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Seed germination characteristics of *Xanthium spinosum* populations from different climatic regions of Türkiye: Implications for weed management

Türkiye'nin farklı iklim bölgelerinden toplanan Xanthium spinosum popülasyonlarının tohum çimlenme özellikleri: Yabancı ot mücadelesi açısından ipuçları

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ABSTRACT

Xanthium spinosum is a troublesome invasive weed widely distributed through many agroecological zones in Türkiye, adversely affecting crop production and local biodiversity. Understanding its seed germination biology is essential for formulating efficient, region-specific management measurements. This study assessed the influence of photoperiod, temperature, pH, salinity, osmotic potential, and seed burial depth on the germination characteristics of *X. spinosum* populations collected from four geographical regions (Southeastern Anatolia, Mediterranean, Black Sea, and Central Anatolia) in Türkiye. Peak germination was observed under a 12-hour light/dark photoperiod, with Southeastern Anatolia and the Mediterranean populations exhibiting higher responsiveness to light. The highest germination occurred at ~30 °C for Southeastern Anatolia and Mediterranean populations, whereas Black Sea and Central Anatolia populations preferred relatively lower temperatures (25–27 °C) for peak germination. Similarly, neutral pH (~7.0–7.6) resulted in the highest germination of all populations, whereas Southeastern Anatolia had better pH tolerance. Salinity and osmotic stress tests revealed significant demographic differences, with the Southeastern Anatolia population exhibiting higher tolerance to salinity and drought stresses. Seedling emergence peaked at lower burial depths (~2–4 cm) and had a sharp decline at increased depths. These results highlight significant population-specific adaptation patterns associated with local climatic and edaphic conditions. Deep tillage and management strategies based on environmental tolerance determined in the current study may restrict the further spread of *X. spinosum*.

Keywords: Invasive weed management, Photoperiod sensitivity, Population variability, Seed germination

ÖZ

Xanthium spinosum, Türkiye'nin birçok agroekolojik bölgesine yayılmış, tarımsal üretimi ve yerel biyoçeşitliliği olumsuz etkileyen sorunlu bir istilacı yabancı ottur. Bu türün tohum çimlenme biyolojisinin anlaşılması, etkili ve bölgeye özgü yönetim önlemlerinin oluşturulması açısından büyük önem taşımaktadır. Bu çalışmada, Türkiye'nin dört farklı coğrafik bölgesinden (Güneydoğu Anadolu, Akdeniz, Karadeniz ve İç Anadolu) toplanan *X. spinosum* popülasyonlarının çimlenme davranışı üzerinde fotoperiyot, sıcaklık, pH, tuzluluk, ozmotik potansiyel ve tohum gömülme derinliğinin etkileri değerlendirilmiştir. En yüksek çimlenme, 12 saat ışık/12 saat karanlık fotoperiyotta gözlenmiş, Güneydoğu Anadolu ve Akdeniz popülasyonları daha yüksek ışık duyarlılığı sergilemiştir. Sıcaklık açısından en yüksek çimlenmenin Güneydoğu Anadolu ve Akdeniz popülasyonlarında yaklaşık 30 °C'de gözlemlenirken, Karadeniz ve İç Anadolu popülasyonlarında ise daha ılıman sıcaklıklarda (25–27 °C) gerçekleştiği ortaya konulmuştur. Benzer şekilde, tüm popülasyonlarda nötr pH (~7.0–7.6) koşullarında en yüksek çimlenme kaydedilmiş, Güneydoğu Anadolu popülasyonu daha geniş bir pH toleransı göstermiştir. Tuzluluk ve ozmotik stres testleri, Güneydoğu Anadolu popülasyonunun tuz ve kuraklık streslerine karşı daha yüksek tolerans sergilediğini ortaya koymuştur. Fide çıkışı, düşük gömülme derinliklerinde (~2–4 cm) zirveye ulaşmış, derinlik arttıkça keskin bir düşüş göstermiştir. Bu sonuçlar, yerel iklimsel ve edafik koşullarla ilişkili önemli popülasyon-özgü adaptasyon kalıplarını vurgulamaktadır. Bu çalışmada belirlenen çevresel toleranslara dayalı derin sürüm teknikleri ve yönetim stratejileri, *X. spinosum*'un gelişimini sınırlayabilir. Bu çalışmada ortaya konulan popülasyon düzeyindeki değişkenlik, bölgeye özgü etkili yabancı ot yönetim stratejileri için kritik öneme sahiptir.

Anahtar Kelimeler: İstilacı yabancı ot yönetimi, Fotoperiyot duyarlılığı, Popülasyon varyasyonu, Tohum çimlenmesi

Introduction

Seed germination is a critical factor in the ecology and management of weed species as it influences timing and pattern of seedling emergence (Batlla & Benech-Arnold, 2014). Soil seed bank is the principal source of future weed infestations as it harbours millions of viable seeds (Schwartz-Lazaro & Copes, 2019). Weed infestation is caused by the seeds that can enter dormancy and endure adverse conditions until germination (Batlla & Luis Benech-Arnold, 2007; Benech-Arnold et al., 2000; Qasem, 2020). Consequently, understanding seed germination biology is essential for predicting weed emergence patterns and developing effective management strategies (Chauhan & Johnson, 2010; Marschner et al., 2024). Weed management methods, such as stale or false seedbeds are designed to use germination cues, facilitating germination of weed seeds (Travlos et al., 2020). Therefore, understanding the environmental factors that facilitate or inhibit weed seed germination is essential for the implementation of available management strategies or designing alternative methods (Batlla & Benech-Arnold, 2014).

Seed germination and dormancy of weed species is altered by several environmental factors. Temperature is the most critical indicator of germination, and each species has an optimal temperature range and often exhibits specific diurnal requirements (Dürr et al., 2015). Numerous summer-annual weeds germinate under temperatures ranging from 25 to 35°C, while others need alternating day/night temperatures (Travlos et al., 2020). Fluctuating temperatures may promote weed species to sprout near the soil surface, where daily thermal variations are more pronounced (Steinmaus et al., 2000).

Numerous weed seeds exhibit positive photoblasticism, indicating that they need light exposure to terminate dormancy (Chauhan et al., 2006a). Seeds buried deeper in darkness remain dormant, while those closer to the surface germinate. Cocklebur (*Xanthium* spp.) seeds germinate well in both darkness and light (Weaver & Lechowicz, 1983). Osmotic potential and soil moisture are the other important factors regulating seed germination in weeds. Seeds may remain dormant if the soil moisture tension is elevated (Hegarty, 1978). Certain weed species may germinate under extreme water stress (i.e., osmotic potentials < –0.5 MPa), whereas others need abundant moisture (Ahmadi et al., 2024; Farooq et al., 2019, 2021; Malka et al., 2023; Önen et al., 2018). Osmotic stress or ion toxicity resulting from elevated salinity may impede germination (Hakim et al., 2011). Local adaptation is crucial for successful germination in saline soils as salt-adapted seeds exhibit superior germination under salinity (DiTommaso, 2004). Soil pH is another major factor influencing seed germination of weeds (Alberto Ortiz et al., 2019). While excessive acidity or alkalinity may restrict germination, most weed seeds thrive throughout a broad pH spectrum (Chauhan et al., 2006b, 2006c). Agricultural weeds may thrive in several soil types owing to their wide pH germination range.

Seed burial depth significantly influences germination and seedling emergence by altering light, temperature, and oxygen exposure (Tian et al., 2024; Yuan et al., 2025). Seeds on the soil surface often fail to germinate or survive owing to light-induced dormancy or desiccation; however, shallow burying may provide moisture and enable light penetration (Kigel, 2017; Nautiyal et al., 2023). Small-seeded weeds are unable to emerge from deep soil layers due to restricted energy resources (Benvenuti & Mazzoncini, 2019), while larger seeds will remain dormant if buried beyond their optimal emergence depth (Grundy et al., 2003). The burs (fruits) of *Xanthium spinosum* buried at depths of 1–4 cm exhibit optimal emergence, whereas surface seeds do not germinate, and emergence rates decline markedly at depths above 5–10 cm (Auld, 1993; Hocking & Liddle, 1986; Tao et al., 2022).

Xanthium spinosum L. is a globally significant annual broadleaf weed. It is native to South America and now distributed across all continents except Antarctica, and regarded as a significant invasive weed in Europe, Asia, Africa, and Australia (CABI, 2022). Its invasive nature and impact make it one of the most noxious weeds (CABI, 2022; Holm et al., 1978). *Xanthium spinosum* infests agricultural fields, pastures, roadsides, and riparian zones, flourishing in warm climates and disturbed habitats (Assefa & Tilaye, 2023). It spreads by adhering to animal fur, sheep wool, vehicles, and agricultural machinery, so contaminating harvested crops and seed lots with its spiny burs (CABI, 2022). It may establish dense monospecific stands, outcompeting crops, forage grasses, and native vegetation (Kelečević et al., 2024). Severe infestations in row crops such as maize, soybean, cotton, and sunflower may decrease yields, threatening agriculture. Hence it is a high-priority target for management in several countries, where it is regarded as a noxious weed (CABI, 2022).

Xanthium spinosum is distributed in many habitats of various regions in Türkiye. It has been reported from ~30 provinces in Mediterranean, Aegean, and southeastern Anatolian regions (Bükün, 2005; Kadıoğlu & Kekeç, 2020; Ozturk et al., 2017). The ability of *X. spinosum* to inhabit cultivated and ruderal areas is because of its resistance to many environments. Different populations of *X. spinosum* in Türkiye may face diverse selection pressures, ranging from the humid Black Sea coast to the arid southeastern Anatolia. Hence, it is essential to understand germination biology of these populations to ascertain the differences in tolerance limits (e.g., temperature or moisture) that might influence management strategies. Understanding germination characteristics will allow to predict peak emergence in Turkish agroecological zones and schedule actions such as soil cultivation or herbicide use to target emerging cohorts of *X. spinosum*.

Although *X. spinosum* is significant threat to agriculture; few studies have investigated its seed germination ecology in various regions of the world (Ahmadi et al., 2024; Kelečević et al., 2024; Tao et al., 2022). It exhibits similar germination to that of other *Xanthium* species (CABI, 2022). It produces twin-seeded burs with one larger and one smaller arranged at bottom and top, respectively (Esashi & Leopold, 1968). The bigger seed is often non-dormant and germinates in the first favorable season, whereas the smaller seed has an intrinsic dormancy and frequently remains viable (CABI, 2022). This dual-seed strategy helps in longer persistence. Seeds of *X. spinosum* have the potential to germinate in the absence of light (Auld, 1993; Weaver & Lechowicz, 1983). Elevated soil temperatures facilitate the germination of *X. spinosum* throughout late spring and summer. Kelečević et al. (2024) discovered that *X. spinosum* seeds germinate between 15 to 40°C, exhibiting reduced rates at lower temperatures. The optimal temperature range is 30–35°C. Optimal germination occurs at pH levels ranging from 5 to 10 and tolerance to high salinity, with a 50% germination threshold at 200-250 mM NaCl (Kelečević et al., 2024).

Another significant component of weed germination biology is variation across different populations of the same species. Weeds often colonize extensive geographic areas and many ecosystems, and they may develop population-specific germination responses adapted to local conditions (Farooq et al., 2019). Several weed species in Türkiye exhibited significant differences among seed germination requirements (Farooq et al., 2019, 2021; Önen et al., 2018; Ozaslan et al., 2017). Therefore, determining the seed germination biology of different populations can help to develop region-specific management strategies. Unfortunately, no such data exist for *X. spinosum* populations distributed across different regions in Türkiye.

This study investigated the seed germination characteristics of *X. spinosum* populations stemming from several regions in Türkiye. The objectives were to (1) determine the effects of photoperiod, temperature, pH, osmotic potential, and seed burial depth on germination and seedling emergence of *X. spinosum*, and (2) evaluate germination responses across various climatic and geographic locations. The results will help to develop region-specific management strategies in the future.

Materials and Methods

Seed collection

Seeds (burs) were obtained from four independent populations distributed across various ecosystems in different geographic regions of Türkiye. Seeds were harvested from 50 mature mother plants, transported to the laboratory, desiccated in the shade, and kept at 25°C until used in the studies. The details of the geographic locations of seed collection sites and habitat are given in Table 1.

Seeds were collected from four different places in Türkiye, i.e., Şanlıurfa (Southeastern Anatolia), Adana (Mediterranean), Samsun (Black Sea), and Kayseri (Central Anatolia). The climatic conditions differed, with Şanlıurfa exhibiting a Hot Semi-Arid Climate (BSh), Adana having Hot-Summer Mediterranean Climate (Csa), Samsun with Warm-Summer Humid Continental Climate (Dfb), and Kayseri with Cold Semi-Arid Climate (BSk). Seed collection habitats ranged from agricultural areas (Şanlıurfa and Adana) to non-agricultural areas (Samsun) and roadside environments (Kayseri). The population size all sites was 100 to 200 plants.

Table 1. Background information on the seed collection sites, their geographic locations, prevailing habitat and climatic conditions

Population	Region	Climatic region/Köppen classification	Geographic location	Habitat	Population size
Şanlıurfa	Southeastern Anatolia	Hot Semi-Arid Climate (BSh)	37.325450 °N 39.656890 °E	Agriculture	> 100 plants
Adana	Mediterranean	Hot-Summer Mediterranean Climate (Csa)	36.875550 °N 35. 567060 °E	Agriculture	> 200 plants
Samsun	Black Sea	Warm-Summer Humid Continental (Dfb)	40.986110 °N 35.641260°E	Non-Agricultural	> 150 plants
Kayseri	Central Anatolia	Cold Semi-Arid Climate (BSk)	38.681333 °N 35.495861 °E	Roadside	> 100 plants

Three soil samples were collected from all seed collection sites and mixed to prepare a composite sample. The soil was analyzed according to standard procedures described in the literature. Soil characteristics of seed collection sites indicated significant variations that may influence seed germination. Soils in Adana had the highest calcium carbonate ($CaCO_3$) concentration (29.58%), indicating more calcareous, alkaline conditions, while Şanlıurfa exhibited a comparatively low $CaCO_3$ content (6.86%), suggesting less calcareous soil. Organic matter (OM) content was typically low across all sites, indicating degraded or intensively cultivated soils, with Samsun exhibiting the highest OM content (2.46%), potentially improving soil moisture retention and nutrient availability. Soil pH indicated a little alkalinity across all locations, ranging from 7.55 to 8.23, with Kayseri and Samsun exhibiting the highest levels of alkalinity. Electrical conductivity (EC) (an indicator of soil salinity) was significantly higher in Şanlıurfa (839 mS/m) and a bit high in Adana (512.89 mS/m), suggesting saline soils that may impede germination. Kayseri had the lowest EC (205.15 mS/m), indicating mild salinity. Soil texture exhibited minor variations. All locations were mostly clayey; however, Kayseri had a comparatively lower clay content (49.5%) than Şanlıurfa, Adana, and Samsun (>60%), possibly facilitating improved drainage. Available phosphorus (P) concentration was highest in Samsun (67.87 ppm), indicating possibly enhanced soil fertility, while Kayseri exhibited a very low level (10.03 ppm) (Table 2).

Table 2. Soil properties of the seed collection sites of Xanthium spinosum populations included in the study

Population	$CaCO_3$ (%)	OM (%)	pH	EC (mS/m)	Clay (%)	Sand (%)	Silt (%)	P (ppm)
Şanlıurfa	6.86	1.69	7.62	839.00	61.10	23.90	15.00	28.10
Adana	29.58	1.93	7.55	512.89	63.22	32.20	25.14	41.20
Samsun	13.24	2.46	8.03	476.00	61.8	25.7	12.5	67.87
Kayseri	10.63	1.17	8.23	205.15	49.50	31.75	18.75	10.03

Experimental protocol

The burs of *X. spinosum* were used for all experiments. Due to the quick release of seed dormancy after seed dispersal, no seed dormancy release treatments were required. Each bur generally carries two seeds, one of which germinates in the current growing season while the other germinates in the subsequent season (CABI, 2022). Therefore, the burs were used in the experiments, i.e., seeds were not removed from the burs.

Germination tests were conducted in 90 × 15 mm Petri dishes infused with two layers of filter paper. The paper was saturated with either 4 mL of deionized water or the appropriate treatment solutions (salinity, pH, or osmotic potential experiments). Petri dishes were sealed with paraffin film to reduce moisture loss and incubated under conditions specific to each experiment. Each treatment had five replications, with 20 seeds placed in each dish. Two dishes constituted a single replication, resulting in a total of 10 dishes (200 seeds) per treatment. Incubation was conducted at 30 °C under a 12-hour photoperiod, unless specified otherwise. Germination was evaluated after 21 days and experiments were terminated.

A factorial experimental design was used for the experiments where populations were the main factor and experimental treatments were sub-factors. Each experiment was repeated over time to validate the findings.

Effect of photoperiod on seed germination

Seeds were exposed to three light/dark regimes, i.e., complete dark (0 h), a 12-hour light/12-hour dark cycle, and continuous light (24 h) to evaluate photoperiod sensitivity. Incubators were illuminated with cool, white, fluorescent lights with an intensity of 350 $\mu Em^{-2}\ s^{-1}$. Dishes in the complete dark treatment were wrapped in four layers of aluminum foil to prevent any light exposure.

Effect of constant temperatures on seed germination

Seeds were exposed to ten constant temperatures (5, 10, 15, 20, 25, 30, 35, 40, 45, and 50 °C). Each treatment was conducted in independently controlled incubators to ensure accurate temperature control.

Effect of different pH levels on seed germination

The effect of pH on seed germination was investigated across a wide range of pH levels, i.e., acidic (3.0, 4.0, 5.0, and 6.0), neutral (7.0), and alkaline (8.0, 9.0, 10.0, 11.0, and 12.0). All solutions were prepared using distilled water as the base. The desired pH values were adjusted using either 1N hydrochloric acid (HCl) to lower the pH or 1N sodium hydroxide (NaOH) to raise it, following the protocol described by Chauhan et al. (2006a). The pH of each solution was verified using a calibrated digital pH meter. Fresh solutions were prepared as needed, and any stored solutions were rechecked for pH stability prior to use.

Effect of different salinity levels on seed germination

To evaluate salinity tolerance, seeds were exposed to NaCl solutions at concentrations of 50, 100, 150, 200, 300, 400, 500, and 600 mM. A control treatment with deionized water was included for the comparison. All saline solutions were prepared by dissolving analytical-grade NaCl in deionized water to get the desired concentrations.

Effect of different osmotic potentials on seed germination

The response of seeds to water stress was evaluated using polyethylene glycol (PEG 8000) solutions prepared to deliver osmotic potentials of 0 (control), -0.2, -0.4, -0.6, -0.8, -1.0, -1.2, -1.4, and -1.6 MPa. Solutions were freshly prepared prior to each use for ensuring consistency and accuracy. The required concentrations of PEG 8000 for each osmotic potential were determined and prepared according to the method described by Michel (1983).

Effect of seed burial depth on seedling emergence

The impact of burial depth on seedling emergence was assessed in plastic pots by planting seeds at depths of 0, 0.5, 1, 2, 4, 6, 8, 10, 12, and 15 cm. Twenty seeds were allocated for each depth, with five replications per treatment. Experiments were performed in a greenhouse regulated at 30 °C with a 12-hour light/dark cycle.

Statistical analysis

Final germination percentages were evaluated using third-degree (cubic) polynomial regression and Gaussian model, depending upon the treatments. Germination percentages across varying salinity and osmotic potential levels were modelled using third-degree (cubic) polynomial regression to accurately describe the nonlinear germination response curves. A third-degree polynomial function has been given in equation 1 (Obam, 2006).

$$Y = ax^3 + bx^2 + cx + d \qquad \text{(Eq. 1)}$$

where *y* is the predicted germination percentage x is either salinity (mM) or osmotic potential (-MPa), and a, b, c, and d are the polynomial coefficients estimated by least squares fitting.

For temperature, pH, and seed burial depth experiments, data were modeled using a three-parameter Gaussian model presented in equation 2 (Mesgaran et al., 2013).

$$G = a \times e\,[-0.5\text{-}\ \{(x - b)/c\}^2] \qquad \text{(Eq. 2)}$$

where a represents the peak germination or emergence percentage, b is the treatment level corresponding to peak response, and c describes the spread of the distribution.

The results from the photoperiod experiment were analyzed using a two-way analysis of variance (ANOVA). Before ANOVA, the assumptions of normality and homogeneity of variance were tested. The means were grouped using the Least Significant Difference (LSD) test at 95% probability level where ANOVA denoted significant differences.

All ANOVA analyses were executed in SPSS version 21.0, and curve fitting was carried out using SigmaPlot version 13.0.

Results and Discussion

Effect of photoperiod on seed germination

Analysis of variance revealed that seed germination was strongly influenced by population, photoperiod, and their interaction ($p < 0.0001$ for all; Table 3). The photoperiod had the most significant effect (F = 272.93), followed by population (F = 10.17) and the population × photoperiod interaction (F = 11.53).

Table 3. Analysis of variance for different photoperiods on seed germination of *Xanthium spinosum* populations stemming from different climatic zones in Türkiye

Source of variation	**DF**	**Sum of squares**	**Mean squares**	**F value**	**P value**
Populations (P)	3	229.22	76.41	10.17	< 0.0001
Photoperiod (PH)	2	4097.79	2048.89	272.93	< 0.0001
P × PH	6	519.70	86.61	11.53	< 0.0001

DF = degrees of freedom, the bold values in P value column denote significant effect of the respective individual or interactive effect on seed germination ($p<0.05$)

Significant variations were observed across studied populations and photoperiods (Figure 1). The highest germination was recorded under a 12-hour light/12-hour dark photoperiod, indicating that alternating light exposure was optimum for seed germination. The Southeastern Anatolia population had the highest germination percentage under 12-hour light/12-hour dark photoperiod, followed by the Mediterranean population. Conversely, the populations from Central Anatolia and the Black Sea had significantly lower germination rates across all photoperiods. Continuous dark caused the lowest germination rates across all populations, while seeds from Central Anatolia exhibited slightly better germination under these conditions relative to other regions. Populations from warmer, sunnier regions (Southeastern Anatolia and Mediterranean) exhibited more receptivity to light, whereas those from colder or variable-light availability (Black Sea and Central Anatolia) had lesser light dependency.

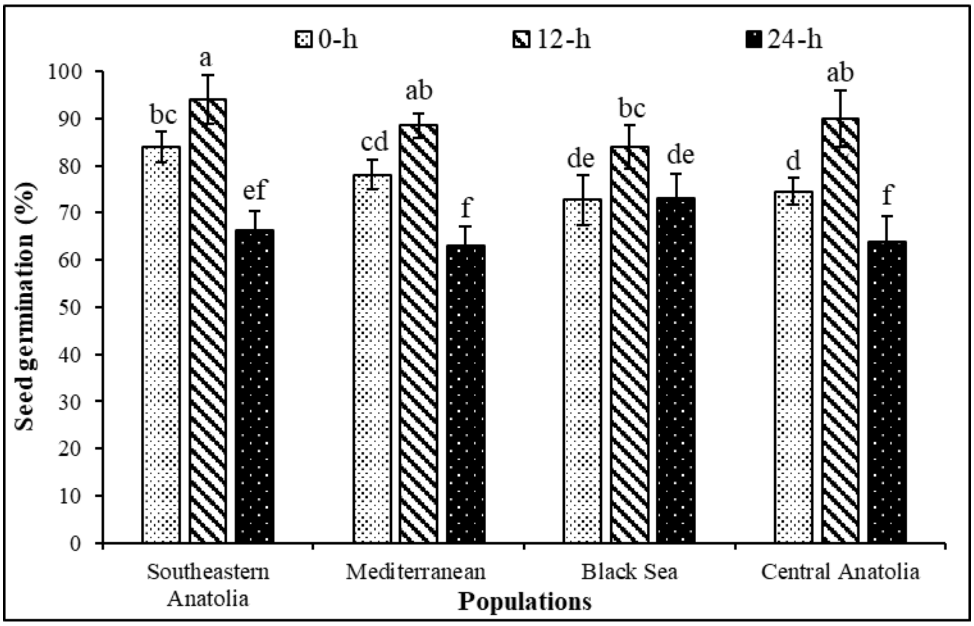

Figure 1. The influence of different photoperiods on seed germination of *Xanthium spinosum* populations stemming from different climatic zones in Türkiye. The data presented are means ± standard errors (n = 5). The means with different letters are statistically different from each other ($p<0.05$).

The strong influence of individual and interactive effects of photoperiods and populations on seed germination demonstrates the importance of environmental cues and genetic variation in regulating the germination characteristics of *X. spinosum*. Higher germination of Southeastern Anatolia and the Mediterranean populations under 12-hour light/12-hour dark conditions indicate adaptability to environments with higher solar radiation and uniform photoperiods. Fluctuating light conditions probably act as a dependable environmental cue in these regions, possibly facilitating germination when circumstances are optimal for seedling establishment (Dürr et al., 2015; Kelečević et al., 2024). The significant relationship between population and photoperiod highlights local ecotypic variation within *X. spinosum*, affecting its invasive potential. Populations requiring excessive sunlight may be controlled by canopy cover methods that limit light penetration; thus, preventing germination. In contrast, populations exhibiting increased tolerance to low-light environments may need comprehensive strategies addressing both seed bank and newly germinated seedlings. The results stress the need to modify weed control strategies to the ecological traits and adaptive behaviors of various *X. spinosum* populations.

Effect of constant temperatures on seed germination

Temperature significantly influenced the germination of *X. spinosum* populations, showing a unique Gaussian response across all populations (Figure 2). Southeastern Anatolia and Mediterranean populations had the greatest germination ability, reaching maximum theoretical germination rates of 101.4% and 89.9%, respectively, with optimum germination temperatures estimated at 30.1 °C (Table 4). Conversely, the Black Sea and Central Anatolia populations had lower optimum temperatures (27.0 °C and 25.5 °C, respectively), with corresponding maximum germination rates of 92.7% and 90.9%, respectively.

Germination was limited at lower temperature (≤15 °C), with all populations exhibiting <35% germination. Germination gradually increased with increasing temperature, reaching its peak at 25–30 °C, followed by a steep decline at temperatures besides 35 °C. Southeastern Anatolia population exhibited comparatively higher germination percentages at supra-optimal temperatures (35–40 °C) relative to other populations, indicating a greater thermal tolerance. The calculated spread (σ) values, between 8.1 and 9.2 °C, indicate significant thermal adaptability among populations. Southeastern Anatolia and Mediterranean populations exhibited adaptation to elevated temperatures, but Black Sea and Central Anatolia populations were better adapted to comparatively colder environments. These variations probably indicate ecological or evolutionary diversity across populations, perhaps influenced by the climatic circumstances of their native environments (Farooq et al., 2019, 2021; Önen et al., 2018).

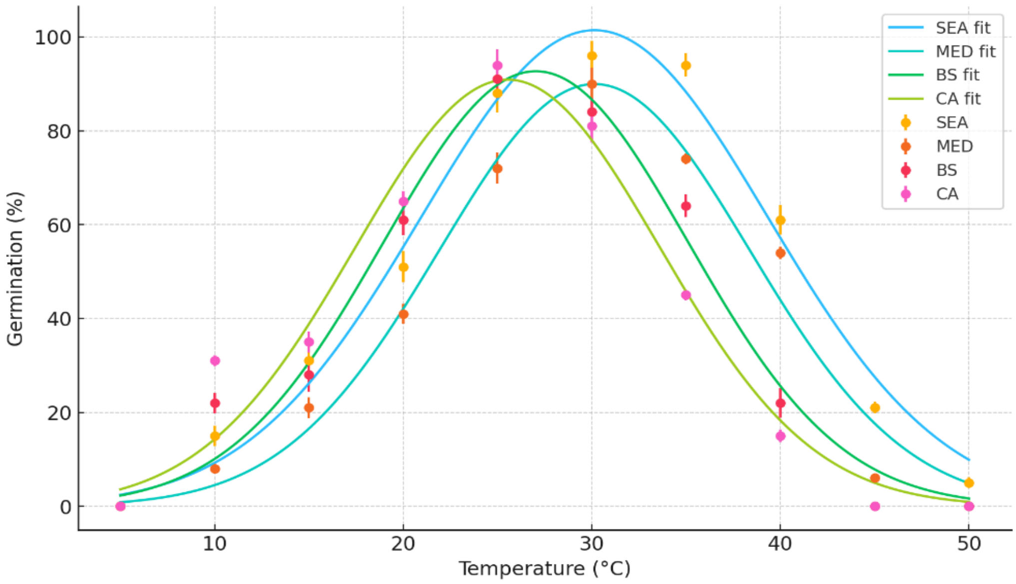

Figure 2. The influence of different constant temperatures on seed germination of *Xanthium spinosum* populations stemming from different climatic zones in Türkiye. The data presented are means ± standard errors (n = 5). The curves are three-parameter Gaussian model fitted on the final germination data.

Table 4. Summary of the fitted temperature response parameters for *Xanthium spinosum* seed germination across four regional populations

Populations	Maximum Germination (%)	Optimum Temperature (°C)	Spread (σ)
Southeastern Anatolia	101.42	30.15	9.20
Mediterranean	89.95	30.15	8.23
Black Sea	92.68	27.04	8.08
Central Anatolia	90.89	25.54	8.08

Maximum germination (%) denotes the estimated highest germination rate determined by Gaussian model fitting. The optimum temperature (°C) denotes the temperature at which highest germination is predicted to occur. The spread (σ, °C) is the standard deviation of the fitted Gaussian curve, reflecting the range of temperature tolerance around the optimum. High σ values imply increased temperature tolerance, whilst lower σ values indicate limited thermal requirements for germination.

The observed variations in optimum temperatures and germination responses among studied populations indicate significant ecotypic heterogeneity possibly influenced by local environmental variables (Cochrane et al., 2015; Walter et al., 2020). Southeastern Anatolia and Mediterranean populations demonstrated higher optimum temperatures (~30 °C) because of warmer and drier conditions in the seed collection sites, which aligns with evidence that *X. spinosum* flourishes in disturbed, open habitats characterized by significant thermal variations (Liu et al., 2025; Xiao et al., 2024). The lower optimal temperatures observed for Black Sea and Central Anatolia populations (~25–27 °C) correspond with adaptations to colder or more temperate habitats, since temperature conditions during early germination stages are crucial for weed establishment and invasion success (Dürr et al., 2015). Temperature breadth (σ values ranging from 8–9 °C) recorded in all populations suggests a level of physiological adaptability, supporting the concept that *X. spinosum* may thrive in a diverse array of thermal niches, a characteristic trait among invasive and cosmopolitan weeds (Fenner & Thompson, 2005). The reduction in germination at temperatures beyond 35 °C highlights thermal thresholds of *X. spinosum*, which may become more significant considering future global warming scenarios (Liu et al., 2025). These findings emphasize the need to consider population-level diversity in germination characteristics when predicting the possible spread and control strategies of *X. spinosum* under changing conditions.

Effect of different pH levels on seed germination

The germination response to pH exhibited a Gaussian pattern, showing significant variations across populations for optimum pH values (Figure 3). The Central Anatolia population had the highest predicted germination rate (91.6%) at an optimum pH of 7.37, indicating strong adaptation to neutral soil conditions. The Southeastern Anatolia population exhibited better performance, reaching a maximum of 90.1% at lower optimum pH of 6.95, indicating a tolerance for moderately acidic soils. The Black Sea population exhibited an optimum pH of 7.59 and a highest germination rate of 89.6%, while the Mediterranean population reached a peak germination rate of 86.3% at an optimum pH of 7.07. These populations exhibited slightly reduced maximum germination but had a distinct preference for neutral to slightly alkaline environments.

Southeastern Anatolia population had the widest pH tolerance (σ = 2.01), indicating greater adaptability in both acidic and alkaline environments. The Mediterranean population had the least variability (σ = 1.76), indicating greater susceptibility to pH variations (Table 5).

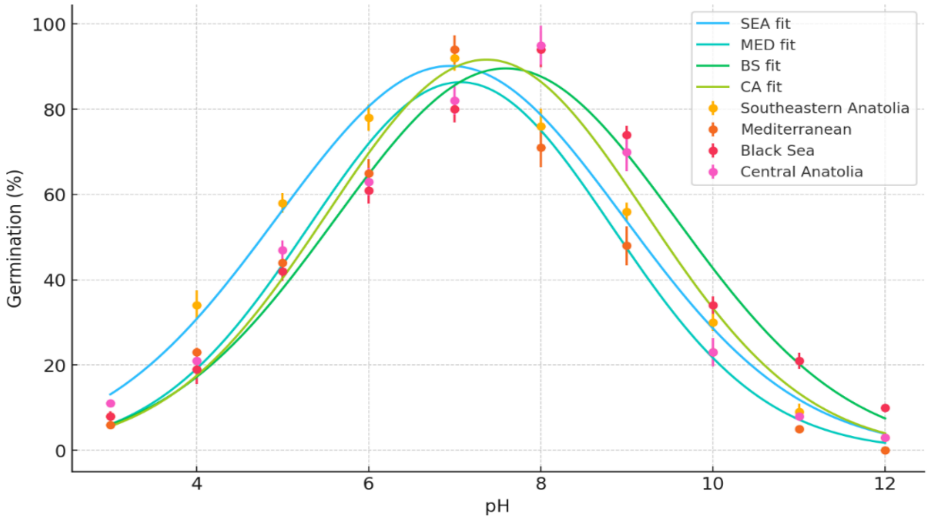

Figure 3. Germination response curves of *Xanthium spinosum* populations stemming from four geographic regions of Türkiye under different pH levels. Points indicate calculated mean germination percentages (± standard error), whereas lines represent fitted Gaussian curves. Each population had a bell-shaped response, with peak germination occurring at neutral pH levels (7.0–7.6). Differences in peak values and spread (σ) indicate population-specific tolerance and adaptation to variations in solution pH.

Table 5. Summary of fitted Gaussian parameters describing the response of *Xanthium spinosum* seed germination to pH across four regional populations

Populations	Maximum Germination (%)	Optimum pH	Spread (σ)
Southeastern Anatolia	90.15	6.95	2.01
Mediterranean	86.33	7.07	1.76
Black Sea	89.57	7.59	1.98
Central Anatolia	91.63	7.37	1.85

Maximum germination (%) denotes the theoretical maximum germination derived from curve fitting analysis. The optimum pH is the pH level at which highest germination is expected to occur. Spread (σ, pH units) indicates the standard deviation of the Gaussian distribution and indicates the range of pH tolerance for each population, where higher values represent a wider tolerance.

The pH-dependent germination responses of studied populations were highly correlated with the soil properties of their native ranges. Populations from Southeastern Anatolia and the Mediterranean region had optimum germination at pH 7.0–7.1, indicating adaptability to moderately alkaline soils (pH 7.55–7.62). Conversely, populations from the Black Sea and Central Anatolia originated in more alkaline soils (pH 8.03–8.23), had somewhat elevated optimum pH values (7.4–7.6). The results align with earlier research indicating that seed germination characteristics of various populations of the same species often correlate with the soil pH conditions of their origin (Baskin & Baskin, 2014; Farooq et al., 2019, 2021; Önen et al., 2018; Ozaslan et al., 2017).

Extensive pH tolerance observed in the Southeastern Anatolia population may be attributed to its origin in extremely saline, clay-dominant soils (EC = 839 mS/m; 61.1% clay), where dynamic soil chemistry encourages a more flexible germination behavior (Benvenuti, 2003). In contrast, the limited tolerance of the Mediterranean population correlates with its calcareous soil environment (29.58% $CaCO_3$), recognized for maintaining more stable pH values. These findings indicate that soil chemistry significantly impacts the germination niche width of *X. spinosum*, hence influencing its potential invasiveness in various habitats.

Effect of different salinity levels on seed germination

The highest germination under non-saline treatment exhibited slight variation across populations, with 91.76% germination in the Black Sea population to 96.65% in the Central Anatolia population (Table 6).

Table 6. Maximum germination percentages at zero salinity, salinity levels required to inhibit 50% germination (EC_{50}), and coefficient of determination (R^2) values for third-degree polynomial fits describing the germination response of four regional populations under varying salinity levels

Population	Maximum Germination (%)	EC_{50} (ppm)	R^2 of Fit
Southeastern Anatolia	94.10	306.30	0.996
Mediterranean	93.48	227.41	0.987
Black Sea	91.76	198.87	0.993
Central Anatolia	96.65	155.76	0.993

EC_{50} = salinity levels required to inhibit 50% of maximum germination

Despite similar baseline germination, populations exhibited varied responses to increasing salinity levels. The Southeastern Anatolia population had the highest salt resistance, requiring a salinity level of 306.30 mM to decrease germination by 50% (EC_{50}). In contrast, the Central Anatolia population had the highest sensitivity, with a 50% drop at just 155.76 ppm. Mediterranean and Black Sea populations exhibited intermediate tolerances, with EC_{50} values of 227.41 ppm and 198.87 ppm, respectively (Figure 4).

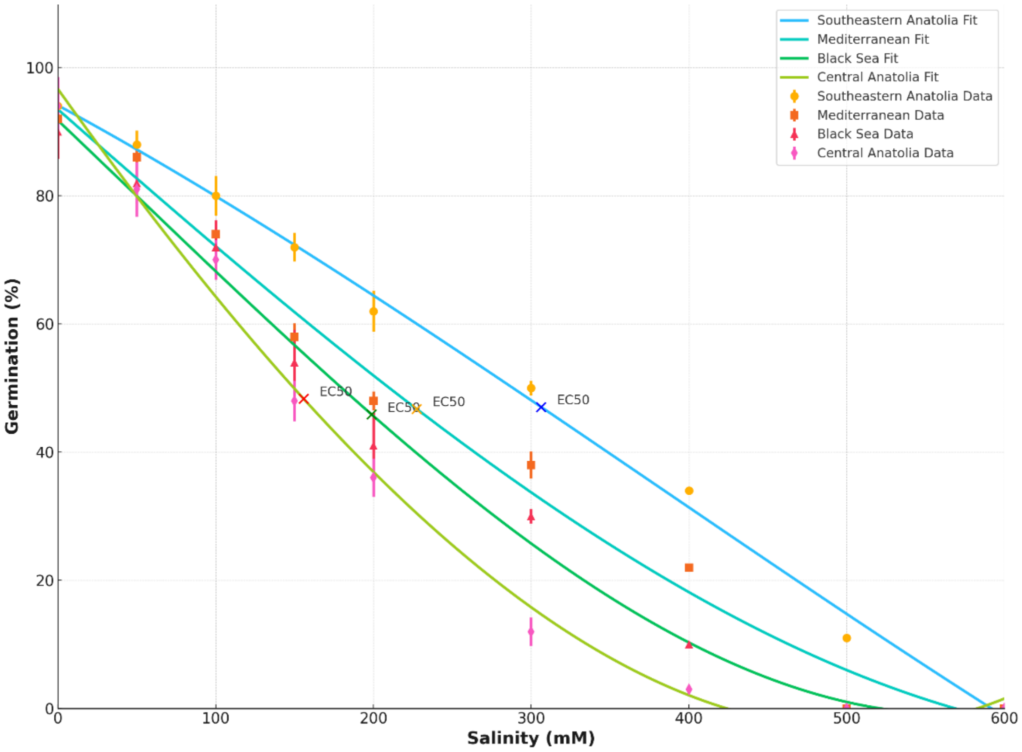

Figure 4. Germination response curves of four *Xanthium spinosum* populations under increasing salinity stress, fitted using third-degree polynomial models. Data points represent observed mean germination percentages ± standard error of the mean at each salinity level (n = 5). The lines indicate fitted curves. EC_{50} points (salinity concentrations causing a 50% reduction in maximum germination) are marked on each curve.

Tested populations had high and constant germination (91.76% to 96.65%) in non-saline conditions (0 mM), whereas tolerance to salt varied among populations. The EC_{50} values significantly varied across populations. Southeastern Anatolia population demonstrated the highest salt resistance, with an EC_{50} of 306.30 mM, demonstrating strong physiological mechanisms for germination under salinity stress. These findings align with the soil properties of the site of origin, which had high electrical conductivity (839.00 mS/m) and a semi-arid climate. Plant populations naturally exposed to highly saline and dry environments evolve seed-level tolerance traits such osmotic adjustments, antioxidant activity, and delayed germination (Gul et al., 2013; Qu & Huang, 2005). Central Anatolia population had the lowest salt tolerance, with an EC_{50} of 155.76 mM. This population stemmed from a cold semi-arid climate with low soil salinity (205.15 mS/m). Other continental steppe-origin plants have higher salinity sensitivity during germination owing to lower seed development selection pressure for salt tolerance (Song et al., 2005). Lower organic matter and phosphorus levels (1.17% OM and 10.03 ppm P) in soils may affect early-stage stress mitigation during germination.

The Mediterranean and Black Sea populations exhibited moderate salt tolerance, with EC_{50} values of 227.41 mM and 198.87 mM, respectively. Hot-summer Mediterranean climate and moderate salinity (512.89 mS/m) of Mediterranean soils may have selected for salt tolerance. These results confirm the ecological concept that local adaptation to soil salinity and moisture regimes considerably affect seed germination (Baskin & Baskin, 2014). High soil salinity favors seed germination delay, and structural resistance, whereas mesic or temperate populations prioritize rapid germination under favorable conditions without costly stress adaptations.

Effect of different osmotic potentials on seed germination

The third-degree polynomial models correctly predicted germination responses under osmotic stress, with good coefficients of determination (R^2 values between 0.990 and 0.997). Peak germination under non-stressed environments varied from 88.84% in the Mediterranean to 94.78% in Southeastern Anatolia populations (Table 7).

Table 7. Maximum germination percentages at zero osmotic stress, osmotic potential values causing 50% reduction in maximum germination (EC_{50}), and coefficients of determination (R^2) for third-degree polynomial fits describing the germination responses of four Xanthium spinosum populations under increasing osmotic stress (-MPa).

Population	**Maximum Germination (%)**	**EC_{50} (-MPa)**	**R^2 of Fit**
Southeastern Anatolia	94.78	0.96	0.9974
Mediterranean	88.84	0.85	0.9900
Black Sea	92.08	0.70	0.9970
Central Anatolia	93.54	0.61	0.9955

EC_{50} = Osmotic potential levels required to inhibit 50% of the maximum germination

The osmotic potential required to inhibit maximum germination by 50% (EC_{50}) varied among population. Southeastern Anatolia had the highest tolerance at -0.96 MPa, followed by the Mediterranean at -0.85 MPa. The Black Sea and Central Anatolia populations were more susceptible, with EC_{50} values of -0.70 and -0.61 MPa. Southeastern Anatolia appeared most resistant to osmotic stress (Figure 5).

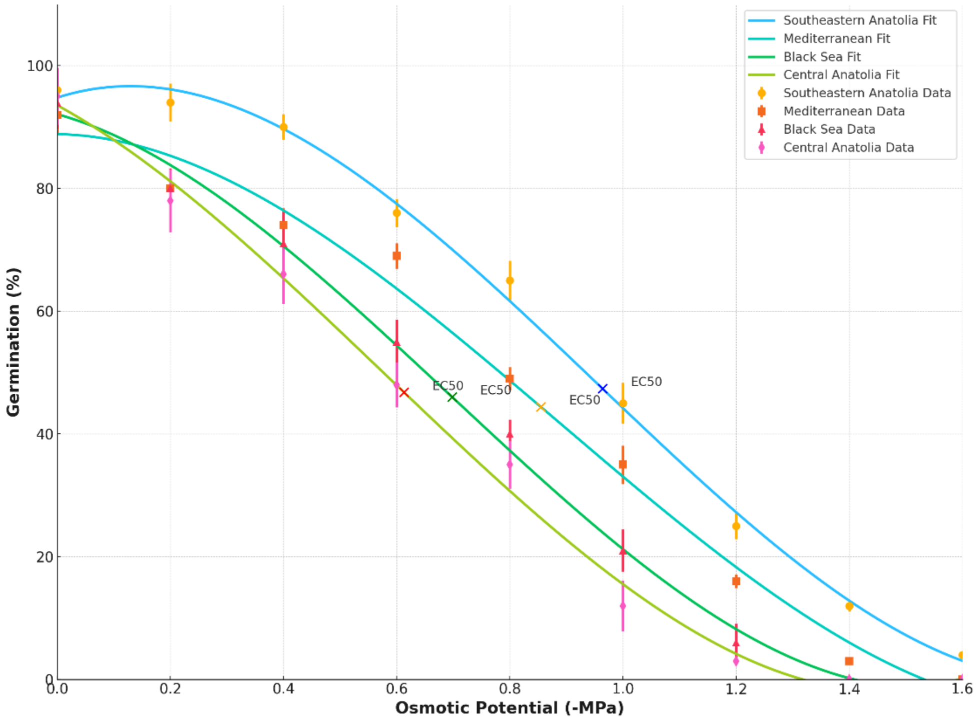

Figure 5. Germination response curves of four *Xanthium spinosum* populations under increasing osmotic stress, fitted using third-degree polynomial models. Data points represent observed mean germination percentages ± standard error of the mean at each osmotic potential level. Solid lines indicate fitted curves. EC_{50} points are marked on each curve.

The results indicated that studied populations exhibit significant variation in germination responses to osmotic stress, strongly associated with their native environments. Southeastern Anatolia population had the highest resistance, with an EC_{50} of -0.96 MPa, while the Mediterranean population followed with an EC_{50} of -0.85 MPa. Conversely, Black Sea and Central Anatolia populations exhibited more susceptibility to water stress, shown by lower EC_{50} values of -0.70 MPa and -0.61 MPa, respectively. These patterns indicate robust ecological adaptability (Sun et al., 2023) to the climatic and soil conditions of the seed collection sites. Southeastern Anatolia had a hot semi-arid climate, very high soil salinity (839.00 mS/m), and frequent drought, which likely help in the production of seeds with improved osmotic stress resistance. This correlates with earlier studies (Farooq et al., 2019, 2021; Önen et al., 2018), which indicated that seeds from dry and saline habitats often have enhanced osmotic adjustment mechanisms, such as osmolyte accumulation and membrane stability, to facilitate germination under water-limited environments.

Effect of seed burial depth on seedling emergence

The seedling emergence from various burial depths was successfully modeled using three-parameter Gaussian functions. Seedling emergence demonstrated a typical bell-shaped curve, characterized by low emergence at surface sowing (0 cm), a rapid rise peaking at shallow to moderate burial depths (~2–4 cm), and a subsequent gradual drop at deeper depths (Table 8).

Table 8. Summary of fitted Gaussian model parameters describing the effect of burial depth on seedling emergence of *Xanthium spinosum* populations collected from four different climatic regions of Türkiye.

Population	Maximum Emergence (%)	Optimum Burial Depth (cm)	Spread (σ, cm)
Southeastern Anatolia	85.61	4.33	3.08
Mediterranean	76.48	4.35	3.11
Black Sea	81.80	4.17	2.66
Central Anatolia	75.90	4.06	2.59

Maximum emergence (%) represents the theoretical peak seedling emergence predicted by the fitted model. Optimum burial depth (cm) indicates the depth at which maximum seedling emergence is expected. Spread (σ, cm) denotes the standard deviation of the fitted Gaussian curve and reflects the breadth of burial depth tolerance; larger σ values indicate broader germination ability across depth variations.

Southeastern Anatolia population had the highest peak emergence, with maximum emergence recorded from 2 cm burial depth. Mediterranean and Black Sea populations had slightly reduced maximum emergence rates while demonstrating comparable optimum burial depths to those in Southeastern Anatolia. Central Anatolia population, although achieving a relatively high peak emergence, had a more significant drop beyond a burial depth of 4 cm, indicating greater vulnerability to deeper burial (Figure 6).

The burial depth responses directly impact integrated weed management strategies. Significant emergence observed at shallow to intermediate burial depths (~2–4 cm) across all populations indicates that *X. spinosum* is particularly sensitive to seed placement within the soil profile. The significant reduction in emergence beyond 6 cm, especially for the Central Anatolia population, suggests that deep burial may function as an efficient cultural control strategy. Techniques like deep tillage, which displace seeds to depths more than 6–8 cm, may significantly diminish seedling recruitment, hence constraining the weed's soil seedbank over time (Chauhan et al., 2006a, 2006c).

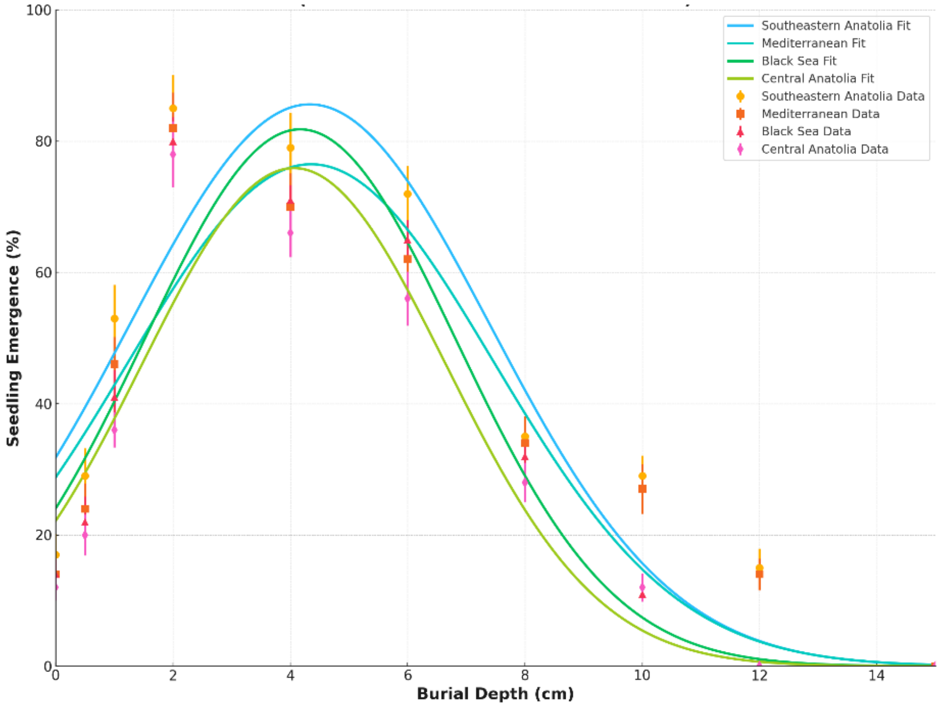

Figure 6. Seedling emergence response curves of four *Xanthium spinosum* in relation to burial depth, modeled using three-parameter Gaussian functions. Data points represent observed mean germination percentages ± standard error of the mean (SEM). Solid lines indicate fitted Gaussian curves. Burial depths are expressed in centimeters (cm).

Conclusion

The study revealed that germination characteristics of *Xanthium spinosum* seeds are significantly affected by environmental cues with considerable population-specific variability associated with climatic and edaphic conditions. The highest germination was recorded under moderate temperature (~30 °C), neutral to slightly alkaline pH, moderate osmotic stress, and shallow burial depths (~2–4 cm). Populations from warmer and more saline areas (Southeastern Anatolia) exhibited enhanced tolerance to thermal, saline, and osmotic stresses, along with a wider range of pH and burial depth tolerance. Conversely, populations stemming from temperate and semi-arid regions had smaller ecological tolerance. The results have significant implications for weed control, i.e., extensive tillage that buries seeds below 6 cm, along with moisture management and residue retention, might significantly reduce the establishment of *X. spinosum*. Moreover, incorporating population-specific responses to light, temperature, salinity, and burial depth into management strategies might enhance the accuracy and robustness of management measures. Predictive emergence models that include these variations in biology will enhance the timing of herbicide application, mechanical control strategies, and soil management techniques. Designing weed management strategies to the ecological adaptations of *X. spinosum* populations is essential for limiting the spread and attaining sustainable suppression across different agroecosystems in Türkiye.

Acknowledgement

Not applicable

Ethics approval and consent to participate

Not applicable as the study is not a clinical trial and did not include any patients.

Competing interests

The author has declared no conflicts of interest.

Authors' contributions

Conceptualization, S.F.; methodology, S.F.; software, S.F.; validation, S.F.; formal analysis, S.F.; investigation, S.F.; resources, S.F.; data curation, S.F.; writing—original draft preparation, S.F.; writing—review and editing, S.F.; visualization, S.F. All authors have read and agreed to the published version of the manuscript.

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