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Seed germination ecology of eclipta (*Eclipta prostrata*) in dry direct-seeded rice fields from China

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Abstract

Eclipta [Eclipta prostrata (L.) L.] is an important tropical weed that has recently emerged as a problematic weed in dry direct-seeded rice (Oryza sativa L.) (DSR) fields in China. Understanding its seed germination biology and ecology is crucial for developing integrated weed management strategies in the DSR system. Laboratory experiments were conducted to investigate seed germination of E. prostrata seeds under varying environmental conditions. Germination was greatest under alternating temperature regimes of 25/15 to 40/30 C, whereas it wa-s significantly reduced at 20/10 C and completely inhibited at 15/5 C. Germination was also fully suppressed under continuous darkness, indicating strong light dependency. Eclipta prostrata seeds tolerated a broad range of pH values (4 to 10) with germination rates consistently greater than 95%. However, germination declined sharply under osmotic potentials, falling below 2% at -0.6 MPa, and being completely inhibited at -0.7 MPa. Seeds also showed moderate salt tolerance, with 50% inhibition at 150 mM NaCl and no germination at 300 mM NaCl. Exposure to radiant heat (>90 C for 5 min) prevented germination, suggesting residue burning may be an effective control measure. Seedling emergence was highest (100%) on the soil surface but declined steeply with increasing burial depth, with no emergence observed beyond 0.5 cm. Similarly, surface application of wheat (Triticum aestivum L.) straw residue (2 to 6 Mg ha⁻¹) significantly reduced seedling emergence and biomass. These findings provide essential insights into E. prostrata germination ecology and offer practical implications for its integrated management in DSR systems.

Introduction

Rice (*Oryza sativa* L.) is a staple food for over half of the global population, with Asia accounting for approximately 90% of global rice production and consumption (Kraehmer et al. 2016; Priya et al. 2019). In many Asian countries, traditional manual transplanting remains the dominant cultivation method, but this practice is labor-intensive and increasingly unsustainable (Barla et al. 2021). Rapid urbanization and rising labor costs have led to severe shortages in rural labor. Additionally, changing climate conditions threaten the availability of irrigation water in major rice-growing regions (Shivashenkaramurthy et al. 2020). Consequently, there is a pressing need to adopt alternative rice production methods that require less labor and water. Dry direct-seeded rice (DSR) is one such method, offering a more sustainable and cost-effective approach by reducing labor demands, water use, and production costs.

China is the world's largest rice producer, contributing approximately 28% of global output. Since the 1990s, there has been a shift from traditional transplanting to DSR, which now accounts for about 30% of China's 30.2 million ha of rice-growing area (Zhang et al. 2018). However, weed infestation poses a major challenge in DSR systems. Unlike transplanted rice, which gains a competitive size advantage and benefits from water submergence that suppresses early weed growth, DSR lacks these natural weed-suppressing conditions. As a result, unchecked weed competition in DSR can lead to yield losses of up to 100% (Singh et al. 2014). Eclipta [Eclipta prostrata (L.) L.] has become increasingly problematic in DSR systems in China. This shift may be linked to the shallow seeding, lack of standing water, and reduced soil disturbance in DSR fields, which create favorable conditions for surface germination.

Eclipta prostrata, an annual broadleaf weed from the Asteraceae family, is native to Asia and widespread across tropical, subtropical, and temperate regions (Holm et al. 1977). It reproduces and spreads primarily through seeds, which are easily dispersed by wind and water, particularly during the rainy season (Quisumbing 1923). Eclipta prostrata is a problematic weed in several crops, including peanut (Arachis hypogaea L.), soybean [Glycine max (L.) Merr.], rice, sugarcane (Saccharum officinarum L.), and corn (Zea mays L.), and it has been reported in DSR systems



across 22 countries (Rao et al. 2007). It also serves as a host for plant viruses such as Alternanthera yellow vein virus (He et al. 2008; Zaidi et al. 2016) and the fungus *Nigrospora sphaerica* (Qiu et al. 2022), further impacting crop health. In China, rice yield losses due to *E. prostrata* infestation have been reported to range from 4% to 70%, depending on weed density (Zhu et al. 2012).

Chemical herbicides remain the most efficient and cost-effective method for weed management (Bastiaans et al. 2008; Singh et al. 2006). However, overreliance on these chemicals has led to the development of herbicide resistance in *E. prostrata* populations in China, resulting in significant agricultural and ecological concerns (Li et al. 2017). Integrated weed management (IWM), which combines multiple control strategies, has emerged as a sustainable alternative (Chauhan et al. 2017). However, successful IWM implementation requires a comprehensive understanding of weed biology, particularly the conditions influencing seed germination and seedling emergence (Chauhan and Johnson 2010).

Environmental factors such as temperature, light, soil pH, osmotic stress, burial depth, and crop residue have been shown to significantly influence weed seed germination and emergence (Ahmed et al. 2015; Chauhan et al. 2006; Ramesh 2015). For instance, redroot pigweed (*Amaranthus retroflexus* L.) and Chinese sprangletop [*Leptochloa chinensis* (L.) Nees] exhibit reduced germination under deeper burial and reduced light (Humphries et al. 2018). Similarly, crop residues such as sage (*Salvia officinalis* L.) and lemongrass [*Cymbopogon citratus* (DC. ex Nees) Stapf] have been found to suppress subterranean clover (*Trifolium subterraneum* L.) by 57% in olive (*Olea europaea* L.) orchards, partly due to reduced light penetration and physical soil disturbance (Restuccia and Scavo 2023).

Previous studies on E. prostrata germination have primarily been conducted in tropical regions and swamp ecosystems (Chauhan and Johnson 2008b; Sharp and Boyd 2019). These studies evaluated responses to temperature, light, salinity, and burial depth. However, comparable data for E. prostrata populations from subtropical monsoon climates, such as those in eastern China, are lacking. These regions exhibit distinct seasonal temperature patterns and soil moisture dynamics, which may influence germination ecology and weed emergence patterns. Germination behavior can vary significantly among populations of the same weed species due to adaptation to local climatic and soil conditions. For instance, prior studies have demonstrated that A. retroflexus, common lambsquarters (Chenopodium album L.), and horseweed [Erigeron canadensis L.; syn.: Conyza canadensis (L.) Cronquist] exhibit population-specific differences in germination responses depending on their geographic origin and habitat (Restuccia and Scavo 2023). This level of ecological variation is particularly important in weed management, as locally adapted ecotypes may respond differently to environmental factors and agronomic practices.

Although the germination ecology of *E. prostrata* has been investigated in tropical and subtropical systems such as the Philippines and southern Florida (Chauhan and Johnson 2008b; Sharp and Boyd 2019), However, comparable data for *E. prostrata* populations from subtropical monsoon climates, such as those in eastern China, where dry DSR is rapidly expanding as a labor- and water-saving cultivation method, are lacking. In recent years, *E. prostrata* has emerged as a dominant weed in DSR fields across the middle and lower Yangtze River plain, posing new challenges to rice production. Therefore, understanding how subtropical *E. prostrata* populations respond to local environmental

conditions is crucial for developing region-specific and sustainable IWM strategies. This study aimed to evaluate the effects of temperature, light, pH, osmotic potential, salt concentration, radiant heat, burial depth, and wheat straw mulch on the seed germination and seedling emergence of *E. prostrata*. The findings will contribute to the development of targeted and sustainable weed management strategies for DSR systems in subtropical monsoon regions, characterized by high temperatures and rainfall coinciding during the growing season and a warm and humid climate, along with increasing risks of droughts and floods.

Materials and Methods

Seed Sampling

Eclipta prostrata seeds were collected in October 2023 from dry DSR fields (\sim 60 ha) in Yancheng, Jiangsu Province, China (33.4°N, 120.07°E). Seeds were harvested from more than 400 random *E. prostrata* plants throughout the fields to ensure genetic diversity, cleaned, and stored in a seed cabinet at 4 C and 40% relative humidity until use. The 1,000-seed weight was determined to be 0.42 g.

Germination Seed Protocol

All experiments were conducted from May to October 2024 in the laboratories of the Jiangsu Academy of Agricultural Sciences (32.20°N, 118.51°E). For each test, 25 seeds were placed in 9-cm-diameter petri dishes lined with two layers of Whatman No. 11 filter paper (Whatman International, Ltd., Maidstone, Kent, UK). Five milliliters of distilled water or treatment solution was added to each dish, which was sealed with Parafilm* PM-996 (Bemis Company, Inc., Sheboygan Falls, WI, USA) to minimize evaporation. Except where noted, all germination trials were performed at 30/20 C (12-h light/12-h dark photoperiod), the regime that supported the highest germination in preliminary testing. Germination was assessed after 14 d and defined by the emergence of the radicle.

Experiment 1. Temperature and Light

Germination was evaluated under six alternating temperature regimes: 15/5, 20/10, 25/15, 30/20, 35/25, and 40/30 C. Each temperature condition was tested under two light regimes: 12-h light/12-h dark and continuous darkness (dishes wrapped in aluminum foil). These conditions were chosen to simulate seasonal variation in Chinese rice-growing regions.

Experiment 2. pH

Buffered solutions of pH 4, 5, 6, 7, 8, 9, and 10 were prepared following the method of Chachalis and Reddy (2000). Seeds were incubated in these solutions, and germination was recorded after 14 d.

Experiment 3. Osmotic Potential

Polyethylene glycol 6000 (PEG 6000) was used to simulate osmotic stress at potentials of 0, -0.1, -0.2, -0.3, -0.4, -0.5, -0.6, and -0.7 MPa, based on the Michel and Radcliffe (1995) protocol. Germination was monitored after 14 d.

Experiment 4. Salinity Stress (NaCl)

Sodium chloride solutions were prepared at concentrations of 0 (control), 25, 50, 100, 150, 200, 250, and 300 mM. Seeds were incubated under the standard germination protocol. Germination was recorded after 14 d.

Experiment 5. Radiant Heat Exposure

To simulate postharvest residue burning, seeds were subjected to six temperature treatments (50, 60, 70, 80, 90, 100, and 110 C) for 5 min in a hot-air oven. Each treatment included four replicates of 100 seeds. Seeds were allowed to cool before incubation using the standard germination protocol. Germination was assessed after 14 d.

Experiment 6. Soil Burial Depth

Twenty-five seeds were placed at depths of 0 (surface), 0.1, 0.2, 0.3, 0.4, 0.5, and 0.6 cm in plastic pots (7-cm diameter by 7.5-cm height) filled with paddy field soil (pH 6.9, 1.2% organic matter). Soil was sieved (3 mm) before use. Pots were maintained at 30/20 C (12-h light/12-h dark) with subirrigation. Seedling emergence (appearance of cotyledons) was monitored daily for 21 d.

Experiment 7. Wheat Straw Residue

Twenty-five seeds were sown on the soil surface in larger pots (15-cm diameter by 15-cm height) and covered with wheat straw mulch at rates of 0, 2, 4, 6, 8, and 10 Mg ha⁻¹. Wheat straw was obtained from the cultivar 'Yangmai 34' and applied uniformly. Pots were subirrigated and incubated at 30/20 C (12-h light/12-h dark). Seedling emergence and shoot biomass were measured at 21 d after sowing.

Statistical Analysis

All experiments followed a randomized complete block design with two independent runs. Each treatment within a run included four replicates (n=4), and the entire experiment was repeated once for validation. As no significant differences (P > 0.05) were observed between runs, data were pooled. The homogeneity of variance and normality of residuals were checked before analysis. Data were analyzed using SPSS v. 25.0 (SPSS, Chicago, IL, USA). Where appropriate, nonlinear regression was performed using SigmaPlot 10.0 (Systat Software, San Jose, CA, USA). The following three-parameter sigmoid model was used:

$$G = G_{max}/\{1 + e[(x - x_{50})/b]\}$$
[1]

where G is the germination or emergence percentage at a given factor level (x), G_{max} is the maximum response, x_{50} is the factor value causing 50% inhibition, and b is the slope.

For burial depth effects, an exponential decay model was also used:

$$E = E_{max} \times exp(-E_{rate} \times x)$$
 [2]

where E is seedling emergence at depth x, $E_{\rm max}$ is the maximum emergence, and $E_{\rm rate}$ is the decay constant.

Results and Discussion

Effect of Temperature and Light on Germination

Germination of *E. prostrata* was influenced by the interaction between temperature and light (Figure 1; P < 0.05), indicating that the effect of temperature on germination depended on light

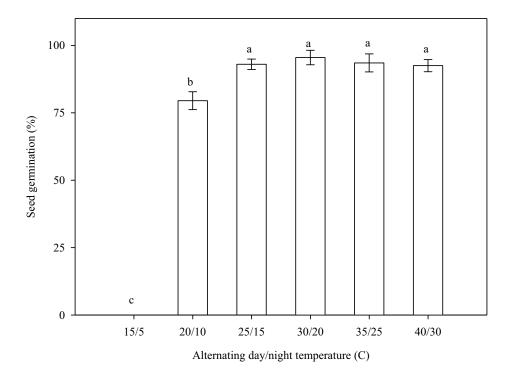


Figure 1. Effect of simulating alternating day/night temperatures (5/15, 20/10, 25/15, 30/20, 35/25, 40/30 C) and photoperiod (day and night) for 14 d in growth chambers on germination of freshly harvested seeds of *Eclipta prostrata*. Vertical bars represent standard error of mean (n = 8). Different letters on the vertical bars denote significant differences at $\alpha = 0.05$.

availability. Under light conditions, germination increased from 87% at 20/10 C to a maximum of 98% at 30/20 C, but declined at both lower (15/5 C; 0%) and higher (40/30 C; 93%) temperature regimes. In contrast, no germination occurred under complete darkness at any tested temperature, confirming that light is an essential environmental cue for germination in this species.

These results suggest that *E. prostrata* seeds from subtropical Chinese DSR fields can germinate across a broad temperature range (20/10 to 40/30 C), provided that light is available. This finding is consistent with earlier studies in tropical environments, where high germination rates were also observed at similar temperatures (Chauhan and Johnson 2008b; Sharp and Boyd 2019).

A limitation of the present study is the absence of constant-temperature treatments, which makes it difficult to disentangle the individual effects of day and night temperature phases in the alternating regimes. This pattern has been observed in other tropical and subtropical weed species, where maximum daytime temperatures often play a greater role in triggering germination than cooler night temperatures (Benech-Arnold et al. 2000; Chauhan and Johnson 2008b). Although alternating temperatures are widely used to simulate natural diurnal fluctuations, the inclusion of constant-temperature controls (e.g., 25 C, 30 C) in future studies would allow more precise identification of the critical temperature thresholds for *E. prostrata* germination.

In contrast, no germination occurred under complete darkness at any tested temperature, confirming that light is an essential environmental cue for germination in this species. This indicates that *E. prostrata* is positively photoblastic, relying on light cues to initiate germination. Such light dependency is characteristic of many small-seeded weed species, which often lack sufficient energy reserves to support seedling emergence in the absence of light (Benvenuti et al. 2001; Forcella et al. 2000). The small seed size of *E. prostrata* (1,000-seed weight ≈ 0.42 g) likely contributes to this

dependency. Similar photoblastic behavior has been reported in other species (Benvenuti et al. 2004; Zhang et al. 2023). From a management perspective, practices that reduce light penetration to the soil surface—such as residue mulching, soil shading, or shallow tillage—may help suppress *E. prostrata* emergence in conservation agriculture systems.

Effect of pH on Germination

Eclipta prostrata seeds exhibited high germination rates (>90%) across the entire tested pH range (4 to 10), with no differences among treatments. These results indicate that E. prostrata can germinate under a wide variety of soil pH conditions, confirming its wide ecological adaptability. Similar tolerance has been reported for other tropical weeds, such as goosegrass [Eleusine indica (L.) Gaertn.] and wild mustard (Sinapis arvensis L.) (Chauhan and Johnson 2008b; Singh et al. 2021). This broad pH tolerance indicates strong ecological adaptability and suggests that E. prostrata may persist in both upland and lowland rice environments. As such, manipulating soil pH is unlikely to be an effective stand-alone strategy for managing this species. Instead, IWM approaches—such as residue mulching, deep tillage, or stale seedbed techniques-may offer better control by targeting other germination-limiting factors (Chauhan and Johnson 2008a; Singh et al. 2021).

Effect of Osmotic Potential on Germination

Seed germination declined sharply under increasing osmotic stress (Figure 2), following a three-parameter sigmoid model with high fit ($R^2 = 0.99$). Maximum germination (95%) occurred at 0 MPa, and remained high up to -0.2 MPa. However, germination dropped significantly at -0.3 MPa (66%) and was nearly absent (<3%) at -0.6 MPa. Complete inhibition occurred at -0.7 MPa. The

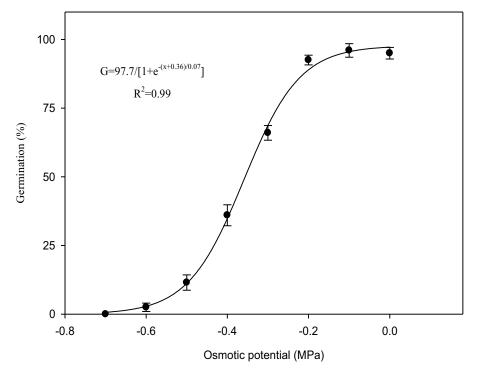


Figure 2. Effect of osmotic potential on germination of *Eclipta prostrata* seeds incubated in a growth chamber at 30/20 C day/night temperatures in a 12-h photoperiod for 14 d. The line represents a three-parameter sigmoid model fit to the data, and vertical bars represent the standard errors of the means (n = 8).

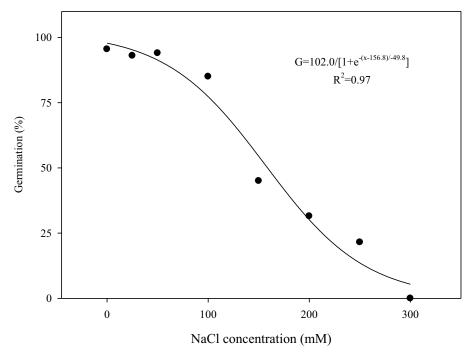


Figure 3. Effect of sodium chloride (NaCl) concentration on germination of *Eclipta prostrata* seeds incubated in a growth chamber at 30/20 C day/night temperatures in a 12-h photoperiod for 14 d. The line represents a three-parameter sigmoid model fit to the data, and vertical bars represent the standard errors of the means (n = 8).

osmotic potential causing 50% inhibition was estimated at -0.36 MPa.

These findings highlight the moisture sensitivity of *E. prostrata*, although it exhibits some tolerance to moderate drought stress. Comparisons with *E. prostrata* populations from tropical regions (Chauhan and Johnson 2008b) suggest slight regional variation in stress response, possibly due to local adaptation. Like other dryland weeds such as African lovegrass [*Eragrostis curvula* (Schrad.) Nees] and Navua sedge (*Cyperus aromaticus*), reduced germination of *E. prostrata* under water-deficit conditions suggests that moisture availability is a key driver of emergence success (Alagbo and Chauhan 2023; Chadha et al. 2021).

Effect of Salt Stress on Germination

Eclipta prostrata germination was moderately tolerant to salinity, following a sigmoid response to increasing NaCl concentrations (Figure 3). Germination remained above 85% at concentrations ≤50 mM, but dropped to 23% to 28% at 200 to 250 mM NaCl. No germination occurred at 300 mM, and the concentration causing 50% inhibition was estimated to be 150 mM. These results indicate a somewhat lower salinity tolerance compared with findings from *E. prostrata* populations studied in tropical regions, where germination remained relatively high even at 150 mM NaCl, with an estimated x_{50} above 220 mM (Chauhan and Johnson 2008b). This difference may reflect population-level adaptations to local soil salinity or climatic conditions.

High salinity negatively impacts seed germination by inducing osmotic and ionic stress. Nevertheless, many weeds exhibit salinity tolerance due to genetic plasticity (Kumar et al. 2024). The ability of *E. prostrata* to germinate under saline conditions suggests that it could become problematic in salt-affected agricultural lands, which comprise approximately 3.69 million ha in China (Yang 2008; Yang et al. 2022).

Effect of Radiant Heat on Germination

Germination was severely affected by short-term exposure to high temperatures, with the three-parameter sigmoid model accurately describing the response (Figure 4). Germination exceeded 75% after 5-min exposure to \leq 80 C, declined markedly at 90 C, and was completely inhibited at 100 C. The temperature required for 50% inhibition was estimated at 84.6 C.

These results suggest that postharvest residue burning—particularly when seeds remain on or near the soil surface—can effectively reduce the *E. prostrata* seedbank. Previous studies have shown that surface temperatures during burning can exceed 500 C, especially at shallow depths (Iizumi and Iwanami 1965). However, straw residue burning may be banned by government due to its adverse environmental impacts, including the destruction of soil microbiota and air pollution (Lin and Begho 2022; Sarkar et al. 2020).

Table 1. Parameter estimates of three-parameter sigmoid model $G = G_{max}/\{1 + e[(x - x_{50})/b]\}$ fit to the seedling emergence to the different soil burial depths in Figure 5.

		Parameter estimates ^a			
Soil burial depth	G _{max} ^b	X ₅₀	b	R ²	
cm	%	d			
0	98.1 a	5.56 d	0.40 d	0.99	
0.1	72.9 b	6.17 c	0.57 c	0.99	
0.2	56.8 c	6.56 c	0.80b	0.99	
0.3	26.3 d	10.52 b	1.10 a	0.82	
0.4	4.0 e	14.98 a	0.02 e	0.99	
0.5	_				
0.6	_				

 $^{a}G_{max}$, maximum emergence (%); x_{50} , the number of days to 50% emergence (d); b, slope. Different letters in the same column indicate a statistical difference at P < 0.05.

^bA dash (—) indicates that no seedlings emerged when seeds were planted at 0.5-cm depth.

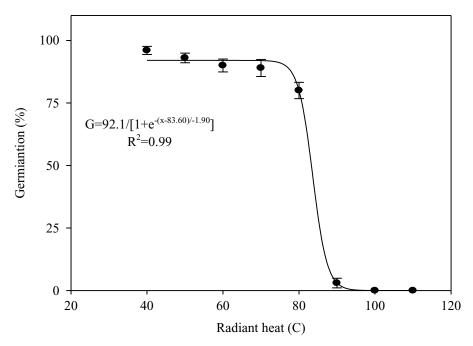


Figure 4. Effect of 5-min exposures at various oven temperatures on germination of *Eclipta prostrata* seeds after 14 d of incubation at 30/20 C day/night temperature. The line represents a three-parameter sigmoid model fit to the data, and vertical bars represent the standard errors of the means (n = 8).

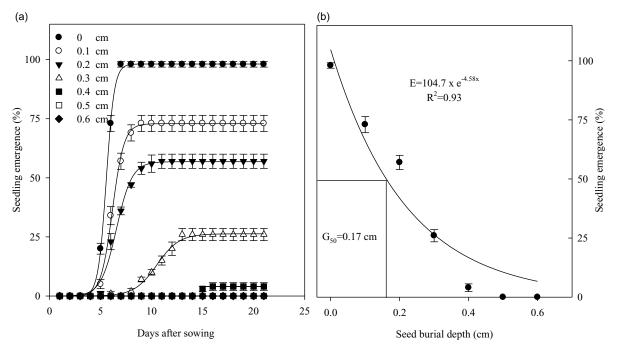


Figure 5. Effect of soil burial depth (cm) on seedling emergence of *Eclipta prostrata*. Seedling emergence was assessed until 21 d after planting (A). The seed burial depth required to inhibit 50% of maximum emergence is 0.17 cm (B). Vertical bars represent the standard errors of the means (n = 8).

Effect of Burial Depth on Seedling Emergence

Seedling emergence was highest (100%) when seeds were placed on the soil surface but declined sharply with increasing burial depth (Figure 5). No emergence occurred at depths \geq 0.5 cm. The burial depth required for 50% inhibition was 0.17 cm. Additionally, deeper burial delayed emergence time and reduced the emergence rate (Table 1).

Eclipta prostrata seeds are small and positively photoblastic, limiting their ability to emerge from deeper soil layers. Generally, *E. prostrata* produces relatively small seeds, with a 1,000-seed weight of approximately 0.42 g and average seed length between 1.2 and 1.5 mm (Quisumbing 1923; Chauhan and Johnson 2008b). This places *E. prostrata* among other small-seeded weed species that are typically light sensitive. For instance, *E. indica* and *L. chinensis*—

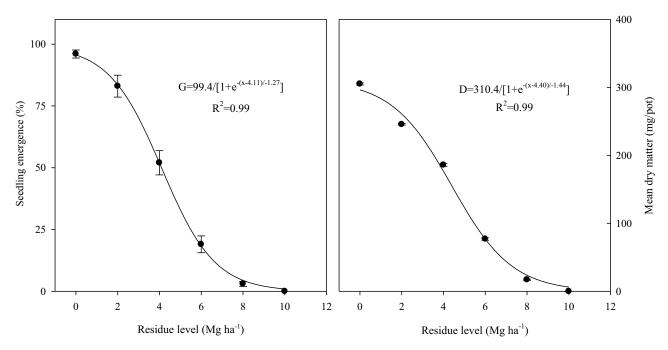


Figure 6. Effect of different amounts of residue $(0, 2, 4, 6, 8, and 10 \text{ Mg ha}^{-1})$ on emergence and mean dry matter of *Eclipta prostrata* seedlings sown in pots for 21 d. Vertical bars represent the standard errors of the means (n = 8).

both positively photoblastic—have 1,000-seed weights of ~0.3 to 0.6 g (Benvenuti et al. 2004; Chauhan and Johnson 2008a). In contrast, larger-seeded weeds such as *S. arvensis* (~2.0 g per 1,000 seeds) tend to be less dependent on light for germination (Ghorbani et al. 1999). The small size of *E. prostrata* seeds may limit energy reserves available for seedling emergence from depth or in darkness, thus reinforcing their reliance on light cues. Smaller seeds lack the energy reserves to support hypocotyl elongation from depth, unlike larger-seeded weeds such as leucaena [*Leucaena leucocephala* (Lam.) de Wit] (Dhawan and Chauhan 2022). The burial depth experiments revealed that *E. prostrata* seedlings failed to emerge from depths greater than 0.5 cm. Rotary tillage that buries seeds below 0.5 cm could effectively reduce emergence in subsequent seasons.

While rotary tillage may reduce surface seed density by disturbing the topsoil, it may not consistently bury all seeds below the critical emergence threshold. In contrast, inversion tillage methods such as moldboard plowing can effectively place seeds deeper into the soil profile, reducing emergence potential and promoting seedbank depletion. Similar strategies have proven effective in controlling other surface-germinating weed species, such as barnyardgrass [Echinochloa crus-galli (L.) P. Beauv.], for which deep burial reduced emergence by more than 90% (Savić et al., 2025). However, inversion tillage is not without limitations it increases soil disturbance, may not be feasible in conservation agriculture systems, and can also redistribute dormant seeds to deeper layers rather than eliminating them. Therefore, tillagebased management should be integrated with other strategies such as stale seedbed or surface residue retention to sustainably suppress E. prostrata emergence.

Effect of Wheat Residue Cover on Seedling Emergence

Straw mulch reduced seedling emergence and aboveground biomass (Figure 6). Emergence declined from 96% (control) to 3% at 8,000 kg

 ha^{-1} residue levels, with complete suppression at 10,000 kg ha^{-1} . The mulch rate for 50% inhibition was estimated at 4,100 kg ha^{-1} . Shoot biomass decreased proportionally with increasing mulch, from 300 mg pot⁻¹ to 100 mg pot⁻¹ at 4,000 to 6,000 kg ha^{-1} .

Residue likely suppresses emergence by blocking light and altering temperature and moisture at the soil surface, and possibly through physical or allelopathic effects (Macías et al. 2014; Sturm et al. 2018; Teasdale 1996; Weston et al. 2013). Although no allelopathic properties have been confirmed for the wheat cultivar used (Yangmai 34), physical suppression appears sufficient to reduce weed pressure. Thus, residue retention can be an effective tool in IWM programs.

In summary, this study demonstrates that *E. prostrata* seeds germinate under a broad range of temperatures and pH values and exhibit moderate tolerance to salt and drought stress. However, they require light for germination and are highly sensitive to deep burial, exposure to high temperatures, and surface residue. These traits suggest that integrated practices such as residue retention, deep tillage, and residue burning could be strategically employed to suppress *E. prostrata* emergence in dry DSR systems.

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Competing interests. The author declare no conflicts of interest.

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