

Responses of seed germination of *Xanthium orientale* L. and *Xanthium spinosum* L. to temperature

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Abstract: Species of the genus *Xanthium* (cocklebur) are invasive plants widespread all over the world. In Bosnia and Herzegovina, *Xanthium orientale* L. was an invasive species, while *Xanthium spinosum* L. was an economically harmful weed species. The reason these species are spread over vast areas and across various climate conditions must be attributed to their biology, particularly the biology of their seeds. Germination of populations of *X. orientale* and *X. spinosum* at a temperature range of 15 °C to 40 °C over 2 to 20 days ranged between 15.0% (*X. spinosum*) and 90.0% (*X. orientale*). By means of the application of a statistical model, a positive correlative dependence of temperature and time on seed germination was determined (*X. orientale* = 80.70%, *X. spinosum* = 62.20%), which provided a possibility of modelling the seed germination of *Xanthium* species in various ecological conditions. The optimal germination temperature for both cocklebur species was 30–35 °C. As the germination of seeds was recorded at all researched temperatures (15, 20, 25, 30, 35 and 40 °C), it points to a wide ecological valence for the considered abiotic factor. These results suggest that the unique germination biological characteristics of the *Xanthium* genus made it extremely easy for the species to form monodominant communities in new habitats and climate-changing environments quickly.

Keywords: *Xanthium orientale* L.; *Xanthium spinosum* L.; temperature; germination

Xanthium is a genus of flowering plants in the Asteraceae family (Compositae, with over 1 600 genera and 2 500 species worldwide), native to the Americas and to eastern and some parts of southern Asia. Although short-day plants can also flower in the tropics, where the day length is constant. Many countries have the status of an economically noxious weed species; in some countries, they are classified as invasive species (CABI 2022). Furthermore, *Xanthium* species are extensively distributed throughout

Bosnia and Herzegovina (B&H), with *X. orientale* categorized as invasive, while *X. spinosum* is regarded as economically harmful (Kelečević et al. 2020). *Xanthium* species have been reported to invade various crops such as maize, soybean, cotton, sunflower, tomato, wheat, orchards, and vineyards, as well as non-crop lands (Pacanoski et al. 2007; Hussain et al. 2014; Seifu et al. 2017; Vrbničanin et al. 2020). Yields of maize decreased by 10.0% at 1 *X. strumarium*/m of the row, but a maximum yield loss of 35.0–45.0%

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was recorded at a density of 12 plants/m². Similarly, Ismail et al. (2016) found a 5.2, 22.0, and 44.4% reduction in maize grain yield at *X. strumarium* densities of 1, 4, and 8 plants/m², respectively. At 16 plants/m² density, *X. strumarium* caused maize yield losses of up to 54.0%, while grain weight was reduced by up to 33.0% (Karimmojeni et al. 2009). The seedlings and seeds are the toxic parts of *X. strumarium* and show significant cytotoxic effects in liver cell lines (Xue et al. 2014). *Xanthium* fruit contains two seeds, one small (upper dormant seed) and one large (lower non-dormant seed). The larger seed has no innate dormancy and has high germination potential, while the smaller seed is not germinable at normal temperatures and notably delays germination (Esashi & Leopold 1968). The dormancy of the smaller seed could be due to a lack of oxygen supply or the presence of an inhibitor or other plant growth hormones that act by derepressing the partially or completely repressed DNA site. According to Khan (1966), antagonism between the biogenic inhibitor and kinetin indicates the involvement of the reversible phytochrome system and DNA-dependent RNA synthesis (not protein synthesis) in the dormancy mechanism of the smaller seed of *X. pensylvanicum*. Apart from endogenous, seed germination/dormancy is influenced by several environmental factors (soil temperature and water potential, light exposure, temperature fluctuations, nitrate concentration, soil pH, and soil gaseous environment) (Travlos et al. 2020). Soil temperature greatly affects dormancy and seed germination (Bouwmeester & Karssen 1992). The biology of dormancy and germination determines whether temporal variations promote or inhibit seed germination. Climate changes have significantly impacted all plant species in recent decades, including crops and weeds (Ramesh et al. 2017). So, thermophilic weed species that require higher temperatures for germination and growth (such as *Xanthium* species) would become more competitive and spread faster under climate change scenarios. Rising CO₂ levels in the atmosphere lead to increased plant photosynthesis, known as the carbon fertilization effect (Cho 2022). The idea that crops are fundamentally C₃ and weeds C₄ and that weed competition decreases when atmospheric CO₂ levels increase should not be considered a universal axiom. For example, relative stimulation of aboveground biomass in *X. strumarium*, (C₃ plant) was significantly greater when grown in mixed crops with sorghum (*Sorghum bicolor*, C₄ plant) compared with monoculture at elevated CO₂ (Ziska 2001). Like

most countries, B&H faces the consequences of climate change, which manifest themselves in floods, drought, heavy rainfall, and extremely high temperatures (Čustović & Marković 2014). These species have heliophobic seeds, i.e. non-photoblastic seeds (Saeed et al. 2020). According to these researchers, under natural conditions, the maximum germination of *X. strumarium* (77.0%) was at the temperature of 35–40 °C, while under controlled conditions it was 25–30 °C. Auld (1993) reported that germination rates at 25 °C, with or without partial seed coat removal, ranged from 53.0–57.5%, with the seed coat showing no effect on dormancy. This study was conducted to determine the effect of temperature on seed germination of *X. orientale* L. and *X. spinosum* L. to understand better the causes of the wide distribution and occurrence of these species in cultivated and non-cultivated lands. Since weather conditions are highly variable, even extreme over the past decade, it is necessary, apart from the optimal temperature of germination, to know the minimum and maximum germination temperatures as well, along with the dynamic of seed germination, to predict the spread and invasiveness of these species. Thus, we can predict the emergence of seedlings and determine an appropriate strategy to control these weed species in the context of highly variable climatic conditions.

MATERIAL AND METHODS

B&H is located in the western part of the Balkan peninsula. The annual precipitation ranges from 792 mm in the northeastern part to 1 707 mm in the south. Annual mean temperatures are 10.6–14.9 °C (Radusin et al. 2016). Usually, the temperature between June and September is higher than 30 °C. The distribution of *Xanthium* species has been recorded across the whole territory of B&H (Figure 1), and 20 populations were selected for seed germination. From each population, fruits from five normally developed plants were collected and transported in paper bags to a laboratory. The fruits were stored at 4 °C until germination tests. For testing, normally developed fruits were used by random selection.

Seeds of 19 *X. orientale* populations were collected, and one for *X. spinosum*, on crop and non-crop lands (Table 1).

Germination tests of the seeds of all 20 populations were performed simultaneously at the respective temperatures of 15, 20, 25, 30, 35 and 40 °C. The

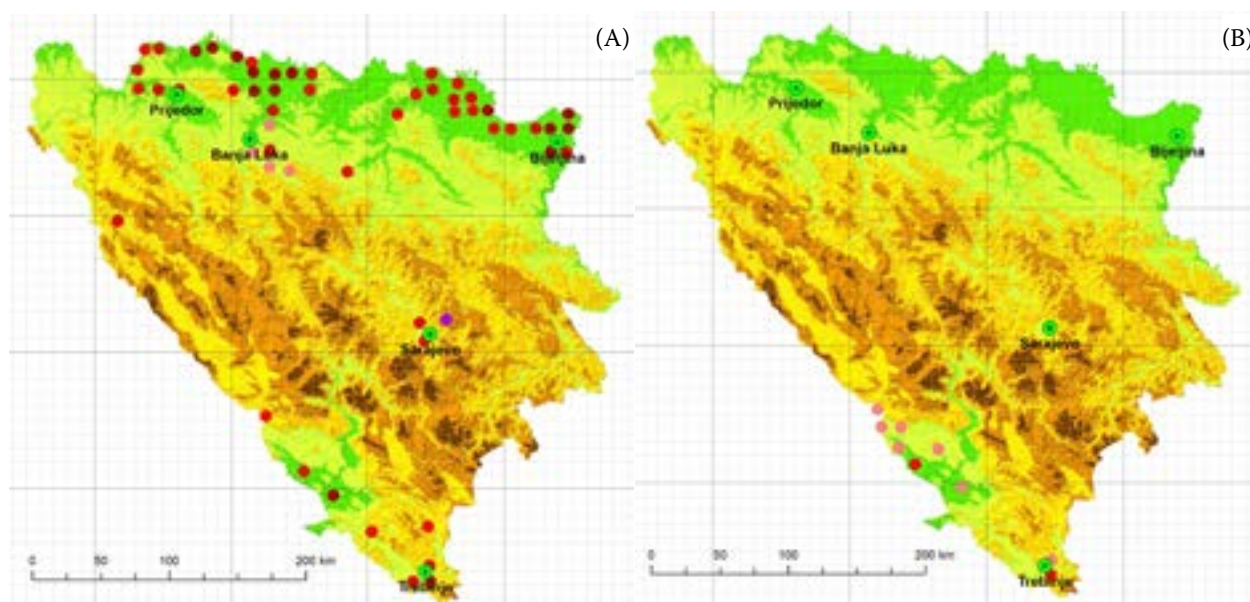


Figure 1. Distribution of *Xanthium orientale* (A) and *X. spinosum* (B) in B&H (Kelečević et al. 2020)

whole fruit was used for testing. Sterilized quartz sand (100 g), grain size 0.5–0.8 mm, pH 6.0–7.5 was used as substrate. Five fruits were randomly placed in 90 × 20 mm Petri dishes, and 35 mL (for *X. orientale*) or 20 mL (for *X. spinosum*) of distilled water was added, sufficient to ensure optimal humidity until the end of the experiment. The fruits of *X. orientale* were

at a depth of 0.61 cm, while the fruits of *X. spinosum* were in sand at depth of about 0.75 cm. Germination of seeds was performed in a Fisher Scientific ET618-4 thermostable incubator, with a volume of 135 L, with the ability to control the temperature within the range of 2–40 °C ± 0.5 °C without lighting. Germinated seeds were counted every second day dur-

Table 1. Localities where fruits of *Xanthium* populations were collected

Population	Latitude (N)	Longitude (E)	Elevation (m a.s.l.)	Habitat
<i>Xanthium orientale</i>				
Agrofin	42°40'14.3"	18°19'38.0"	272	vineyard
Aleksandrovac 1	44°58'09.7"	17°18'25.9"	120	roadside
Aleksandrovac 2	44°58'09.7"	17°18'25.9"	120	ruderal area
Balatun	44°52'57.1"	19°19'56.9"	81	roadside
Bardača	45°05'22.5"	17°26'32.4"	81	ditch
Berek	45°02'35.5"	17°14'30.6"	104	maize field
Cerovljani	45°02'29.4"	17°15'24.1"	103	maize field
Dolgođi 1	43°52'03.3"	18°17'01.5"	486	wasteland
Dolgođi 2	43°51'41.5"	18°17'41.4"	483	maize field
Domanovići	43°08'13.2"	17°47'01.5"	144	vineyard
Gorica	42°42'54.8"	18°21'05.6"	285	riverside
Lončari	44°56'44.7"	18°39'50.7"	85	maize field
Lukavac	45°04'19.1"	17°12'44.0"	104	maize field
Mašići	45°01'43.6"	17°15'57.6"	103	maize field
Popovo polje	42°39'54.2"	18°19'33.0"	270	vineyard
Seferovci	44°59'52.9"	17°20'59.9"	106	ruderal area
Velino Selo	44°53'17.6"	19°19'28.2"	82	maize field
Vilusi	45°00'30.0"	17°16'53.0"	108	maize field
Volujac	42°41'06.9"	18°19'25.0"	269	vineyard
<i>X. spinosum</i>				
Trebinje	42°41'06.9"	18°19'25.0"	269	vineyard

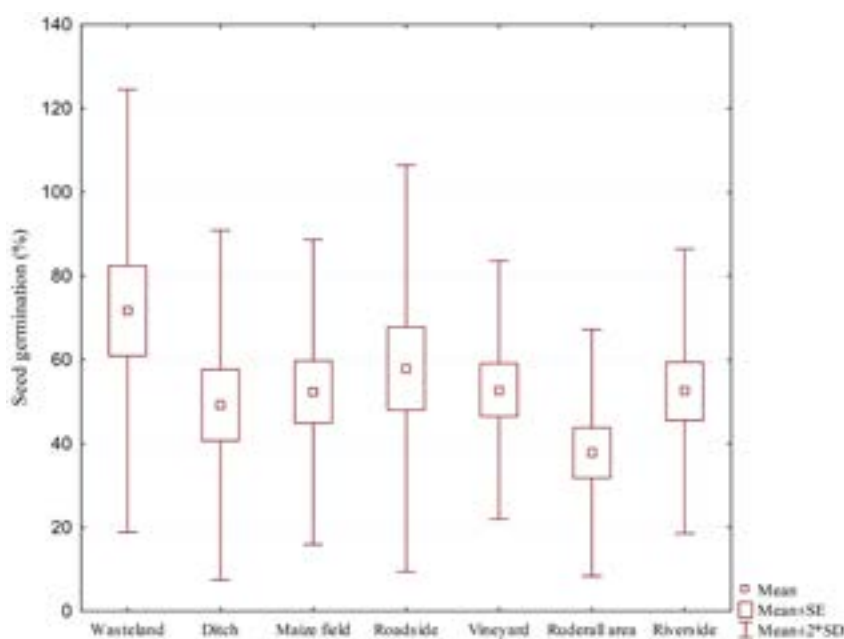


Figure 2. The total germination percentage of *Xanthium orientale* to habitat

ing a 20-day testing period. The seed was considered germinated when a radicle could be spotted on the surface of a fruit. All trial variants were performed in four replications and two cycles. A germination rate (GR, sum of germination per day) was calculated using a formula described by Maguire (1962):

$$GR = n_1/t_1 + n_2/t_2 + n_3/t_3 + \dots + n_x/t_x \text{ (fruits/day)} \quad (1)$$

where: $n_1, n_2, \dots, n_x$ – are the numbers of the germinated seeds at times; $t_1, t_2, \dots, t_x$ – time in days

The data was analyzed by two-factor analysis of variance (ANOVA) using the Statistica (version 10.0). The Tukey test was used to determine the significance of differences between the populations studied. The partial and multiple correlation coefficient was used to determine the effect of temperature and time on seed germination.

RESULTS

In terms of habitat (related to all temperatures), the best germination (%) was found in seeds collected from wasteland and the lowest in seeds that developed in ruderal areas (Figure 2).

The research does not state the temperatures above or below which the germination of *Xanthium* species occurs. Most seeds of all populations could germinate in a wide range of temperatures. The minimum germination was 15.0%, and the maximum was 90.0% within the 15–40 °C temperature range. The highest seed germination was achieved at 35 °C in both species, and germination decreased with a further increase in temperature. The percentage of total germination of all *X. orientale* populations was high (up to 90.0%) compared to *X. spinosum* (15.0%) (Figure 3).

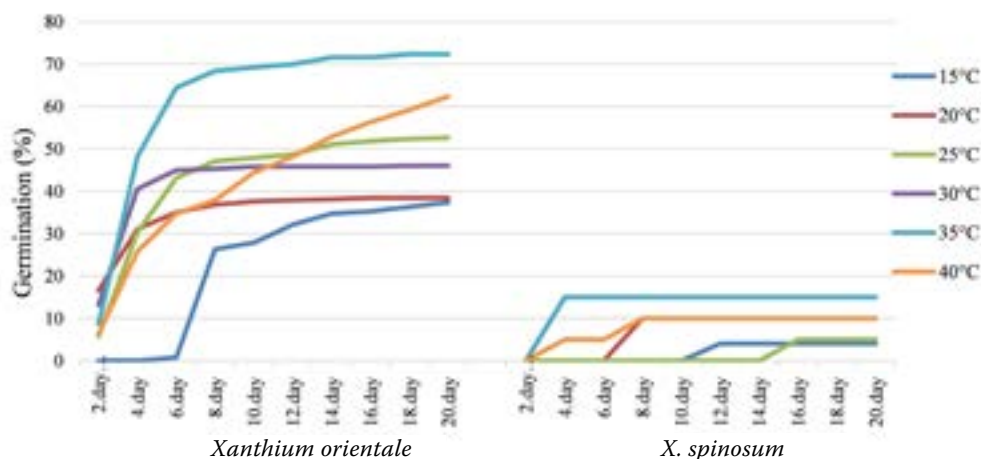


Figure 3. Total percentage of seed germination of *Xanthium orientale* and *X. spinosum*

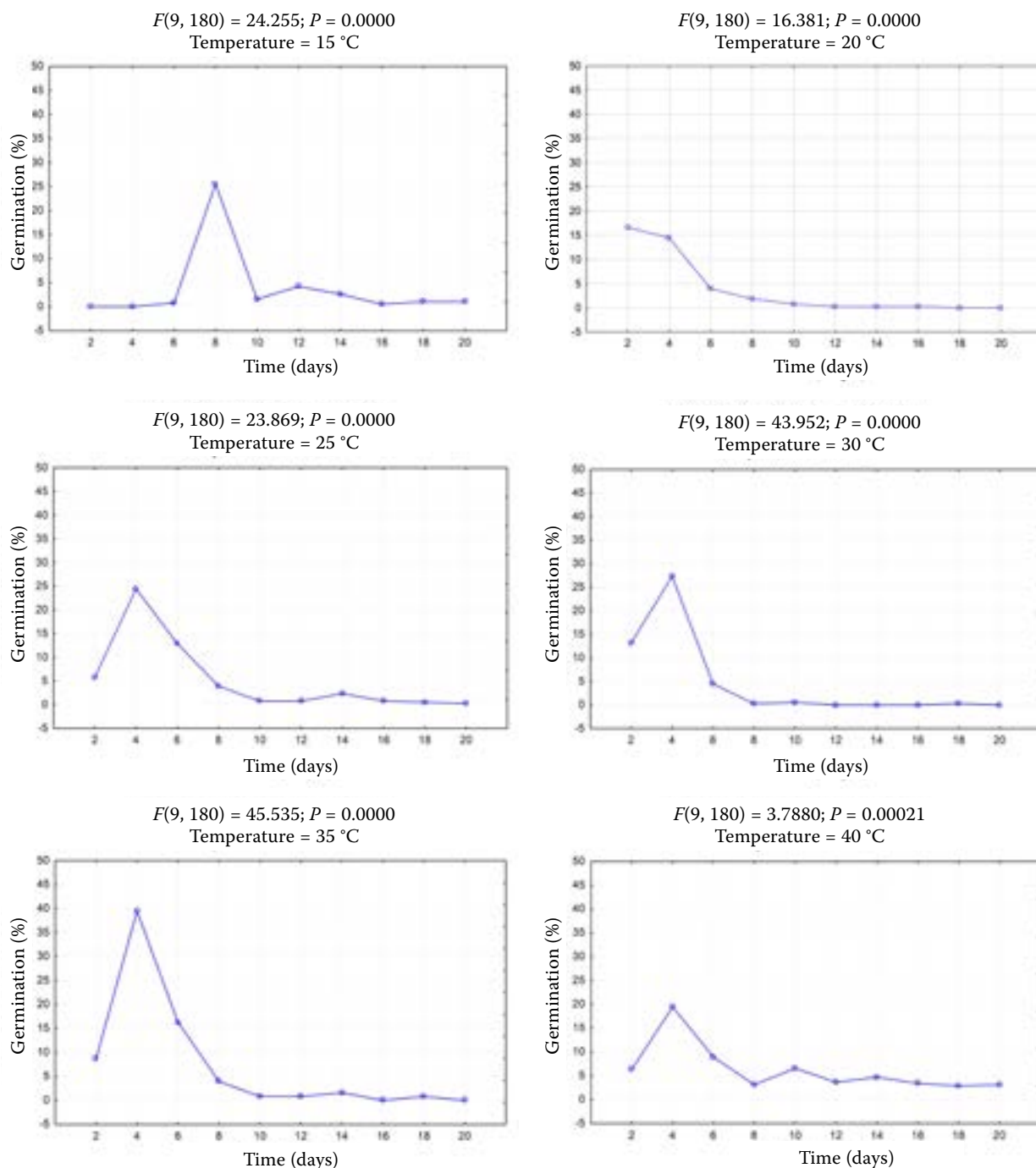


Figure 4. Dynamic of seed germination of *Xanthium orientale* at respective temperatures of 15 °C, 20 °C, 25 °C, 30 °C, 35 °C and 40 °C

The dynamic of seed germination. The average seed germination of *X. orientale* in the temperature interval of 15 °C to 40 °C ranged from 37.4% to 72.4%, where the best germination was achieved at 35 °C on the fourth day (Figure 4). As for the germination of *X. orientale* is at its lowest point (37.4%) at the lowest temperature (15 °C). The dynamic of germina-

tion was rather stretched; the germination process lasted up to day 20, with its pinnacle on the eighth day of the research. At the temperatures of 25 °C, 30 °C, and 35 °C, the highest germination of *X. orientale* was reached on the fourth day of germination. At such temperatures, seeds germinated vigorously, so we can state that the optimal temperatures for *X. orientale*

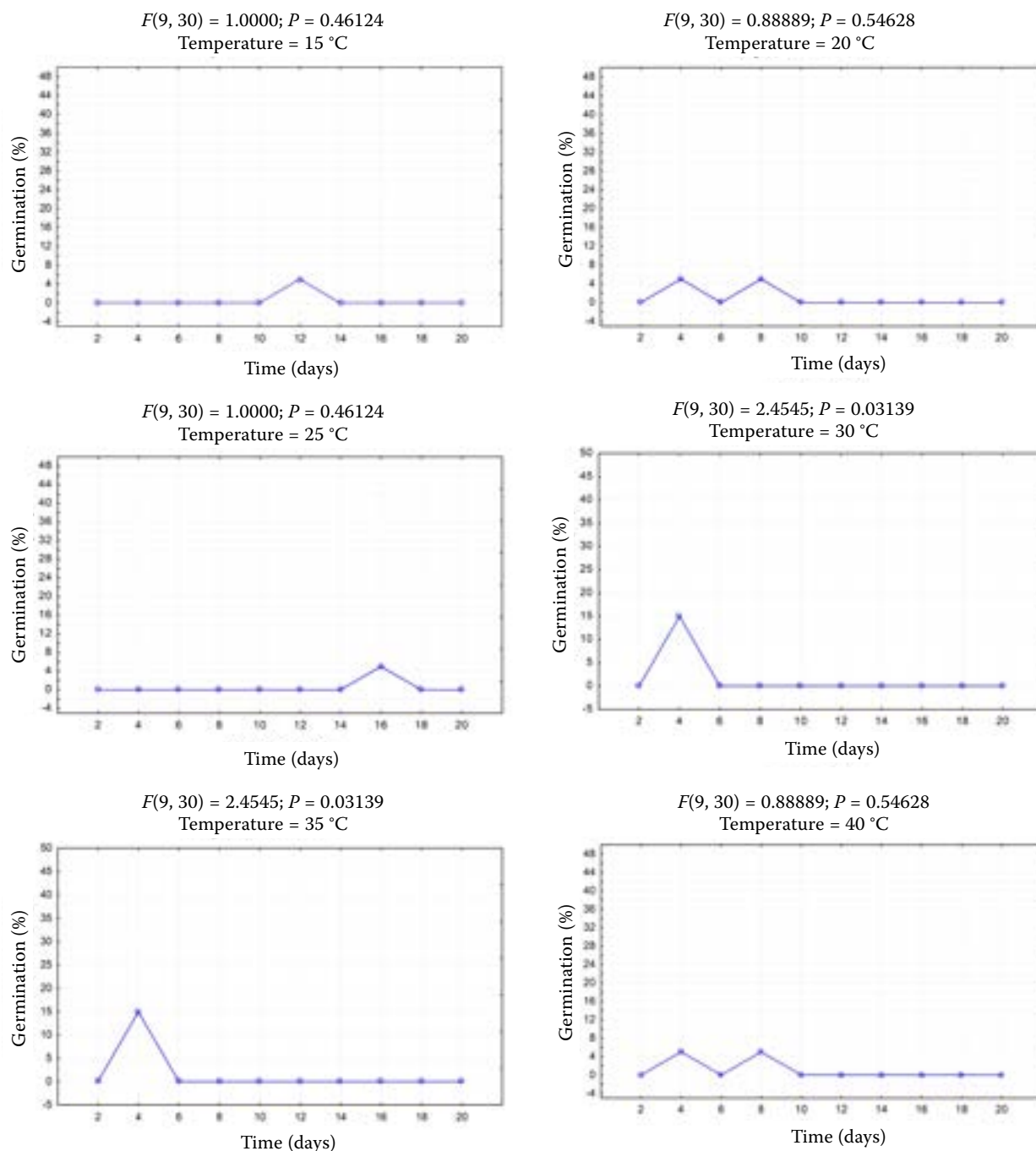


Figure 5. The dynamic of seed germination of *Xanthium spinosum* at respective temperatures of 15 °C, 20 °C, 25 °C, 30 °C, 35 °C and 40 °C

ranged from 30 °C to 35 °C. At 40 °C, the percentage of germinated seeds was also very high (62.4%), although germination was protracted and lasted throughout the study period (2–20 days) (Figure 4).

In contrast to *X. orientale*, the germination of *X. spinosum* at 15 °C, 25 °C, 30 °C, and 35 °C was lower and lasted only two days, but the germination dynamic was different (Figure 5). Average seed

germination of *X. spinosum* within the temperature interval of 15–40 °C ranged from 4.0–15.0%. The lowest percentage of seed germination was at respective temperatures of 15 °C and 25 °C, only 4.0%, and the germination process was very protracted, being reached on the twelfth and sixteenth day, respectively. The highest and fastest germination of seeds was achieved at 30–35 °C.

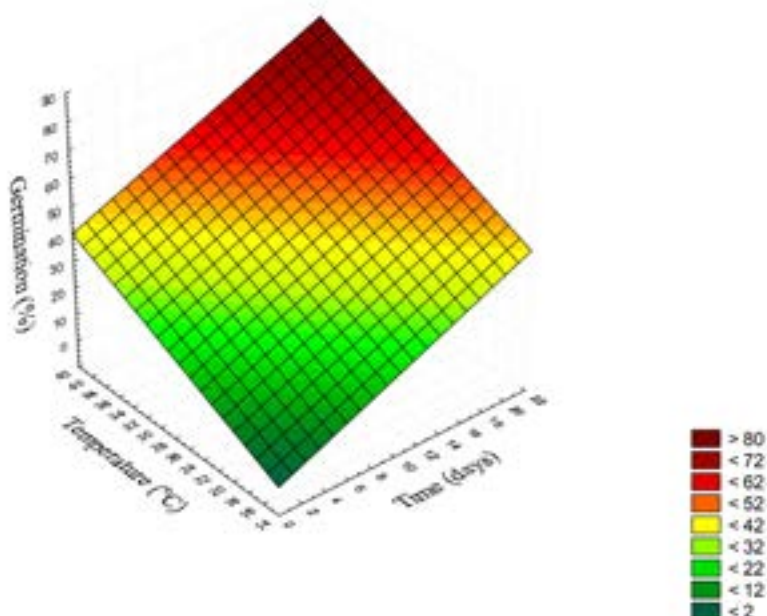


Figure 6. Multiple correlations of seed germination dependence on temperature and time of populations *Xanthium orientale* ($F_{2,57} = 53.325^{**}$; $P = 8.827 \times 10^{-14}$; $R = 0.807^{**}$)

The germination of *X. orientale* populations occurred within the temperature range of 15–40 °C over 2–20 days, with rates ranging between 50.0% and 90.0%. Positive partial ($r_{yTi-Te} = 0.675$; $r_{yTe-Ti} = 0.713$) and multiple ($R = 0.807$) correlational dependence were confirmed between temperature and elapsed time to the achieved germination of these populations (Figure 6).

The effect of temperature and time on seed germination of *X. spinosum* is also highly statistically significant. Germination within the 15–40 °C temperature range in 2–20 days ranged between 4.0–15.0%. A positive partial ($r_{yTi-Te} = 0.373$; $r_{yTe-Ti} = 0.566$) and multiple ($R = 0.622$) correlation between temperature and time was confirmed. (Figure 7).

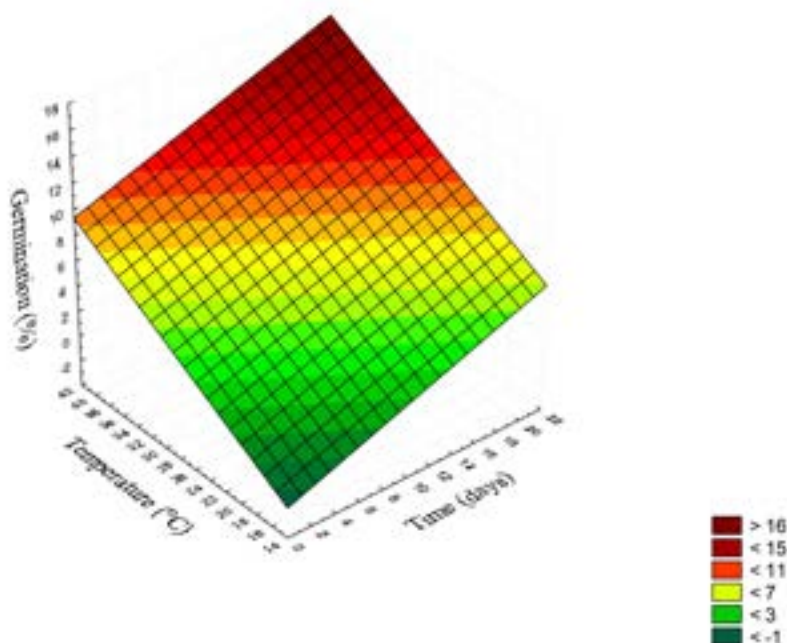


Figure 7. Multiple correlations of seed germination dependence on temperature and time of populations *Xanthium spinosum* ($F_{2,57} = 18.019^{**}$; $P = 8.619 \times 10^{-7}$; $R = 0.622^{**}$)

The linear correlation coefficient shows that the germination of *X. orientale* seeds is higher compared to *X. spinosum*. When the temperature increases by 1 °C, the germination of *X. orientale* increases by 1.4% (Figure 6), while the germination of *X. spinosum* increases by 0.4% (Figure 7). As a function of time (day), germination increased by 1.9% for *X. orientale* (Figure 6), while it increased by 0.3% for *X. spinosum* (Figure 7).

DISCUSSION

Xanthium species' distribution is influenced by intrinsic and extrinsic factors (i.e., temperature amount of precipitation), which in anthropogenic habitats are often the result of human activity. The highest and fastest germination of *X. orientale* were observed at temperatures ranging 30–35 °C (Figure 4), consistent with other *Xanthium* species (section *Euxanthium* DC.): *X. strumarium* (Saeed et al. 2020), *X. sibiricum* (Wang et al. 2014), *X. canadense* (Shitaka & Hirose 1993), *X. italicum* (Georgescu et al. 2015) etc. The optimality of these temperatures is confirmed by the fact that, at 30 °C and 35 °C, respectively, the germination process was the shortest and most intense, with the highest percentage of germination recorded on the fourth day of the research (Figure 4). While the germination process was extended on other referent temperatures (15 °C, 20 °C, 25 °C and 40 °C), it was the longest at the temperature of 40 °C (up to 20 days). Saric et al. (2012) showed similar results concerning germination dynamics in *X. strumarium*. At 15 °C, the seeds took a longer period to start germinating (about five days); however, at higher temperatures (25 °C, 30 °C, and 35 °C), germination began the very next day of the experiment.

The average seed germination of *X. spinosum* ranged from 4.0–15.0% (Figure 5). The highest and fastest germination of seeds was also achieved at temperatures of 30–35 °C. In addition, these temperatures are responsible for the initial germination time since the highest germination rate was achieved on the fourth day, whereas, with regard to the respective temperatures of 15 °C, 20 °C, 25 °C, and 40 °C, the germination process was either extended (it lasted up to 10 days) or belated (start after the day 10), resulting in a lower percentage of germination as well (Figure 5). According to Tao et al. (2022), the initial germination time was shortest at

28 °C (about 5 days), and the highest germination rate was 71.5% at a sand depth of 1 cm, while in this study, seeds were at a sand depth of 0.75 cm. These results are also in contrast to the studies of Auld (1993), where the highest germination in the soil was found at the temperature of 25 °C with 62.0 % to 95.0%. The differences between the percentage of germination in this paper and the results from previous studies could be related to the adaptation process of weed populations to local environmental conditions (Loddo et al. 2018). The low percentage of germination of *X. spinosum* can also be explained by the burial depth and the gradual decomposition of the fruit coat in the soil.

In general, temperature and time positively affect seed germination, i.e., with the percentage of germinating seeds increasing as the temperature (until 35 °C) and time (until the sixteenth day) increase. Although the effect of temperature and time on seed germination was significant (Figures 6 and 7), we can point out that other factors are exerting great influence on seed germination, such as the conditions under which the mother plant developed (Figure 2), as well as endogenous processes in the seed (Chiu et al. 2012). Seed germination depends on the characteristics of the seed (hard coats, impermeability of the coats to oxygen, need for a certain post-ripening period in dry storage), chilling requirements, need for special light or dark conditions, phytohormones, a network of transcription factors) (Chiu et al. 2012) and environmental factors (Travlos et al. 2020). Despite the protracted nature of the germination process, the seeds could germinate within the 20–40 °C range of temperatures (Figures 4 and 5). Germination at high temperatures has been found in a large number of weed species. However, they belong to tropical plants, such as *Echinochloa crus-galli*, *Amaranthus albus* and *Portulaca oleraceae*, which can germinate at 42 °C (Dahlquist et al. 2007). Seed germination at high temperatures is due to a special group of proteins that protect the germ from heat, so species with high-temperature requirements have higher levels of these protein groups (Medina & Cardemil 1993). The possibility of germination at high temperatures, given the increasingly pronounced climatic changes resulting from global warming and the expected rise in temperature, indicates the possibility of spreading this species to new areas and increasing abundance in the areas where it already occurs. The lower germination

capacity of the *X. spinosum* regarding *X. orientale* could be one of the reasons for the lower distribution of this species (Greuter 2006+).

B&H has several climate types: temperate continental climate (northern and central parts), submontane and mountainous (central parts), and Adriatic and modified Adriatic climate type (southern parts) (Radusin et al. 2016). The maximum soil temperature at a depth up to 5 cm (in April and May) has ranged from 19.1 °C to 34.0 °C in the past decade [Bijedić (ed.) 2013–2023; Supić et al. 2013–2023]. These temperature differences may result in later germination in the northern and central parts of B&H with a temperate continental climate, compared to the southern part, where germination begins earlier. Nevertheless, since the differences in germination time (up to 9 days) do not result in a major delay in flowering (Shitaka & Hirose 1993), plants in different climates can complete their development and form fruits. This suggests great plasticity of *X. orientale* regarding temperature requirements and the possibility of development in different climates, which may explain the wide distribution and character of the invasive species in many countries (CABI 2022). Although *X. spinosum* has similar temperature requirements, the overall percentage of germination was very low (only 15.0%), and it appears that other factors influenced germination and dispersal and thus, a smaller area of introduction into Europe compared to *X. orientale* (Greuter 2006+). The dynamic of seed germination shows that the largest amount of seeds (seed bank) germinates energetically under optimal temperature conditions. The adaptability of *Xanthium* species to temperature, water inundation (Wang 2014), high soil salinity, and soil pH (He & Ma 2018) may explain the wide distribution (Greuter 2006+) and character of the invasive species under different environmental conditions.

CONCLUSION

Species of the genus *Xanthium* have high requirements regarding the optimal temperature for seed germination, which ranges 30–35 °C. The germination rate of the larger seed in the fruit of *X. orientale* is up to 90%. The germination rate of one seed of the *X. spinosum* was much lower, only 15%. The influence of two independent variables (temperature and time) on the seed germination percentage is significant. Thus, based upon determined regres-

sion dependence, it is possible to model the emergence of *Xanthium* species. Species of the genus *Xanthium* have a great ability to germinate under a wide range of temperatures and other environmental factors, which explains their invasive status in many countries. In this context, it is argued that the increasing damage to crops and the wide distribution of *X. orientale* is due to the universality of suitable habitats regarding temperature conditions, such as cultivated and non-cultivated lands. Because *X. orientale* is an ecological threat and given the universality of its suitable habitats, we recommend monitoring *X. orientale* in all habitat types. Given the current projected potential range of *X. orientale* in light of climate change, these results could be useful for decision-makers in developing short- and long-term conservation strategies for planning weed control measures.

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