435.2008.01477.x
- Onofri, A., Gresta, F., and Tei, F. (2010). A new method for the analysis of germination and emergence data of weed species. *Weed. Res.* 50, 187–198. doi: 10.1111/j.1365-3180.2010.00776.x
- Oveisi, M., Alizadeh, H., Lorestani, S. A., Esmaili, A., Sadeghnejad, N., Piri, R., et al. (2024). Triangle area model (TAM) for predicting germination: An approach to enhance hydrothermal time model applications. *Curr. Plant Biol.* 39. doi: 10.1016/j.cpb.2024.100356
- Pichtel, J., Kuroiwa, K., and Sawyerr, H. T. (2000). Distribution of Pb, Cd and Ba in soils and plants of two contaminated sites. *Environ. Pollut.* 110, 171–178. doi: 10.1016/S0269-7491(99)00272-9
- Prentis, P. J., Wilson, J. R. U., Dormontt, E. E., Richardson, D. M., and Lowe, A. J. (2008). Adaptive evolution in invasive species. *Trends Plant Sci.* 13, 288–294. doi: 10.1016/j.tplants.2008.03.004
- Puteh, A. B., Rosli, R., and Mohamad, R. B. (2010). Dormancy and cardinal temperatures during seed germination of five weedy rice (*Oryza* spp.) strains. *Pertanika. J. Trop. Agric. Sci.* 33, 243–250.
- Putra, A. R., Hodgins, K. A., and Fournier-Level, A. (2024). Assessing the invasive potential of different source populations of ragweed (*Ambrosia artemisiifolia* L.) through genomically informed species distribution modelling. *Evol. Appl.* 17, 1–13. doi: 10.1111/eva.13632
- Qiu, J., Bai, Y., Fu, Y. B., and Wilmshurst, J. F. (2010). Spatial variation in temperature thresholds during seed germination of remnant *Festuca hallii* populations across the Canadian prairie. *Environ. Exp. Bot.* 67, 479–486. doi: 10.1016/j.envexpbot.2009.09.002
- Ramesh, K., Matloob, A., Aslam, F., Florentine, S. K., and Chauhan, B. S. (2017). Weeds in a changing climate: Vulnerabilities, consequences, and implications for future weed management. *Front. Plant Sci.* 8. doi: 10.3389/fpls.2017.00095
- Ranieri, B. D., Pezzini, F. F., Garcia, Q. S., Chautems, A., and França, M. G. C. (2012). Testing the regeneration niche hypothesis with Gesneriaceae (tribe Sinningiae) in Brazil: Implications for the conservation of rare species. *Austral Ecol.* 37, 125–133. doi: 10.1111/j.1442-9993.2011.02254.x
- Rodriguez, C. M., and D'Alessandro, M. (2019). Indoor thermal comfort review: The tropics as the next frontier. *Urban. Clim.* 29, 100488. doi: 10.1016/j.uclim.2019.100488
- and RStudio Team, (2023). RStudio | Open source & professional software for data science teams - RStudio (RStudio Inc). Available online at: <https://rstudio.com/> (Accessed February 10, 2021).
- Saint-Louis, S., DiTommaso, A., and Watson, A. K. (2005). A common ragweed (*Ambrosia artemisiifolia*) biotype in southwestern Québec resistant to linuron. *Weed. Technol.* 19, 737–743. doi: 10.1614/wt-04-276.1
- Scalone, R., Lemke, A., Štefanić, E., Kolseth, A. K., Rašić, S., and Andersson, L. (2016). Phenological variation in *Ambrosia artemisiifolia* L. facilitates near future establishment at northern latitudes. *PLoS One* 11, 1–15. doi: 10.1371/journal.pone.0166510
- Schneider, C. A., Rasband, W. S., and Eliceiri, K. W. (2012). NIH Image to ImageJ: 25 years of image analysis. *Nat. Methods* 9, 671–675. doi: 10.1038/nmeth.2089
- Schroeder, A. B., Dobson, E. T. A., Rueden, C. T., Tomancak, P., Jug, F., and Eliceiri, K. W. (2021). The ImageJ ecosystem: Open-source software for image visualization, processing, and analysis. *Protein Sci.* 30, 234–249. doi: 10.1002/pro.3993
- Scruggs, E., Sciences, E., Tech, V., and Tech, V. (2019). Common ragweed (*Ambrosia artemisiifolia*) control in soybeans. Blacksburg, VA: Virginia Cooperative Extension SPES143NP.
- Silveira, F. A. O., Negreiros, D., Araújo, L. M., and Fernandes, G. W. (2012). Does seed germination contribute to ecological breadth and geographic range? A test with sympatric *Diplusodon* (Lythraceae) species from rupestrian fields. *Plant Species. Biol.* 27, 170–173. doi: 10.1111/j.1442-1984.2011.00342.x
- Silvertown, J., and Bullock, J. M. (2003). Do seedlings in gaps interact? A field test of assumptions in ESS seed size models. *Oikos* 101, 499–504. doi: 10.1034/j.1600-0706.2003.12247.x
- Skálová, H., Guo, W. Y., Wild, J., and Pyšek, P. (2017). *Ambrosia artemisiifolia* in the Czech Republic: History of invasion, current distribution and prediction of future spread. *Preslia* 89, 1–16. doi: 10.23855/preslia.2017.001
- Smith, M., Cecchi, L., Skjøth, C. A., Karrer, G., and Šikoparija, B. (2013). Common ragweed: A threat to environmental health in Europe. *Environ. Int.* 61, 115–126. doi: 10.1016/j.envint.2013.08.005
- Song, X. J., Liu, G., Qian, Z. Q., and Zhu, Z. H. (2023). Niche Filling Dynamics of Ragweed (*Ambrosia artemisiifolia* L.) during Global Invasion. *Plants* 12, 1–16. doi: 10.3390/plants12061313
- Šostarčić, V., Masin, R., Loddo, D., Brijačak, E., and Šćepanović, M. (2021a). Germination parameters of selected summer weeds: Transferring of the alertinf model to other geographical regions. *Agronomy* 11. doi: 10.3390/agronomy11020292

- Šoštarić, V., Masin, R., Loddo, D., Svečnjak, Z., Rubinić, V., and Šćepanović, M. (2021b). Predicting the emergence of *echinocloa crus-galli* (L.) p. beauv. in maize crop in Croatia with hydrothermal model. *Agronomy* 11. doi: 10.3390/agronomy11102072
- Stradford, J., Sakhare, A., Ravichandran, R., Schroeder, E. T., Michener, L. A., and Pa, J. (2021). Conducting a VR clinical trial in the era of COVID-19. *Front. Virtual. Real. 2*. doi: 10.3389/frvir.2021.639478
- Sun, Y., Bossdorf, O., Grados, R. D., Liao, Z. Y., and Müller-Schärer, H. (2020). Rapid genomic and phenotypic change in response to climate warming in a widespread plant invader. *Glob. Change Biol.* 26, 6511–6522. doi: 10.1111/gcb.15291
- Taylor, R. A. J. (2019). *Plants* (Elsevier: Taylor's Power Law), 103–142. doi: 10.1016/B978-0-12-810987-8.00006-9
- Trudgill, D. L., Squire, G. R., and Thompson, K. (2000). A thermal time basis for comparing the germination requirements of some British herbaceous plants. *New Phytol.* 145, 107–114. doi: 10.1046/j.1469-8137.2000.00554.x
- van Boheemen, L. A., Lombaert, E., Nurkowski, K. A., Gauffre, B., Rieseberg, L. H., and Hodgins, K. A. (2017). Multiple introductions, admixture and bridgehead invasion characterize the introduction history of *Ambrosia artemisiifolia* in Europe and Australia. *Mol. Ecol.* 26, 5421–5434. doi: 10.1111/mec.14293
- Van Mólken, T., Jorritsma-Wienk, L. D., Van Hoek, P. H. W., and De Kroon, H. (2005). Only seed size matters for germination in different populations of the dimorphic *Tragopogon pratensis* subsp. *pratensis* (Asteraceae). *Am. J. Bot.* 92, 432–437. doi: 10.3732/ajb.92.3.432
- Wang, H., Liu, T., Zhao, W., Liu, X., Sun, M., Su, P., et al. (2022). Reduced invasiveness of common ragweed (*Ambrosia artemisiifolia*) using low-dose herbicide treatments for high-efficiency and eco-friendly control. *Front. Plant Sci.* 13. doi: 10.3389/fpls.2022.861806
- Weaver, S. E. (2001). Impact of lamb's-quarters, common ragweed and green foxtail on yield of corn and soybean in Ontario. *Can. J. Plant Sci.* 81, 821–828. doi: 10.4141/P01-057
- Xian, X., Zhao, H., Wang, R., Huang, H., Chen, B., Zhang, G., et al. (2023). Climate change has increased the global threats posed by three ragweeds (*Ambrosia* L.) in the Anthropocene. *Sci. Total. Environ.* 859, 160252. doi: 10.1016/j.scitotenv.2022.160252
- Zhou, L., Yu, H., Yang, K., Chen, L., Yin, W., and Ding, J. (2021). Latitudinal and longitudinal trends of seed traits indicate adaptive strategies of an invasive plant. *Front. Plant Sci.* 12. doi: 10.3389/fpls.2021.657813
- Ziska, L. H. (2002). Sensitivity of ragweed (*Ambrosia artemisiifolia*) growth to urban ozone concentrations. *Funct. Plant Biol.* 29, 1365–1369. doi: 10.1071/FP02039