

Exploring germination requirements of *Iva xanthiifolia*: Implications for potential spread in Europe

Nebojša Nikolić^{*}, Roberta Masin

Department of Agronomy, Food, Natural Resources, Animals and Environment, University of Padova, 35020, Legnaro PD, Italy

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ABSTRACT

Iva xanthiifolia, an invasive annual weed species native to North American prairies, is an agricultural problem in different parts of the world and represents a health hazard as an allergen to humans. This study addresses the limited literature on its germination requirements, focusing on base temperature, base water potential, and salinity tolerance. Seeds from a Serbian population near Belgrade were tested to various conditions. The experiments were conducted using temperatures ranging from 1 °C to 30 °C and water potentials ranging from 0 to −2 MPa, while salinity tolerance was tested at three temperatures (1, 3, and 6 °C) and five salinity levels (0 to 16 dS/m). Results indicate higher germination rates at lower temperatures (1 °C) compared to higher temperatures (30 °C), with a base temperature of 0.7 ± 0.37 °C. Germination decreased with increased water potential, showing a base water potential of -1.58 ± 0.07 MPa. Salinity tolerance was observed, with germination even at 16 dS/m (the final germination rate was $54.5\% \pm 2.88$). Additionally, germination was observed declining with increasing temperature in a saline environment. As germination is one of the major determinants of a species' success, the possible spreading of this species under different climate change scenarios was simulated. Results of future distribution modelling suggested sensitivity to precipitation changes and potential northward expansion of this species. This research enhances our understanding of *Iva xanthiifolia* traits, useful for supporting management strategies for its control and mitigation of its impact, even under future climate change and land-use scenarios.

Introduction

Iva xanthiifolia (Nutt.), synonym *Cyclachaena xanthiifolia* Fresen., EPPO code—IVAXA, is an invasive annual weed species from the Asteraceae family native to the North American prairies and commonly found on sandy alluvial soils (Follak et al., 2013). The species was introduced and naturalized into the European flora in the nineteenth century and is now widespread throughout most of central and south-eastern Europe, mainly in the basins of large rivers such as the Danube and Rhine. Invasion hotspots have been identified in parts of Slovakia (Bratislava, Nitra, Košice districts), in the northern region of Serbia (Vojvodina), in southeastern Hungary (Csongrád and Békés counties), in eastern parts of Austria (Burgenland, Lower Austria) and in eastern Germany (Dresden Basin). It also occurs in Ukraine and in southern and central Russia (Abramova and Nurmieva, 2014; Aistova, 2012; Follak et al., 2013). Information on the current spread and level of establishment of this species in Europe can be found in the Compendium of the Center for Agriculture and Bioscience International (CABI; <https://www.cabidigitallibrary.org/product/QI>) (Fig. 1).

[//www.cabidigitallibrary.org/product/QI](https://www.cabidigitallibrary.org/product/QI)) (Fig. 1).

I. xanthiifolia is a robust plant and can grow to over 2 m, sometimes as much as 3 m. Fast growth and high seed production are the main characteristics of this species, which therefore has high competitive potential (Follak et al., 2013). The number of seeds produced per plant ranges from 35,000 to 50,000 on average, while the maximum recorded seed production per plant was 105,000 (Milanova, 1999). This species mainly colonizes ruderal habitats and is found on roadsides, canals, rubbish dumps, and abandoned or neglected urban areas (Krstić et al., 2007). It is wind-pollinated, producing allergenic pollen that can cause severe respiratory difficulties and skin irritation (Konstantinović et al., 2009; Krstić et al., 2007). Some authors, such as Abramova and Nurmieva (2014), point out that *I. xanthiifolia* is no less allergenic than *Ambrosia artemisiifolia*, a known allergenic species of the same family (Déchamp, 1999; Möller et al., 2002). Its growth potential and competitive capability also make it problematic for arable crops, such as maize, sunflowers, various vegetables, and sugar beet (Hodi and Torma, 2002; Marisavljević et al., 2005; Stefanović and Simić, 2006). Moreover,

^{*} Corresponding author.

E-mail address: nebojsa.nikolic@unipd.it (N. Nikolić).

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milk from cows ingesting *I. xanthiifolia* has a bitter taste and is unsuitable for consumption (Muenscher, 1975). To our knowledge, there are few reports in the literature on the physiological requirements for germination of this invasive species, such as temperature and water potential, usually found in the so called 'grey literature' whose accuracy and results are difficult to verify. Considering that these information are the cornerstone for different emergence predictive models (Gonzalez-Andujar et al., 2016; Masin et al., 2014; Roman et al., 2000), this topic becomes of crucial importance and needs to be seriously studied. Furthermore these could be important information for determining the success of the further spread of *I. xanthiifolia*, and understanding whether it has the potential to invade much larger areas than it currently occupies (Follak et al., 2013). Information on the temperature, water potential and salinity thresholds for germination could provide insights into its dispersal patterns and highlight those areas that may be at risk of invasion, by indicating whether a certain area is suitable for germination and emergence of this species. Therefore, in this work, the primary objective was to fill the knowledge gap by determining the parameters of base temperature and base water potential governing the germination process in a Serbian population of this species collected near Belgrade. In addition, the effect of salinity induced stress on germination was examined. The problem of soil salinization due to rising groundwater and improper irrigation in different parts of the world is well known (Zaman et al., 2018). According to some estimates, saline soils or salt-affected soils account for about 23 % of total arable land (Tanji, 2002), a percentage that is expected to increase in the coming years due to low precipitation, high surface evaporation, weathering of native rocks, irrigation with saline water and poor agricultural practices (Jamil et al., 2011). Although the literature indicates that *I. xanthiifolia* does not

commonly grow on saline soils, the findings from Radanović et al. (2011) in Serbia suggest that this species can easily colonize saline habitats. Indeed, the authors have found this species growing in the vicinity of the Velebit village in northern Serbia on a soil that is defined as 'continental inland salt steppes'. Furthermore, considering that this species is often found in ruderal areas and along the roads that in some parts of Europe could be salted to prevent the troubles caused by snow. Investigation of its response to salinity could therefore be important in predicting its potential area of invasion. Finally, an assessment of possible future distribution of this species in Europe, based on the characteristics of the population investigated in this study, was conducted considering various scenarios related to climate change.

Materials and methods

Temperature threshold

Seeds of *I. xanthiifolia* were collected in October 2016 from a ruderal site near Belgrade, Batajnica municipality, Serbia (Fig. 2). They were cleaned and stored at low temperature before sowing. 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 °C. Four replicates of 100 seeds each were tested for each temperature. The seeds were sown on filter paper in Petri dishes with 2 ml of distilled water. After sowing, the Petri dishes were sealed with parafilm and placed inside the climate chambers set to the predetermined temperature, and 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



Fig. 1. Current distribution of the *Iva xanthiifolia* in Europe.

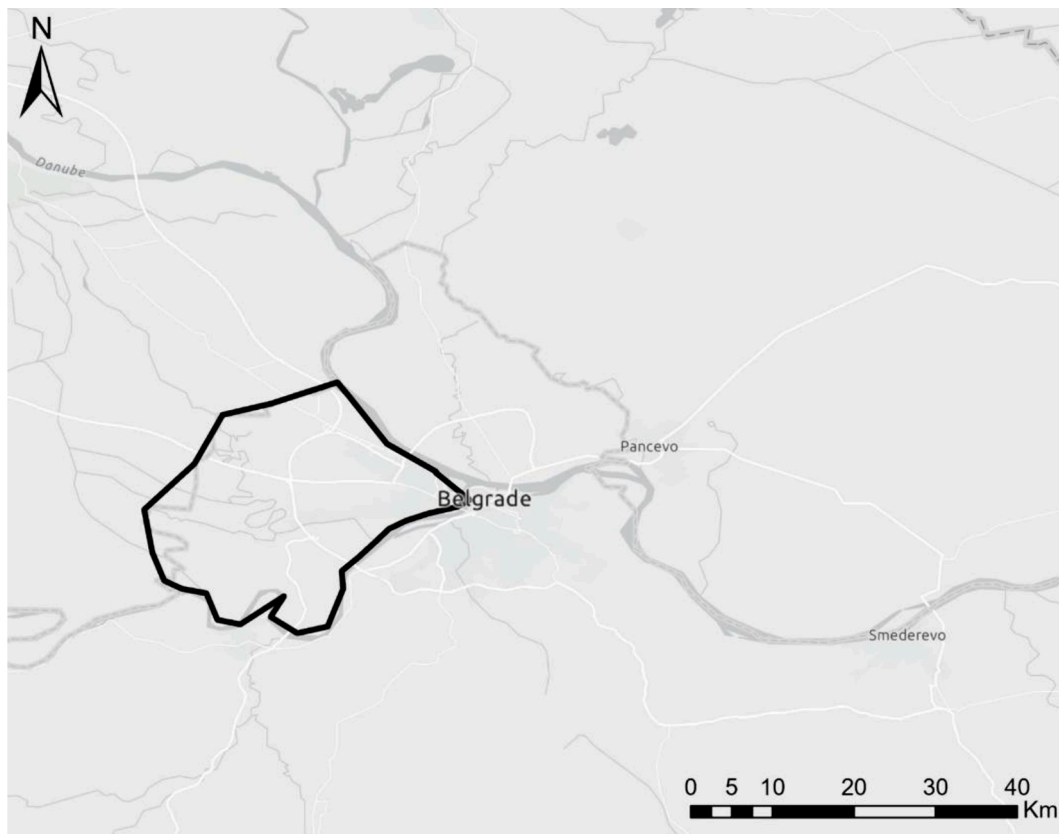


Fig. 2. Area from where the seeds of *Iva xanthiifolia* were collected and that was used as a training area.

elapsed without further germination, as proposed by Baskin and Baskin (2014). All germinated seeds were counted and removed.

Water potential threshold

The water potential threshold was determined using the same seeds collected near Belgrade, Batajnica municipality, Serbia (Fig. 2). Polyethylene glycol 6000 (PEG-6000) 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 , -0.25 , -0.40 , -0.60 , -1.00 , -1.50 , and -2.00 MPa; controls consisted in distilled water alone. The seeds were sown on filter paper and placed in plastic containers 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 100 seeds each. After sowing, the plastic containers were closed and placed in climate chambers at 6°C with a photoperiod of 12 h light and 12 h dark. In the experiment to determine the base temperature described above, 6°C was the optimal temperature for a high germination percentage and high germination rate for *I. xanthiifolia*. Germination was monitored every 2–3 days and was considered concluded after 10 days had elapsed without further germination (Baskin and Baskin, 2014). All germinated seeds were counted and removed.

Salinity tolerance

The effect of salinity on seed germination was tested at five different salinity levels: 0 (control, distilled water), 4, 8, 12 and 16 dS/m. Saline solutions were prepared by adding NaCl to distilled water until the desired salinity level was reached, measured by electrical conductivity using an XS Instruments COND 80 conductivity meter (Giorgio Bormac s.r.l.). Each salinity level was tested with four replicates of 100 seeds,

each at three different temperatures: 1, 3 and 6°C , these being the temperatures at which *I. xanthiifolia* showed the highest germination rates in the experiment to determine the base temperature described above. The seeds were sown in Petri dishes on a filter paper moistened with 2 ml of saline solution or distilled water in case of the controls. After sowing, the Petri dishes were sealed with parafilm and placed in climate chambers set to the three temperatures. Germination was monitored every 2–3 days, the germinated seeds were counted and removed, and the trial was considered concluded after 10 days had elapsed without germination (Baskin and Baskin, 2014).

Statistical analysis

All statistical analyses were performed in the R environment (RStudio Team, 2020). To determine whether there were significant differences in germination at the different temperatures and water potentials. A one-way ANOVA was performed followed by Tukey's HSD test ($p < 0.05$) for post hoc analysis. The same procedure was used to determine the differences in mean germination time (MGT) at the different temperatures. MGT was calculated using the formula proposed by Ellis and Roberts (1980):

$$\text{MGT} = \Sigma(nD) / \Sigma n$$

where D is the number of days since the start of the trial, and n is the number of newly germinated seeds at day D, which is also in accordance with Borsai et al. (2018).

Base temperature (T_b) and base water potential (Ψ_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. 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; G_{\max} , maximum germination as t approaches infinity; b , slope around the inflection point; t_{50} , time at which germination is half G_{\max} .

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 (Ψ_b), substituting the different temperatures with the different levels of water potential (from 0 to -2 MPa), while the temperature was a constant 6°C .

To assess the response to salinity stress, the final germination percentage (FGP) was calculated as the mean of the replicates per treatment (salinity level) for each temperature. Finally, after verifying homoscedasticity and normality, FGP was statistically analyzed by factorial ANOVA with salinity (5 levels) and temperature (3 levels) as the experimental factors. The significance of the differences between the means was evaluated with Tukey's HSD test ($p < 0.05$).

Distribution assessment

Considering that weed species distribution across large areas is usually climate dependent (Hortal et al., 2010; Soberón, 2010; Zhang et al., 2022), possible future distribution assessment of *Iva xanthiifolia* was performed. This was based on future predictions of minimum monthly temperatures and mean precipitations available at the WorldClim website (<https://www.worldclim.org/data/index.html>). The data used are part of WorldClim 2.1 version (Fick and Hijmans, 2017), known for providing accurate future climate variable predictions (van der Merwe et al., 2023). The data are based on the Coupled Model Inter-comparison Project Phase 6 (CMIP6), a more recent and improved version of this project, including also four different climate change scenarios based on shared socio-economic pathways (SSP): SSP1-2.6, SSP2-4.5, SSP3-7.0, and SSP5-8.5, ranging from best to worst case scenario, that is from the scenario where the fossil fuels are in continuous use and the agreements for mitigating the climate change effects are not respected leading to rapid increase in mean temperature and greenhouse gasses emission. To the scenario where all of the goals for climate change effects mitigations are met, resulting in successful reduction of mean temperature increase and to a halt of greenhouse gases emission. (Eyring et al., 2016; Lovato et al., 2022; Meinshausen et al., 2020; Tebaldi et al., 2021). As for the global climate model (GCM), the choice was to use the second generation CMCC Earth System Model (CMCC-ESM2), developed by the Euro-Mediterranean Centre on Climate Change

(CMCC) Foundation. This model showed reliable predicting outcomes when compared to historical data (Cherchi et al., 2018; Lovato et al., 2022). The GCM has already been used in different research activities concerning species spatial distribution, providing satisfying results. Additionally, it offers both historical data and also future predictions divided into 20-years period from 2021 to 2100 (Ali et al., 2023; Arntzen, 2023; Fan et al., 2022; Hussein and Estifanos, 2023; Naimi et al., 2022; Yebeyen et al., 2022). Based on the available data from the WorldClim website and considering the spatial scale at which this work was performed, it was decided to use the 2.5 min spatial resolution for both the monthly minimum temperature and mean monthly precipitation, ensuring high spatial accuracy. The dataset obtained from the WorldClim website was processed within a GIS environment using different tools from the open-source QGIS (v3.32.0) and ESRI ArcGIS Pro© software (v3.1.2).

Training dataset

To obtain a training dataset, similar to what was done by van der Merwe et al. (2023), historical data of monthly average values of minimum temperature and mean precipitations, for the area where seeds were collected (Fig. 2), was used. This data ranged from 2010 to 2016.

The downloaded rasters were clipped to the training area using Clip Raster by Mask Layer tool in QGIS. From these newly obtained rasters, those where the minimum temperature was equal or exceeded the base temperature for species germination during the first five months were selected. Among these, those with the lowest mean precipitation were selected. Using these data, the mean value was derived by employing

Raster Calculator tool in QGIS and the obtained value was then adopted as the precipitation threshold for species germination.

Future dataset

Future datasets obtained from WorldClim included data of four different SSPs and of monthly data averaged on 20-years scale, for four different periods (2021–2040; 2041–2060; 2061–2080; 2081–2100). Considering that *I. xanthiifolia* is described as a spring species, it was decided to test the possible spreading of this species only in the first five months of the year. Rasters containing the minimum temperature were clipped to the extent of Europe using the Clip Raster by Mask Layer tool in QGIS. These rasters were then transformed to polygons using the Pixels to Polygons tool in QGIS to facilitate data assessment. Subsequently, only polygons where the minimum temperature was equal or exceeded the base temperature were selected using the Extract by Attribute tool in QGIS, applying the following formula:

$$T_{\min} \geq T_b$$

where T_{\min} is the average minimum temperature predicted for the 20 years period and T_b is the base temperature for *I. xanthiifolia* germination.

The process was repeated for all the rasters examined. Since T_b is only one of the limiting factors for this species germination, the polygon shapefiles obtained were then used to clip out the areas from the rasters containing precipitation data for each specific month. These rasters were then transformed to polygons using the Pixels to Polygons tool in QGIS. Finally, from each of the polygons obtained, the areas where mean monthly precipitations were equal or exceeded the minimum precipitation needed for *I. xanthiifolia* germination were selected. This was done using the Extract by Attribute tool in QGIS, applying the following formula:

$$P_{\text{mean}} \geq P_{\min}$$

where P_{mean} is the average monthly precipitation for the 20-years

period and Pmin is the minimum precipitation needed for *I xanthiifolia* germination in the training area.

To delineate the maximum potential range of *I. xanthiifolia* distribution in Europe, for each specific SSP, the shapefiles obtained for each 20-years period were merged using the Merge tool in ArcGis Pro, thus obtaining the maximum area suitable for the germination of this species, or more precisely this population, in Europe.

Results

Temperature thresholds

Final germination percentages (FGP) and mean germination times (MGT) at the different temperatures are shown in Fig. 3. For both FGP and MGT, ANOVA resulted in significant differences, at different temperatures, as can be seen in Table 1. It is interesting that both the highest germination percentages and the highest germination rates were at low temperature. With increasing temperature, FGP decreased, and MGT was shorter, but at 30 °C, MGT increased again while FGP remained low.

Given the results of this experiment, it was decided to use from 1 °C to 9 °C as the sub-optimal temperatures for determining the base temperature.

The base temperature for germination of this species resulted to be around 0.7 ± 0.37 °C (Fig. 4).

Base water potential

Mesgaran's (2019) model was also used to estimate the base water potential (Ψ_b) of *I. xanthiifolia*. Unlike the model for base temperature, where only suboptimal temperatures were used, here all the tested water potentials were used. ANOVA resulted in statistically significant differences for FGP and MGT at different water potentials (Table 2). As Fig. 5 shows, as water potential decreases, the germination percentage gradually decreases (from 88.75 % with only distilled water, 0 MPa, to 2.5 % with -1.5 MPa). No germination was observed at -2 MPa, which was therefore not included in further analyses. Mean germination time also increased with decreasing water potential (Fig. 5).

The model used for determining the water potential estimated a Ψ_b value of -1.58 ± 0.07 MPa (Fig. 6).

Salinity tolerance

A statistically significant effect of both factors (salinity and temperature) and their interaction on the final germination percentage FGP is showed in Table 3.

FGP decreased with rising salinity levels, as shown in Fig. 7. The highest germination percentage was at 0 dS/m (control), 97.6 % \pm 0.87, while the lowest was at 16 dS/m, 54.5 % \pm 2.88.

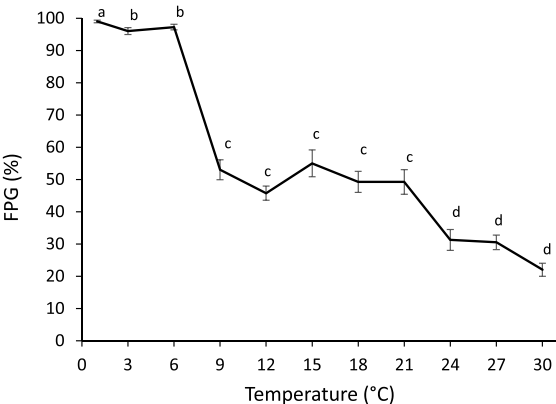


Fig. 3. Final germination percentages (FGP) and mean germination time (MGT) at different temperatures. Different letters indicate significant differences ($p > 0.05$).

Table 1
Results of the ANOVA for the Temperature factorial experiment on FGP and MGT.

FGP	Factors	Df	F-value	p-value
	Temperature	10	104.39	<0.0001
MGT	Factors	Df	F-value	p-value
	Temperature	10	100.21	<0.0001

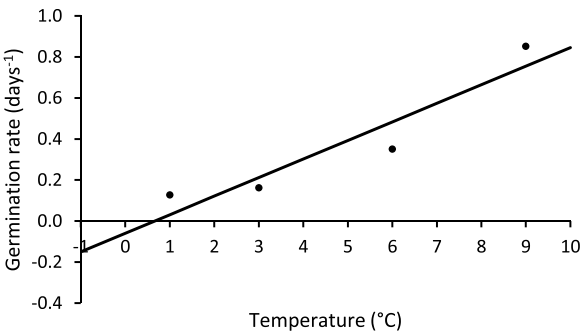


Fig. 4. Estimation of base temperature for *Iva xanthiifolia*.

Table 2
Results of the ANOVA for the Water Potential factorial experiment on FGP and MGT.

FGP	Factors	Df	F-value	p-value
	Water Potential	7	86.6	<0.0001
MGT	Factors	Df	F-value	p-value
	Water Potential	7	49.89	<0.0001

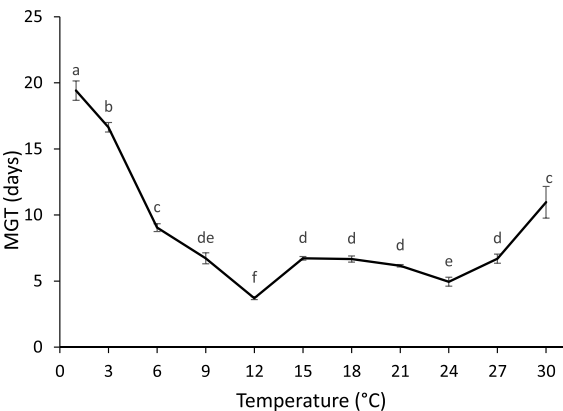
The interaction between temperature and level of salinity was also significant, the results are shown in Fig. 8.

In the control with no salinity, the FGP at the three different temperatures did not exhibit any statistically significant differences. As salinity levels increased, the FGP decreased with each increasing temperature and differences were observed between the various temperatures. The most significant reduction was at 6 °C. As expected, rising salinity also increased the MGT of *I. xanthiifolia* seeds, as shown in Fig. 9.

Although FGP was lower at the higher temperature, germination was faster (low MGT). The same trend was observed in the experiments with different temperatures, with salinity stress increasing these differences.

Possible future distribution

As expected, the possible future distribution of *I. xanthiifolia* is



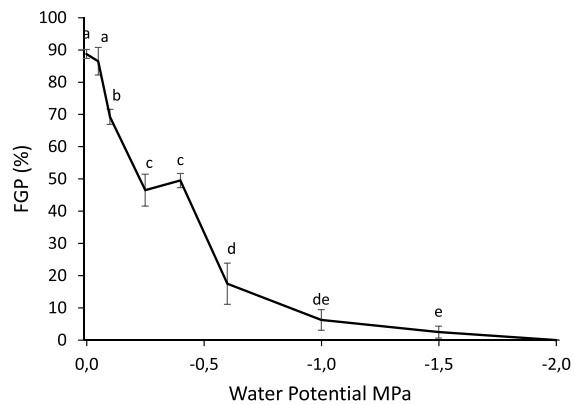


Fig. 5. Final germination percentages (FGP) and mean germination time (MGT) at different water potentials. Different letters indicate significant differences ($p > 0.05$).

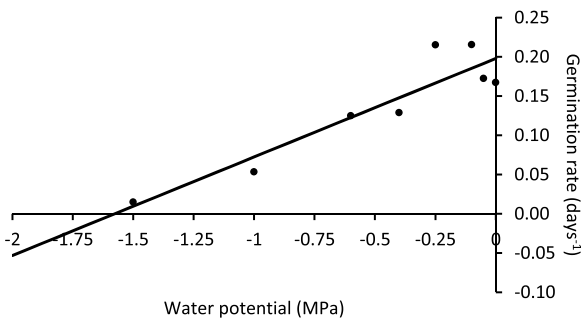
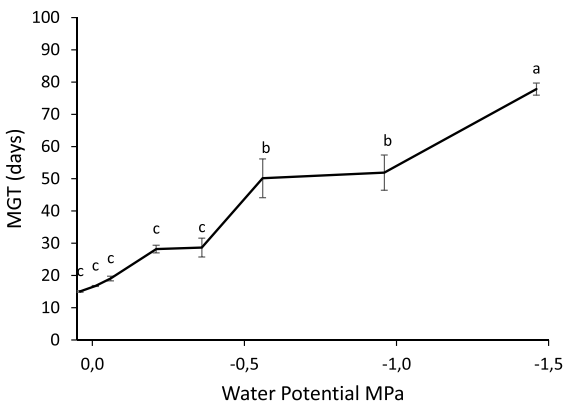


Fig. 6. Estimation of base water potential for *Iva xanthiifolia*.

Table 3
Results of the ANOVA for the Salinity x Temperature factorial experiment on FGP.

Factors	Df	F-value	p-value
Salinity	4	158.86	<0.000
Temperature	2	46.72	<0.000
Salinity x Temperature	8	2.65	0.02

Df, degrees of freedom.

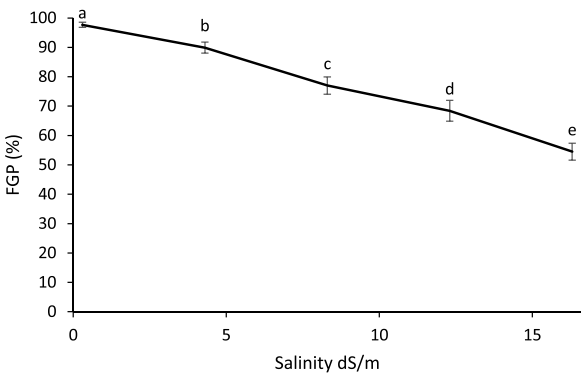


Fig. 7. Final germination percentages of *Iva xanthiifolia* at different levels of salinity. Different letters indicate significant differences ($p < 0.05$), and the bars indicate the standard error.

largely dependent on the climate. Given its capacity to germinate even under high soil salinity and its relatively low base temperature requirement for germination, coupled with predictions pointing towards rising temperatures in the future, it becomes evident that precipitation will emerge as the primary limiting factor influencing its spread.

From the Fig. 10, it is possible to observe that in the best-case

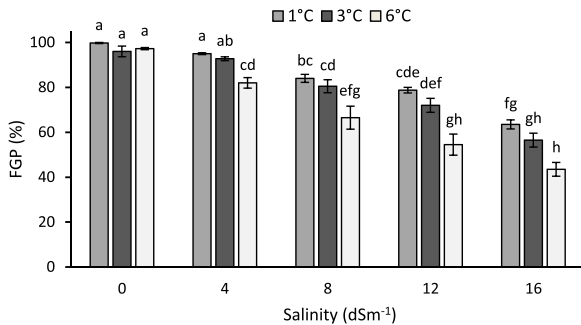


Fig. 8. Final germination percentages of *Iva xanthiifolia* at different temperatures and levels of salinity. Different letters indicate significant differences ($p < 0.05$), and the bars indicate the standard error.

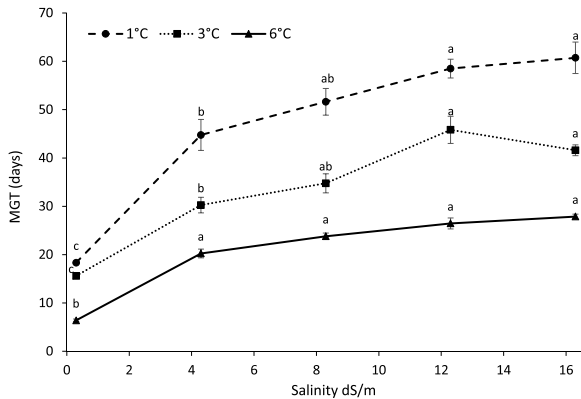


Fig. 9. Mean germination time in days at different temperatures (°C) and salinity levels (dS/m). Different letters indicate significant differences ($p > 0.05$).

scenario, represented by SSP 1–2.6, the potential habitat for *I. xanthiifolia* could expand, especially to the north of Europe and at higher altitudes in mountain ranges. Some southern and eastern areas may either remain or become inhospitable due to arid conditions. The area susceptible of invasion in different time periods under SSP 1–2.6 are detailed in Table 4.

Fig. 11 shows the possible spread of *I. xanthiifolia* under the SSP 2–4.5. Similar to the previous scenario, it is also possible to observe the spread of suitable habitat for the species across the continent, especially towards the north. At the same time, in the later time periods, it is possible to observe the increasing inhospitability of the southern and

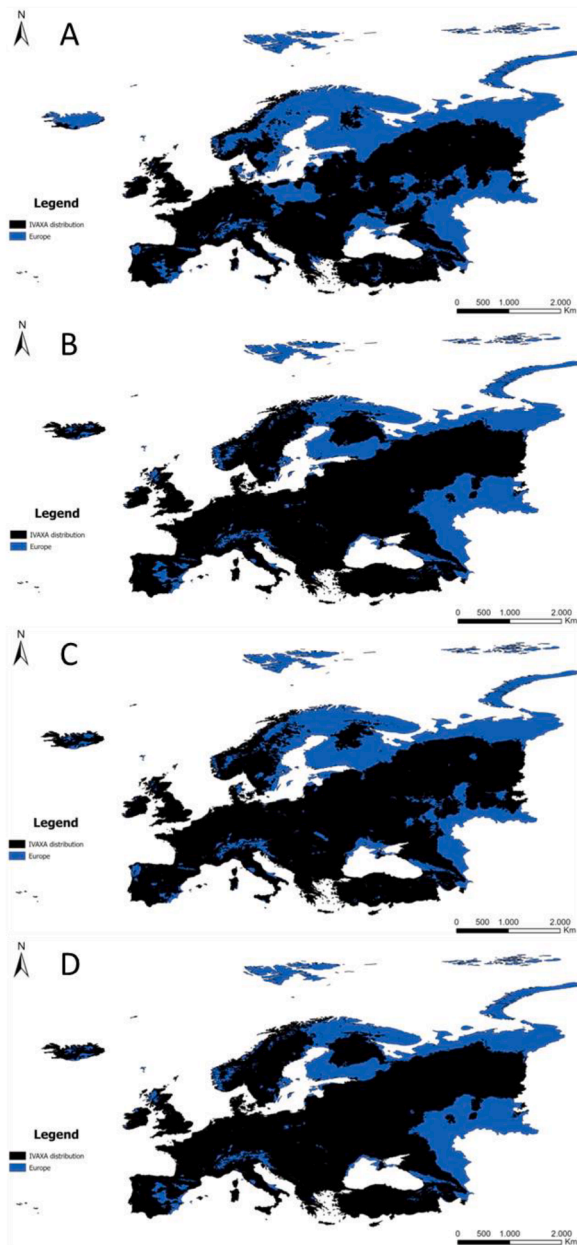


Fig. 10. Distribution of the *Iva xanthiifolia* in the SSP 1–2.6, A-2021–2040, B-2041–2060, C- 2061–2080, D- 2081–2100.

Table 4
Suitable area for *I. xanthiifolia* germination under the SSP 1–2.6 in different time periods.

SSP	Time period	Area (km ²)
1–2.6	2021–2040	14,887,552
1–2.6	2041–2060	16,995,184
1–2.6	2061–2080	19,493,264
1–2.6	2081–2100	19,673,424

south-eastern regions. The area at risk of invasion in different time periods under SSP 2–4.5 are detailed in Table 5.

As noted in the previous simulations, Fig. 12 shows the possible spread of *I. xanthiifolia* across the European continent. A significant and fast spread to the north is evident. Conversely, areas in the south and east of Europe, as along with certain mountain ranges, will become unsuitable for the germination of this species. Details on the area at risk

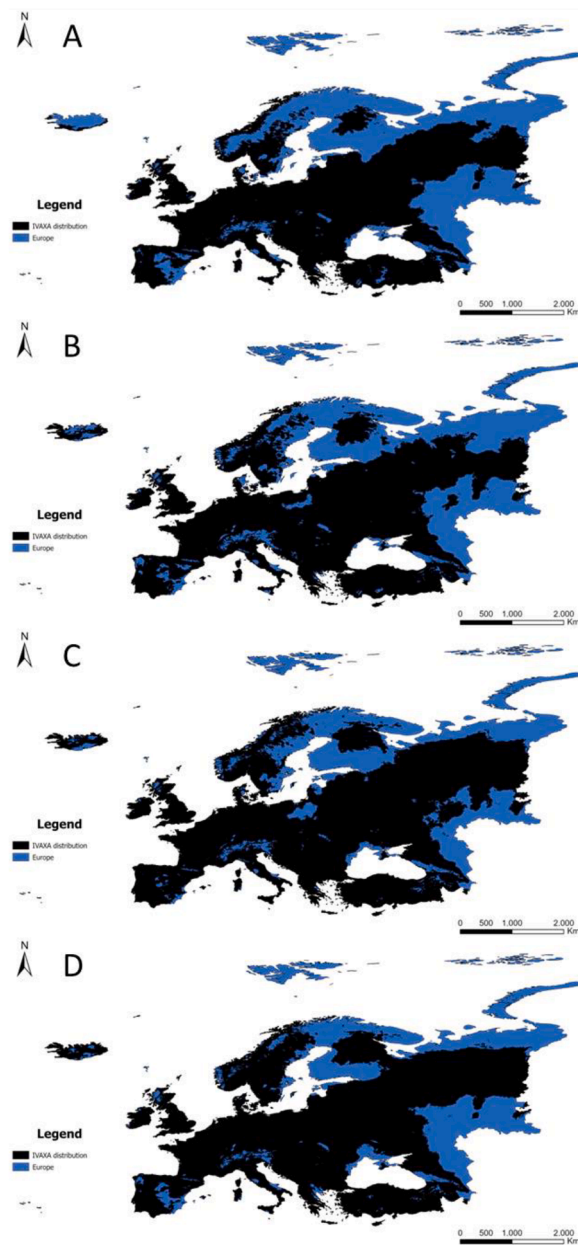


Fig. 11. Distribution of the *Iva xanthiifolia* in the SSP 2–4.5, A-2021–2040, B-2041–2060, C- 2061–2080, D-2081–2100.

Table 5
Suitable area for *I. xanthiifolia* germination under the SSP 2–4.5 in different time periods.

SSP	Time period	Area (km ²)
2–4.5	2021–2040	14,923,376
2–4.5	2041–2060	17,730,144
2–4.5	2061–2080	19,122,976
2–4.5	2081–2100	20,445,184

of invasion in different time periods under SSP 3–7.0 can be further examined in Table 6.

Differently from the previous SSPs, the simulation with the data from SSP 5–8.5, shown in Fig. 13, suggests that the spread to the north of this species may not be so pronounced. Additionally, the spread to the east seems to be inconsistent across different time periods and in general the suitable area in the eastern part of the continent appears to diminish

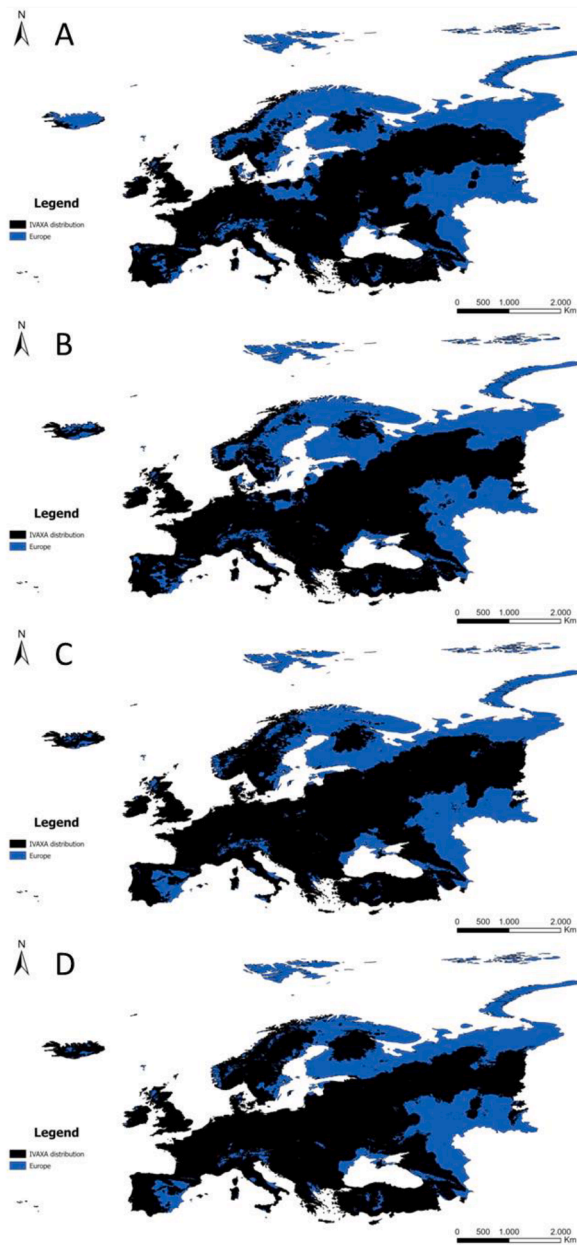


Fig. 12. Distribution of the *Iva xanthiifolia* in the SSP 3–7.0, A-2021–2040, B-2041–2060, C- 2061–2080, D-2081–2100.

Table 6
Suitable area for *I. xanthiifolia* germination under the SSP 3–7.0 in different time periods.

SSP	Time period	Area (km ²)
3–7.0	2021–2040	15,133,680
3–7.0	2041–2060	16,671,680
3–7.0	2061–2080	18,367,392
3–7.0	2081–2100	19,055,104

more rapidly than in other scenarios. Apart from the southern areas that will become unsuitable, it is also possible to observe that some areas of central Europe will become inhospitable for this species. The areas at risk of invasion in different time periods under SSP 5–8.5 are detailed in [Table 7](#).

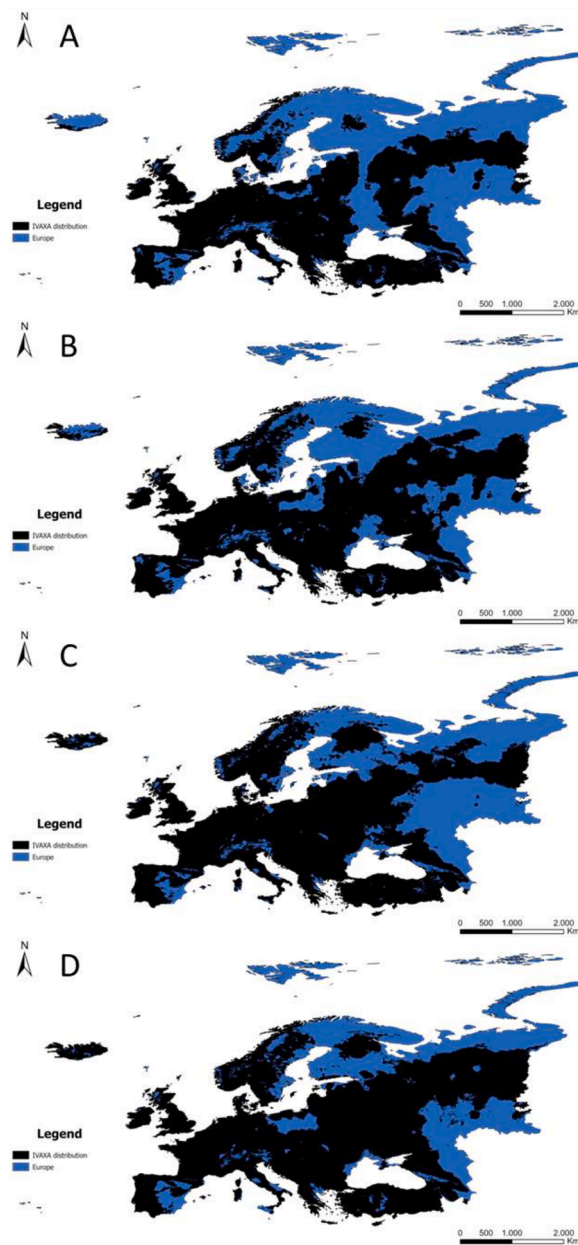


Fig. 13. Distribution of the *Iva xanthiifolia* in the SSP 5–8.5, A-2021–2040, B-2041–2060, C- 2061–2080, D-2081–2100.

Table 7
Suitable area for *I. xanthiifolia* germination under the SSP 3–7.0 in different time periods.

SSP	Time period	Area (km ²)
5–8.5	2021–2040	13,316,688
5–8.5	2041–2060	15,996,464
5–8.5	2061–2080	17,872,816
5–8.5	2081–2100	21,442,928

Discussion

This study investigated the germination requirements and response to salinity stress of the invasive annual weed, *I. xanthiifolia*, to shed light on its potential invasive behaviour in Europe. The findings reveal important insights into the ecology and distribution of this species, with implications for predicting its future spread.

The results for MGT show the optimal temperature for germination to be 12 °C, although the germination percentage at this temperature was lower than at the lower temperatures (1–6 °C). It is important to note that MGT decreased again at 24 °C, and then rose again at higher temperatures, indicating that some of the seeds may have a different optimal temperature for germination. The high FGP at low temperatures could be explained by this species having originated from the North American prairies, a cold weather region with a mean annual temperature of around 1 °C (Millett et al., 2009). The limited data on this species in the literature agree that the germination percentage decreases with rising temperatures (Maguire and Overland, 1959). As the species has been spreading to the southern regions of North America and across Europe, in areas with different climatic conditions, some seeds may be able to germinate at high temperatures. For instance, in certain regions where seeds have been collected, such as the extreme south of the Pannonian Plain, it is not uncommon that a dry, hot autumn period occurs when mature, non-dormant seeds may germinate (Gavrilov et al., 2020; Ruman, 2020). As different authors have suggested (Simons, 2011; Venable, 2007; Yi et al., 2019), these differences in germination periods and temperatures may represent survival strategies adopted by the species to allow it to adapt to a new environment and changing climate.

It is evident from the data in Fig. 3 that, although requiring more time, far more of the *I. xanthiifolia* seeds germinate at a lower temperature than at high temperature: At 1 °C, the mean germination rate reaches 99 %, while at 30 °C it is 22 %. The cold climate of its place of origin may explain this effect.

The estimated base temperature aligns with the temperature thresholds observed for the germination of other plant species from the same region, such as *Krascheninnikovia lanata*, native of the North American prairies, with an estimated base temperature of −3 °C (Wang et al., 2006). Furthermore, as this weed species is usually found on moist soils (Follak et al., 2013), it would be expected to suffer from a lack of water at germination, which is reflected in our findings on germination dynamics, although the estimated base water potential of -1.58 ± 0.07 MPa is not very high.

There is limited information in the literature on the soil preferences of *I. xanthiifolia*. However, it is often found on sandy alluvial soil (Follak et al., 2013; Krstić et al., 2007), which may exposed it to salinity stress. Several studies suggest that alluvial soils worldwide, near both saline and freshwater bodies, could be at risk of salinization (Kováčová and Velísková, 2012; Li et al., 2011). *I. xanthiifolia*'s tolerance to salinity stress is therefore a cause for even greater concern as it might influence its spread and the implementation of control measures. Salt reportedly has an inhibitory effect on seed germination, creating low osmotic potential, or ion toxicity (Na^+ , Cl^+), or both (Munns, 2002; H. Zhang et al., 2012). Salinity can therefore delay, reduce or completely suppress germination (Al-Hawija et al., 2012; Kashmir et al., 2016; Khan and Gulzar, 2003; Qu et al., 2008; Zhang et al., 2012). Nevertheless, although there was a significant drop in the germination of *I. xanthiifolia* with rising salinity levels, more than half of the seeds still germinated at the highest salinity level tested (16 dS/m). Salinity tolerance in plants is not easy to characterize: Grieve et al. (2007) define it as the ability to withstand the effects of high salinity without significant adverse effects, such as reduced growth or yield, or foliar salt damage. Since only germination was monitored in this study, an even more challenging task would be to establish whether this species is salinity tolerant. Nevertheless, other studies define as extremely tolerant those species able to germinate at 18 dS/m (Cirillo et al., 2018), which means that *I. xanthiifolia* could also be highly tolerant to salinity. According to Bhatt and Santo (2016), the salinity-temperature interaction may alter seed sensitivity and influence the germination of seeds. Other studies (Kashmir et al., 2016; Song et al., 2006; Zhang et al., 2012) have also reported the same significant influence of the salinity-temperature interaction on the germination of weed species. Still, it is important to bear in mind that weed species are often more tolerant to salinity than

crops. Although it is not appropriate to classify them as halophytes, the majority have conserved some halophytic traits, such as early germination and emergence, fast growth, heteromorphic seeds, and high seed longevity. It has been suggested that these traits, alone or in combination, may enhance the spread and competitiveness of weeds (Cirillo et al., 2018). This may be the case with *I. xanthiifolia*, considering the species' high potential for germination even at high salinity levels. However, although *I. xanthiifolia* was observed to tolerate high salinity levels during germination, this does not mean that the plant would be able to conclude its life cycle when exposed to such conditions. As some studies indicate, the adverse effects of salinity tend to be expressed more strongly in the early and subsequent growth stages than in germination (Fogliatto et al., 2020). There is a need, therefore, to study the response of plants to salinity stress in different growing stages to determine whether *I. xanthiifolia* would colonize saline soils if it reached maturity and produced seeds there.

The results presented here regarding the base temperature and base water potential could help in designing models for predicting the spread of this species and in developing new and innovative management strategies, focused on spatial and temporal precision weed control, which would also allow a development of or the inclusion of this species into an already existing Decision Support System (DSS). This would offer an important help to farmers, stakeholders and decision makers in controlling the spreading and negative effects caused by this species. Furthermore, the tests of salinity tolerance conducted could provide further insights into the soil types on which this species could thrive, thus helping to assess the risk of colonization. Finally, some of the data obtained in this study have also presented us with the possibility to evaluate the potential distribution of this species to new areas across the European continent. It is crucial to note, however, that any model is inherently limited by the available data and assumptions made during its development, moreover models and assessments could also be subject to uncertainties and the dynamic nature of ecological systems. Comparing the data of the current distribution of *I. xanthiifolia* (Fig. 1) with the one obtained with our simulations of the potential spreading of this species (Figs. 10 to 13), it becomes apparent that numerous countries might face an increased risk of invasion by this species in the near future. The simulations generated in this study offer a more precise understanding of the specific areas at risk. Moreover, these simulations can illustrate how the distribution of these vulnerable habitats evolves over different time periods and under various Shared Socioeconomic Pathways (SSPs), reflecting the temperature and precipitation changes outlined in the dataset employed (Carvalho et al., 2021; Tebaldi et al., 2021). For example, global temperatures are projected to increase by 2.1–3.5 °C above pre-industrial levels under SSP 2–4.5 and by 3.3–5.7 °C under SSP 5–8.5 by the end of the 21st century, while for the SSP 1–2.6, the predictions are that the temperatures will increase in a range of 1.3 to 2.4 °C. This temperature increase will likely be responsible for the simulated spreading of *Iva xanthiifolia* further to the north and far east of the continent. However, in some scenarios, predictions are that the precipitations will be reduced and some southern and eastern parts of Europe could become more arid, leading to *I. xanthiifolia* disappearing from these regions. The most interesting results can be observed for SSP 5–8.5, which suggests that in the near future some parts of eastern and central Europe might become unsuitable for *I. xanthiifolia*, but they could become suitable again towards the end of the century. Therefore, the data obtained in this work highlights that the climate change will have a significant impact on the invasive potential of *Iva xanthiifolia*, by modifying the conditions in different areas of Europe, but also by influencing the species itself forcing it to adapt to new conditions and therefore evolve, as also seen in this work. Furthermore, they confirm the well-known hypothesis that the climate change will have a significant impact on the future distribution of plant species as suggested by different authors (Kelly and Goulden, 2008; Kosanic et al., 2018; Lai et al., 2023; L. Wang et al., 2019).

Conclusions

This work enhances our understanding of the ecological traits of *I. xanthiifolia*, an important invasive weed species, which has not been studied enough. The adaptability to diverse environmental conditions, rapid growth, and prolific seed production emphasize the necessity for monitoring and effective management strategies, as described before. Investigating the impacts of temperature, water potential, and salinity stress on seed germination and projecting its potential distribution under various climate scenarios, as conducted in this study, provides useful insights for policymakers and agricultural stakeholders to prevent its further spread throughout the European continent. However, considering that only one ecotype was examined in this study, further research is necessary to assess the behaviour of other ecotypes of this species grown in various locations and under different climatic conditions. Collecting more data about the ecological requirements of invasive alien plants would enable more precise simulations of their potential spread, supporting efforts to safeguard European ecosystems and agricultural areas from the threats posed by them through coordinated actions and continued research.

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CRedit authorship contribution statement

Nebojša Nikolić: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Resources, Software, Writing – original draft. **Roberta Masin:** Data curation, Formal analysis, Investigation, Methodology, Supervision, Visualization, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at [doi:10.1016/j.stress.2023.100312](https://doi.org/10.1016/j.stress.2023.100312).

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