Herbicide response and germination behavior of two goosegrass (*Eleusine indica*) populations in the Australian environment

Virender Singh Hooda[1] and Bhagirath Singh Chauhan[2]

[1]Assistant Scientist, Department of Agronomy, College of Agriculture, Chaudhary Charan Singh Haryana Agricultural University (CCSHAU), Hisar, Haryana, India and [2]Professor, Queensland Alliance for Agriculture and Food Innovation (QAAFI) and School of Agriculture and Food Sustainability (AGFS), University of Queensland, Gatton, Queensland, Australia

Abstract

Goosegrass [*Eleusine indica* (L.) Gaertn.] is one of the most problematic grassy weeds in the world. It is considered to be an important weed in summer fallows and crops grown in the eastern region of Australia. To examine the seed germination ecology of two populations (Gatton and Ingham) of *E. indica* and their response to postemergence herbicides in Australian conditions, experiments were carried out in the laboratory and screenhouse. Seedling survival, spike production, and plant biomass of both *E. indica* populations declined markedly with the application of postemergence herbicides such as butroxydim, clethodim, glufosinate, haloxyfop, and propaquizafop, whereas the application of paraquat failed to control the Ingham population. A dose–response study verified the presence of paraquat resistance in the Ingham population. In this regard, it was observed that the paraquat doses required to achieve a 50% reduction in survival and plant biomass were 27 and 21 times greater in the Ingham population compared to the Gatton population, respectively. Higher alternating temperatures (35/25 and 30/20 C) resulted in greater germination of both populations than lower alternating temperatures (20/10 and 25/15 C). At 20/10 C, the Ingham population failed to germinate; however, about 15% germination in the Gatton population was observed. At the lowest alternate temperature range (15/5 C), neither population germinated. The germination of both populations of *E. indica* was severely reduced under completely dark conditions compared with the alternating light/dark period. Germination was more tolerant of salt and water stress in the Ingham population compared with the Gatton population. *Eleusine indica* seedling emergence was comparable among populations, and the greatest emergence (83%) was observed for seeds buried at a depth of 2 cm but then declined dramatically, and no seedlings emerged from an 8-cm burial depth. The information acquired from this study could be used in developing effective management strategies for *E. indica*.

Introduction

Weed infestation is a pervasive problem that affects agricultural crop production systems worldwide. In Australia, weeds produce major economic, environmental, and social impacts by causing significant damage to natural landscapes, agricultural land, waterways, and coastal areas. Weeds cost Australian grain growers more than AU$3 billion yr^{-1} (Llewellyn et al. 2016). This financial impact extends beyond just grain cultivation, affecting cotton (*Gossypium hirsutum* L.), sugarcane (*Saccharum officinarum* L.), fruit, and vegetable cultivation as well. Goosegrass [*Eleusine indica* (L.) Gaertn.] is a C$_4$ annual diploid grass species ($2n = 18$) of rainfed agriculture that can produce 140,000 seeds plant^{-1} (Chin 1979). Considered native to Africa and Asia, it is currently distributed in warm and temperate areas worldwide, infesting cultivated land, plantation crops, vegetable farms, gardens, fallows, uncultivated land, and roadsides (Holm et al. 1977). In all Australian states, *E. indica* is found in disturbed habitats within natural areas as well as on the margins of natural forests, grasslands, marshes, stream banks, and coastal areas (QDPIF 2011). Additionally, it is prevalent as a weed along pavements and power line corridors. Furthermore, this weed also acts as a secondary host for several nematodes and diseases of sugarcane, peanut (*Arachis hypogaea* L.), corn (*Zea mays* L.), and rice (*Oryza sativa* L.) (e.g., Bendixen 1986).

Herbicide applications are the method most frequently used to control weeds, and a number of weeds have evolved resistance to herbicides as a result. Herbicide resistance in weeds is not a recent phenomenon, but it is appears to be becoming more prevalent (Coble and Schroeder 2016). Wild carrot (*Daucus carota* L.) was the first weed biotype that acquired resistance to 2,4-D (Switzer 1957), and then common groundsel (*Senecio vulgaris* L.) evolved resistance to triazine (Ryan 1970). Today, herbicide resistance has occurred in 267 weed species (154 dicotyledons and 113 monocotyledons) in 72 countries involving 21 of the 31 known herbicide

sites of action and 165 different herbicides (Heap 2023). More than 150 cases of herbicide resistance have been reported from Australia.

Eleusine indica has developed herbicide resistance to several herbicide modes of action used on both annual and perennial crops worldwide. Paraquat resistance in *E. indica* was first reported in Malaysia in 1990, while the first report of paraquat resistance in *E. indica* in Australia was in 2015 (Preston 2019). The evolution of herbicide (e.g., clethodim, cyhalofop, fenoxaprop, glufosinate, glyphosate, imazapyr, metribuzin, pendimethalin, and trifluralin) resistance in *E. indica* is attributed to widespread herbicide applications across various global regions. This resistance phenomenon has been substantiated in many countries, including Argentina, Australia, Bolivia, Brazil, China, Colombia, Costa Rica, Indonesia, Italy, Japan, Malaysia, Mexico, and the United States (Heap 2023).

Paraquat belongs to the bipyridylium family, and this herbicide is considered to be a contact herbicide due to its reduced mobility in plants (Tahmasebi et al. 2018). It is quickly absorbed by plant leaves after its application. Depending on the light intensity, this herbicide produces reactive oxygen species that damage membranes and act as electron acceptors of photosystem I (PSI) within chloroplasts, inhibiting the photosynthesis process and causing the quick mortality of plant cells (Hawkes 2014).

Studies on seed germination ecology provide important information on the emergence of weeds, their establishment, and their seedbank dynamics, all of which is vital knowledge for any program to control weeds (Chauhan and Johnson 2010). For effective control of any weed, the capacity to accurately estimate when weed seeds would germinate could improve timing of cultural practices. To develop an effectual weed control program, knowledge of seed biology is necessary for developing plant simulation models (Martinson et al. 2007; Nonogaki 2014, 2017; Schutte et al. 2008). In an agroecosystem, seed germination of a weed is a key event in determining its success, and light, temperature, moisture, soil salinity, burial depth, and other factors can all affect it. One of the most crucial elements affecting a seed's ability to germinate is temperature. Due to varying temperature requirements, differential seed germination and emergence behavior have been seen in different populations of weed species such as African mustard (*Brassica tournefortii* Gouan) and wild mustard (*Sinapis arvensis* L.) (Chauhan et al. 2006a; Singh et al. 2021; Singh et al. 2022); although, for the Australian populations of *E. indica*, such information has not been published.

Weed seeds that require light for their germination would emerge when they are near the soil surface, and these weed species may be more common in no-till cropping systems or non-cropped areas (Chauhan and Johnson 2008; Travlos et al. 2020). Similarly, weeds that can germinate in environments with severe salinity or moisture stress can benefit from conditions that prevent the growth of other species.

Crop residues applied to the soil surface (as mulches) may also restrict weed growth (Chauhan and Johnson 2008; Teasdale et al. 1991); however, the amount and type of plant material employed will determine whether crop residues stimulate or hinder weed growth. Thus, crop residue retention could play a significant role in an integrated weed management strategy. The germination and emergence of *E. indica* seedlings can be impacted by the depth at which seeds are buried (Chauhan and Johnson 2008). The vertical seed distribution in the soil can be affected by tillage (Chauhan et al. 2006b), and weed population dynamics may be influenced by this varying weed seed dispersal in the soil profile (Buhler 1991).

There is little information on the ability of *E. indica* to emerge from different depths under Australian conditions. The objectives of this research study were to (1) evaluate the performance of different postemergence herbicides on *E. indica*, and (2) determine the effects of environmental factors on seed germination and seedling emergence of *E. indica*.

Materials and Methods

Seed Description

Two Australian populations (Gatton and Ingham) of *E. indica* were selected for seed collection. In the Queensland (QLD) region of the Lockyer Valley, where Gatton is situated, there is a humid subtropical climate with hot, muggy summers and pleasant, sunny winters. During the summer months, Gatton experiences average minimum and maximum temperatures ranging from 17 to 32 C, while in winter, these temperatures range from 5 to 23 C. The humidity levels typically hover around 50% to 60% during the afternoon. Ingham is situated in the tropical monsoon region of Hinchinbrook Shire, QLD. During the summer months, Ingham experiences average minimum and maximum temperatures ranging from 22 to 34 C, while in winter, these temperatures range from 14 to 26 C. The humidity typically hovers around 70% to 80% during the afternoon hours. Seeds of *E. indica* were collected in March 2021 from fallow fields in Gatton and Ingham. There is distance of about a 1,500 km between the two sites. To obtain experimental samples for the Gatton and Ingham populations, seeds were collected from approximately 50 plants at each site and then bulked by population. After being dehulled by rubbing them between the hands, seeds were manually cleaned, dried in the shade, and kept in airtight containers at room temperature (25 + 2 C) until being used in the experiments. The field history and herbicide usage details for each site remain unknown. Nevertheless, it is important to note that sugarcane cultivation is prevalent in the Ingham region, where paraquat sees extensive use. In contrast, the Gatton site likely has a minimal history of paraquat application.

Performance of Postemergence Herbicides

Ten seeds from each population of *E. indica* were planted in 14-cm-diameter pots at a depth of 1 cm. The pots were filled with a commercial potting mix (Platinum® potting mix, Centenary Landscaping, Brisbane, QLD, Australia). The potting mix contained biological organic-based products and had a pH of 5.6. Immediately after emergence, thinning of plants was done to maintain 5 plants pot^{-1}. These plants were kept on benches outdoors and regularly irrigated using an automated sprinkler system. However, the amount of water used was not measured. To measure the effectiveness of postemergence herbicides, plants were sprayed the 4- to 5-leaf stage (5- to 6-cm plant height) with different postemergence herbicides at recommended label rates typical for most grass species (Table 1). A nontreated control treatment devoid of any herbicide application was included for each population.

A research track sprayer and TeeJet® XR110015 flat-fan nozzles (Sprayshop, Toowoomba, QLD, Australia) were utilized to spray herbicides with a water volume of 108 L ha^{-1}. Data on plant survival and biomass were recorded at 28 d after treatment, and plants that had grown a new leaf in that time were considered to have survived. The surviving plants were harvested at the soil

Table 1. Herbicide treatments, trade names, sites of action, doses, and adjuvants used in the postemergence herbicide trial.

Herbicide treatment	Trade name	Manufacturer	Sites of action[a]	Dose	Adjuvant[b]
				g ae/ai ha^{-1}	
Amitrole + paraquat[c]	Alliance®	Nufarm Australia Ltd, Laverton, VIC, www.nufarm.com/au/	Carotenoid biosynthesis + photosystem I inhibitor	560	—
Butroxydim	Factor®	Nufarm Australia Ltd, Laverton, VIC, www.nufarm.com/au/	ACCase inhibitor	30	1% Supercharge®
Clethodim	Havoc®	Nufarm Australia Ltd, Laverton, VIC, www.nufarm.com/au/	ACCase inhibitor	120	1% Supercharge®
Glufosinate	Biffo®	Nufarm Australia Ltd, Laverton, VIC, www.nufarm.com/au/	Glutamine synthetase inhibitor	750	—
Glyphosate	Roundup Ultra® MAX	Bayer Cropscience Pty Ltd, Hawthorn East, VIC, www.crop.bayer.com.au	EPSPS inhibitor	570	—
Haloxyfop	Verdict™	Corteva Agriscience Australia Pty Ltd, Chatswood, NSW, www.corteva.com.au	ACCase inhibitor	78	1% Hasten™
Imazamox + imazapyr[c]	Intervix®	BASF Australia Ltd, Southbank, VIC, crop-solutions.basf.com.au	ALS inhibitor	36	1% Hasten™
Iodosulfuron	Hussar® OD	Bayer Cropscience Pty Ltd, Hawthorn East, VIC, www.crop.bayer.com.au	ALS inhibitor	10	—
Mesosulfuron	Atlantis® OD	Bayer Cropscience Pty Ltd, Hawthorn East, VIC, www.crop.bayer.com.au	ALS inhibitor	10	1% Hasten™
Paraquat	Gramoxone®	Syngenta Australia Pty Ltd, Macquarie Park, NSW, www.syngenta.com.au	Photosystem I inhibitor	600	1% Hasten™
Pinoxaden	Axial®	Syngenta Australia Pty Ltd, Macquarie Park, NSW, www.syngenta.com.au	ACCase inhibitor	20	0.5% Adigor®
Propaquizafop	Shogun®	Adama Australia Pty Ltd, St Leonards, NSW, www.adama.com	ACCase inhibitor	30	1% Hasten™

[a]Abbreviations: ACCase, acetyl-coenzyme-A carboxylase; ALS, acetolactate synthase; EPSPS, 5-enolpyruvylshikimate-3-phosphate.
[b]Adjuvants: Adigor® (Syngenta Australia Pty Ltd, Macquarie Park, NSW) contains 440 g L^{-1} methyl esters of canola oil fatty acids; Hasten™ (BASF Australia Ltd, Southbank, VIC) contains 704 g L^{-1} ethyl and methyl esters of vegetable oil with 196 g L^{-1} nonionic surfactants; and Supercharge® (Nufarm Australia Ltd, Laverton, VIC) is 471 g L^{-1} paraffin oil.
[c]Commercial mixture.

surface, put in paper bags, and dried for 72 h at 70 C in an oven. The dry biomass was weighed.

This trial found differential responses of both populations to paraquat. The Gatton population was completely controlled, but the Ingham population survived (100%) at the field rates of amitrole + paraquat (560 g ai ha^{-1}) and paraquat (600 g ai ha^{-1}). To further examine these differences, both populations were evaluated for paraquat in a dose–response study using the procedure described above. Plants of both populations were treated with paraquat at the 4- to 5-leaf stage (5- to 6-cm plant height) with doses of 0, 17.75, 37.5, 75, 150, 300, 600, 1,200, 2,400, 4,800, and 9,600 g ai ha^{-1} (with the 1× rate of paraquat being 600 g ai ha^{-1}). Data were measured using the methods stated previously.

General Germination Test Protocol

To evaluate the effect of different environmental factors on seed germination of *E. indica*, various germination tests were conducted in 9-cm-diameter petri dishes containing a double layer of filter paper (Whatman® No. 1, Maidstone, UK). Each petri plate contained 25 seeds distributed equally, then 5 ml of distilled water or a treatment solution was added. To avoid any water vapor loss, petri dishes were placed inside plastic ziplock bags, and then these bags were placed in temperature- and light-controlled incubators (ICCBOD-300, Laboratory Equipment, Marrickville, NSW, Australia). The fluorescent light inside the incubator emitted a white light with a photosynthetic photon flux density of 85 µmol m^{-2} s^{-1}.

Studies on the effects of light, salt stress, and water stress were conducted in an incubator that was set at 30/20 C with a 12-h

photoperiod that coincides with the higher temperature, because this temperature range was found to be optimum for seed germination in the temperature experiment (described in the following section). As there was no germination after 28 d of incubation, the number of germinated seeds was counted at that time, and seeds were deemed to have germinated when the radicle was at least 1 mm in length.

Effect of Temperature on Germination

Seed germination was measured in incubators set at five different day/night temperatures (15/5, 20/10, 25/15, 30/20, and 35/25 C) in the light/dark (12/12-h) environment to study the best temperature conditions for germination of *E. indica* populations. These temperature regimes were chosen to reflect the temperature conditions present in Australia's eastern cropping region at various times of the year.

Effect of Light on Germination

Seeds from both populations of *E. indica* were exposed to two light regimes (either complete darkness for 24 h or an alternating light/dark [12/12-h] period) to assess germination under the two different light regimes (light/dark and dark). The incubator was set for treatment that alternated between light and darkness so that the high temperature (i.e., 30 C) was set during the light period and the low temperature (i.e., 20 C) was set for the dark period. For the dark treatment (30/20 C; 12 h/12 h), petri dishes were wrapped in three layers of aluminum foil to prevent any light from reaching the seeds. The foil was removed after the 28-d incubation period.

Effect of Salt Stress on Germination

To measure the impact of salt stress on *E. indica* germination, 25 seeds from each population were placed in petri plates with 5-ml solutions of 0, 20, 40, 80, 160, and 320 mM sodium chloride (NaCl). Before the germination percentage was recorded, these plates were incubated at 30/20 C day/night temperatures for 28 d. The NaCl concentration levels were chosen to represent the ranges of soil salinity that exist in different parts of Australia (Rengasamy 2002).

Effect of Osmotic Stress on Germination

To evaluate the impact of water stress on seed germination of *E. indica*, seeds from both populations were incubated in a wide range of water-deficient conditions, including 0.0, −0.1, −0.2, −0.4, −0.8, and −1.6 MPa. Following the procedure of Michel and Radcliffe (1995), solutions with the necessary osmotic potentials were made using polyethylene glycol 8000 (Sigma-Aldrich, St Louis, MO, USA).

Effect of Burial Depth on Emergence

At the University of Queensland, Gatton, seeds from both populations of *E. indica* were used to measure the impact of seed burial depth on the emergence of weed seedlings. Each 14-cm-diameter plastic pot contained 50 seeds that were either sown on the top or at a depth of 1, 2, 4, or 8 cm. The soil utilized had a clay loam texture, 2.7% organic matter content, and a pH of 7.2. The soil was sterilized after being passed through a 2-mm sieve to prevent contamination. Control pots without any additional *E. indica* seeds were utilized to ensure that there were no seeds of *E. indica* in the soil. To maintain an appropriate soil moisture level, pots were subirrigated, and seedlings were considered to have emerged when a cotyledon appeared on the soil surface. The trial was terminated at 28 d after seed placement, as no further emergence occurred after that.

Statistical Analyses

All laboratory and screenhouse experiments were carried out using a randomized complete block design. Each experiment was carried out twice, and each treatment included three replications. The ANOVA revealed no interactions between treatments and runs; thus the data from the two runs were merged. Each replication served as a block in the laboratory studies and was set up on a distinct shelf in the germination chamber. Before statistical analysis (GenStat® 21), the variance of the data was visually evaluated by plotting the residuals. Regression analysis was used where appropriate; otherwise, means were separated using the LSD at 5%. The studies of the paraquat dosage response, salt, osmotic potential, and burial depth experiments were done using nonlinear regression (SigmaPlot v. 14.5, Systat Software, Palo Alto, CA, USA). Models displaying biologically relevant interpretation of coefficients were selected. In the dose–response experiment for paraquat, seedling survival, spike production, and biomass production (percent of nontreated control) data were regressed against paraquat doses using a three-parameter logistic model:

$$Y = a / \left[1 + (x/H_{50})^b \right] \qquad [1]$$

In this model, Y represents the survival, spike, or biomass data at the x dose of herbicide; a represents the maximum seedling survival or production of spike/biomass; H_{50} represents the herbicide dose (g ai ha^{-1}) required for a 50% reduction in seedling survival (LD$_{50}$), spike number (SR$_{50}$), or plant biomass production (GR$_{50}$); and b represents the slope. Germination (%) values at different concentrations of NaCl were modeled using a three-parameter logistic model:

$$y = a / \left[1 + (x/x_{50})^b \right] \qquad [2]$$

In this model, y represents the germination percentage at the x concentration of NaCl, a is the maximum germination (%), x_{50} is the NaCl concentration necessary for inhibiting 50% germination, and b represents the slope. A three-parameter sigmoid model was fit to the germination data obtained in response to different osmotic potentials:

$$y = a / \left\{ 1 + \exp\left[-(x - x_{50})^b \right] \right\} \qquad [3]$$

In this model, y represents the germination percentage at osmotic potential x, a represents the maximum germination (%), x_{50} is the osmotic potential necessary for 50% inhibition of maximum germination, and b represents the slope. The seedling emergence values obtained from the seed burial experiment were fit using a three-parameter gaussian model. The model was:

$$y = a * e\left\{ -0.5 * \left[(x - b)/c \right]^2 \right\} \qquad [4]$$

The model's graph is shaped like a bell curve. In the model, y represents the percentage of seedling emergence at burial depth x, a represents the peak of the curve (i.e., the maximum emergence), b represents the center of the peak (i.e., the depth required to achieve maximum seedling emergence), and c is the width of the "bell."

Results and Discussion

### Performance of Postemergence Herbicides

In this study, the interaction between populations and herbicide treatments had an impact on seedling survival, spike, and biomass production of *E. indica* (Table 2). These parameters declined markedly for both populations with the application of post-emergence herbicides, with the exceptions of iodosulfuron, mesosulfuron, and pinoxaden. Control with the application of imazamox + imazapyr was lower for the Gatton population than for the Ingham population, whereas the application of paraquat (alone and in combination with amitrole) failed to control the Ingham population. Despite the Ingham population's seedlings surviving at 100% at the field rates of amitrole + paraquat (560 g ha^{-1}) and paraquat (600 g ha^{-1}), their growth was severely hampered, as evidenced by reductions of 47% to 64% in biomass production when compared with the nontreated control plants (Table 2). Iodosulfuron, mesosulfuron, and pinoxaden demonstrated ineffectiveness on both populations, with more than 70% of the seedlings surviving the application of these herbicides. In the current investigation, butroxydim, clethodim, glufosinate, glyphosate, haloxyfop, and propaquizafop were observed to be efficient herbicides for managing both populations of *E. indica*. Therefore, depending on the crop situation, farmers should rotate these herbicides to control this weed.

The populations of *E. indica* responded differently to different doses of paraquat (Figure 1; Table 3). The doses of paraquat

Table 2. Effect of herbicide treatments on survival, spike number, and biomass of the two Australian populations (Gatton and Ingham) of *Eleusine indica*.

Herbicide treatments	Seedling survival		Spike production		Biomass	
	Gatton	Ingham	Gatton	Ingham	Gatton	Ingham
	%		no. pot^{-1}		g pot^{-1}	
Control	100	100	18.2	22.3	29.60	34.82
Amitrole + paraquat[a]	0	100	0	19.2	0	18.58
Butroxydim	3.3	3.3	0	0	0.03	0.01
Clethodim	0	10	0	0	0	0.01
Glufosinate	6.7	10	0	0	0.02	0.05
Glyphosate	33.3	13.3	0	0	0.13	0.06
Haloxyfop	0	6.7	0	0	0	0.01
Imazamox + imazapyr[a]	90	6.7	16.2	0	13.83	0.06
Iodosulfuron	100	100	20.3	21.0	24.67	20.55
Mesosulfuron	96.7	100	19.5	20.3	26.30	17.53
Paraquat	0	100	0	18.7	0	12.68
Pinoxaden	83.3	76.7	6.0	5.3	6.38	7.28
Propaquizafop	3.3	3.3	0	0	0.03	0
LSD	14.1		2.3		3.22	

[a]A commercial mixture
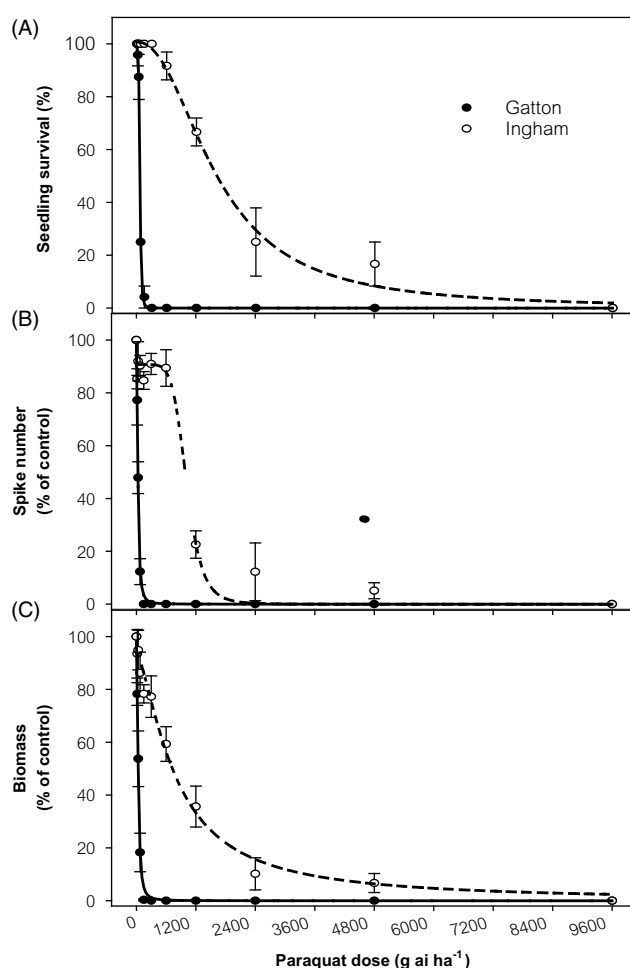
Figure 1. Effect of paraquat dose on (A) seedling survival, (B) spike number (percent of nontreated control), and (C) aboveground biomass (percent of nontreated control) of the two Australian populations (Gatton and Ingham) of *Eleusine indica*. Error bars represent the standard error of the mean.

Table 3. Estimated paraquat dose required for a 50% reduction in survival (LD_{50}), spike number (SR_{50}), and plant biomass production (GR_{50}) of the two Australian populations (Gatton and Ingham) of *Eleusine indica*.
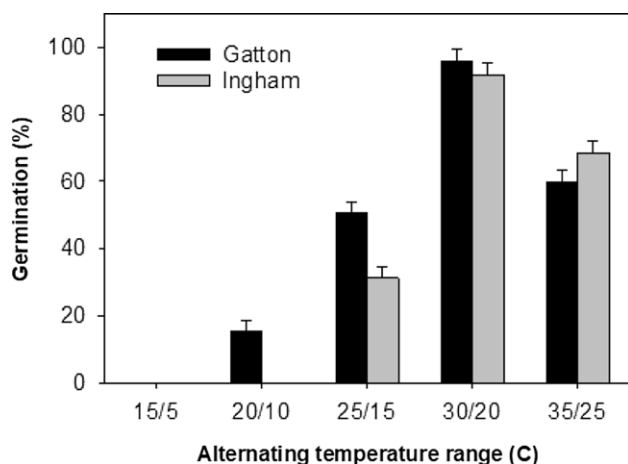
Parameters	Paraquat dose[a]	
	Gatton	Ingham
	g ai ha^{-1}	
LD_{50}	59.2 (1.0)	1,606.1 (84.6)
SR_{50}	34.3 (1.4)	1,017.0 (104.5)
GR_{50}	38.4 (1.9)	796.9 (81.8)

[a]Values in parentheses are standard errors (SE).

USA, showed 30 times more resistance than a susceptible population (Buker et al. 2002). The Ingham population had 1.3 to 2.7 times greater LD_{50} (1,606 g ha^{-1}), SR_{50} (1,017 g ha^{-1}), and GR_{50} (797 g ha^{-1}) values than the field rate (600 g ha^{-1}) of paraquat (Figure 1; Table 3).

Paraquat is a light-activated nonselective herbicide from the bipyridylium family. This herbicide is immediately absorbed into plant leaves after application, acting as a PSI electron acceptor to limit photosynthesis and then transfer electrons to an oxygen molecule to produce hazardous reactive oxygen species (Qian et al. 2009) that efficiently induce membrane damage and cell death. Paraquat therefore effectively controls annual grasses and broadleaf weeds due to its high efficiency and low cost (Fuerst and Vaughn 1990).

Sugarcane is a major resource for sugar production in Australia, and weed infestation constitutes a serious threat hindering its potential (Di Bella et al. 2021). Sugarcane crops are grown in the Ingham area, and farmers use paraquat very frequently to control weeds during fallow periods. Long-term overreliance on chemical herbicides to control weeds imposes a high selection pressure on weeds to evolve resistance. In our study, paraquat resistance in the Ingham population of *E. indica* could be due to the long-term application of paraquat to control weeds. Similarly, resistance in *E. indica* against paraquat was reported from sugarcane fields in China (Li et al. 2022). During the decades-long course of paraquat applications, many paraquat-resistant weeds have been reported. The continuous use of paraquat may result in a shift toward harder-to-control weeds, including *E. indica*. There have been reports of paraquat resistance in weeds due to the *PAR* 1 gene,

needed for a 50% reduction in survival (LD_{50}), spike number (SR_{50}), and plant biomass (GR_{50}) for the Ingham population were 27, 30, and 21 times greater, respectively, than those for the Gatton population. Similar to this, an *E. indica* population from Florida,

Figure 2. Effect of alternating day/night temperatures (15/5 to 35/25 C) on the germination of the two Australian populations (Gatton and Ingham) of *Eleusine indica*. Error bars represent the LSD at the 5% level of significance.

which lowered paraquat uptake through plasma membrane–localized transporters (Li et al. 2013).

To address glyphosate-resistant weed species, the usage of paraquat and glufosinate is expected to increase in Australia (Chauhan et al. 2021). The "double-knock" technique used to counter glyphosate resistance involves a sequential herbicide approach in which different groups of herbicides are applied with a minimum of 1 wk between the first and second applications. This typically involves using glyphosate (Group 9) as the initial herbicide, followed by paraquat (Group 22) to target survivors from the first application. The aim of the double-knock strategy is to bolster glyphosate efficacy and address glyphosate resistance by employing paraquat to eliminate the remaining weeds that have survived the initial glyphosate application.

The first case of paraquat resistance was reported in *Erigeron philadelphicus* in Japan in 1980, and paraquat resistance in *E. indica* was first reported in 1990 (Heap 2023). Alternative herbicides, such as butroxydim, clethodim, glufosinate, glyphosate, haloxyfop, and propaquizafop, can be used to control *E. indica* as reported in our study. Farmers should rotate these herbicides to control this weed and adopt integrated weed management strategies to delay the evolution of resistance by involving nonchemical methods of weed control, such as tillage and harvest weed seed control practices (Manalil et al. 2020; Walsh et al. 2013, 2018).

Effect of Temperature on Germination

An interaction between varying day/night temperature regimes and populations influenced the seed germination of *E. indica* (Figure 2). The response of both populations was similar at 15/5 and 30/20 C, whereas it was different at other alternating day/night temperature regimes. There was no germination of either population at the lowest alternating-temperature range (15/5 C). At an alternating-temperature range of 20/10 C, the Ingham population failed to germinate; however, about 15% germination was observed for the Gatton population. When the temperature was raised to 25/15 C, germination of both populations increased drastically, with a 20% higher germination of the Gatton population (51%) as compared with the Ingham population (31%). Germination of both populations was maximum (96% for Gatton and 92% for Ingham) at the alternating temperature of 30/20 C. When the temperature was raised from 30/20 to 35/25 C,

germination of the Gatton population decreased from 96% to 60%, while germination of the Ingham population decreased from 92% to 69%.

These results reveal that *E. indica* seeds may germinate under a variety of temperature conditions, demonstrating the ability of this weed to invade a wide range of environments. *Eleusine indica* may grow year-round at low altitudes in subtropical and tropical regions due to its ability to germinate over a wide range of temperatures. The optimum temperature regime (30/20 C) for germination of *E. indica* in Australian conditions is comparable to that found for this weed in the Philippines (Chauhan and Johnson 2008). The level of adaptation to the changing temperature regimes was higher in the Gatton population as compared with the Ingham population, which would provide this population with many more opportunities for establishment and reproduction. Characteristically for a tropical weed, greater germination of both populations of *E. indica* was observed at higher temperature regimes (30/20 and 35/25 C) rather than lower temperature regimes (25/15, 20/10, and 15/5 C). When compared with the Gatton population, the Ingham population was more tolerant to high temperatures, as it was able to retain higher germination at the highest temperature (35/25 C).

Between October and March, Gatton experienced long-term (30 yr on average) monthly mean maximum and minimum temperatures that varied from 28.9 to 32.5 C and 13.3 to 19.4 C, respectively (BOM 2023). Similarly, Ingham experienced long-term monthly mean maximum and minimum temperatures that varied from 30.4 to 32.8 and 18.6 to 23.4 C, respectively, between October and March. The surface seeds of the Ingham population experience relatively warmer environmental conditions after reaching maturity than the Gatton population, according to the long-term temperature conditions of the two locations. This suggests that, in comparison to the Gatton population, the Ingham population may exhibit adaptational features for better germination under higher temperatures (35/25 C) and reduced germination under lower temperatures (25/15 and 20/10 C). Despite this, it is still entirely feasible that the Gatton population can germinate earlier and can continue to germinate in higher temperature conditions. Differential germination behavior as a result of various environmental circumstances was also reported in *S. arvensis* (Singh et al. 2022) and *B. tournefortii* populations from Queensland and southern Australia (Chauhan et al. 2006a; Singh et al. 2021).

In the current study, germination of both populations (51% for the Gatton population and 31% for the Ingham population) at 15/25 C suggests that, due to climate change, this summertime weed may adapt to Australia's winter season and become more invasive in winter crops. Because the Gatton population had some germination (15%) at 20/10 C compared with the Ingham population, which failed to germinate under this temperature regime, chances of adaptation to the winter season are higher for the Gatton population. In this study, reduced germination of *E. indica* at 20/10 C and no germination at the lowest temperature regime (15/5 C) suggest that adjusting crop planting dates can reduce the likelihood of this weed becoming an infestation; however, executing this agronomic technique may be influenced by various factors, such as the crop's potential yield and its competitiveness, prevailing weather conditions, and other factors.

Effect of Light on Germination

An interaction between populations and light treatment affected the seed germination of *E. indica* (Figure 3). Under light/dark
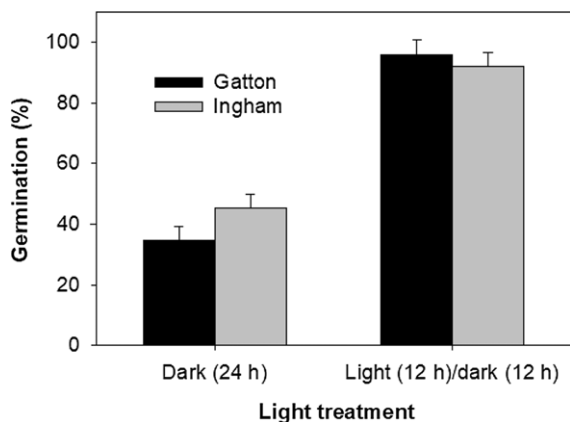
Figure 3. Effect of light/dark regimes on the germination of the two Australian populations (Gatton and Ingham) populations of *Eleusine indica*. Seeds were incubated for 28 d at alternating day/night temperatures of 30/20 C. Error bars represent the LSD at the 5% level of significance.

Figure 4. Effect of sodium chloride concentration on the germination of the two Australian populations (Gatton and Ingham) of *Eleusine indica* incubated under alternating light/dark for 28 d at 30/20 C. The lines represent a three-parameter logistic model fit to the germination data in response to sodium chloride concentrations.

conditions, as compared with total darkness, higher germination of both populations was noted. Both populations exhibited comparable germination (96% for Gatton and 92% for Ingham) under light/dark conditions; however, under complete darkness, higher germination of the Ingham population (45%) was observed as compared with the Gatton population (35%).

Singh et al. (2021) noticed that two populations of *S. arvensis* in Australia responded differently to light treatment and reported that, the Queensland population had higher germination (61%) than the Victoria population (21%) under complete darkness; however, under the light/dark regime, both populations had similar germination (78% to 86%, respectively). Similarly, seed germination of Australian fingergrass (*Chloris truncata* R. Br.) improved in the presence of light; however, 51% to 71% of these seeds germinated even under the dark condition (Chauhan et al. 2018). Similar to our study, Chauhan and Johnson (2008) reported greater germination (72%) of *E. indica* in the Philippines under light/dark regimes as compared with complete darkness (25%) at 30/20 C.

While light exposure is an important factor for seed germination, it is worth noting that not all species share similar light requirements. Some species prefer to germinate in the presence of light, while others thrive in complete darkness (Baskin and Baskin 1998). Certain species may show no clear preference at all. Based on our findings, it appears that *E. indica* has a preference for light, but it is still capable of germinating in the absence of light (Chauhan and Johnson 2008). In our study, populations were gathered from different geographic or agroecological circumstances; it is possible that adaptive features or genetic variations might be responsible for the distinct germination behavior of the two populations in the absence of any light.

Effect of Salt Stress on Germination

Varying salt concentrations affected the *E. indica* seed germination (Figure 4). A decreasing response was observed in the germination of *E. indica* seeds with the increase in NaCl concentration from 0 to 320 mM. Both populations germinated similarly (>90%) under the control treatment and at a salt concentration of 20 mM NaCl. Lower germination was observed for the Gatton population as compared with the Ingham population at 40 to 160 mM NaCl.
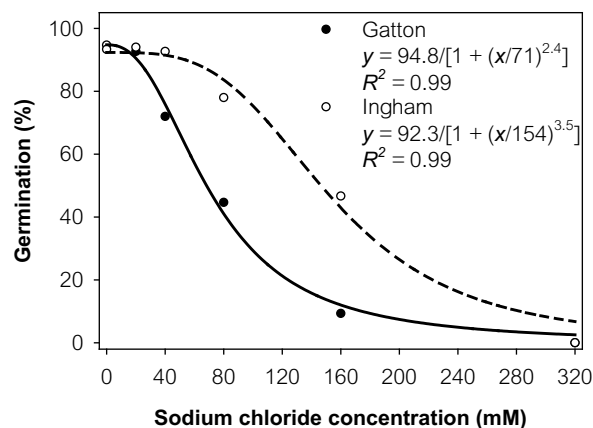
The Ingham population's germination was unaffected (>90%) at 40 mM NaCl, but the germination of the Gatton population was drastically reduced (<80%). The required concentration for 50% inhibition of the maximum germination was 71 mM NaCl for the Gatton population and 154 mM NaCl for the Ingham population, whereas both populations did not germinate at all at 320 mM NaCl.

A study in the Philippines revealed that the required concentration for 50% inhibition of maximum germination of *E. indica* was 78 mM NaCl, and no germination occurred at 200 mM NaCl (Chauhan and Johnson 2008). In our study, germination of both populations occurred up to 160 mM NaCl, which suggests that even in high-saline conditions, competition from *E. indica* could limit crop production, because *E. indica* could grow in high-saline conditions. Also, the findings imply that both populations behaved differently under varied salt concentrations.

The Ingham population continued to germinate more readily between 40 and 160 mM NaCl concentrations, indicating that under Australia's salinized soil conditions, the Ingham population could grow and pose a larger threat to crops compared with the Gatton population. Deng et al. (2019) also reported differential germination response of paraquat-resistant and paraquat-susceptible *E. indica* to salt stress, wherein the susceptible biotype was more sensitive to salinity than the resistant biotype. Genetic variations or adaptation to specific local climatic circumstances may be responsible for the varied germination behavior of populations at high salt concentrations, as these populations were gathered under different agroecological or topographical circumstances (Dehnavi et al. 2020). The area where the Ingham population was drawn from is situated near the sea, which may make a suitable ecosystem for excessive salt content in the soils.

Osmotic stress and ion toxicity under excessive salinity could affect the germination of seeds (Bliss et al. 1986). Earlier research also showed that elevated levels of Cl^- and Na^+ concentration under high salt concentrations could affect the process of seed germination by restricting cellular activity, energy production, and the uptake of essential micronutrients (Gupta and Huang 2014; Maathuis et al. 2014). In addition, osmotic stress, a result of an increased salt content, may change the water and nutrient intake as well as hormonal and enzymatic activity in seeds, resulting in poor germination (Thiam et al. 2013). Consequently, in the present
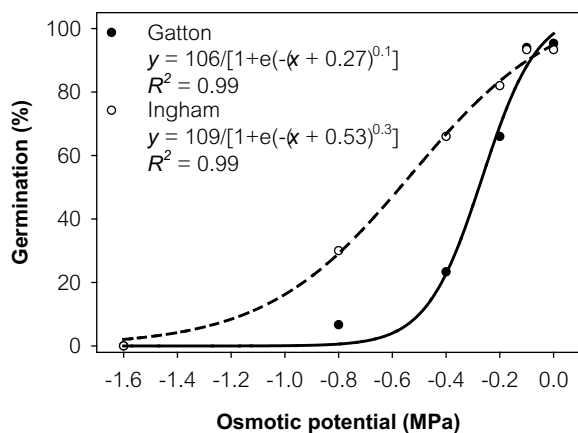
Figure 5. Effect of osmotic potential on the germination of the two Australian populations (Gatton and Ingham) of *Eleusine indica* incubated under alternating light/dark for 28 d at 30/20 C. The lines represent a three-parameter sigmoid model fit to the germination data in response to concentrations of osmotic potentials.
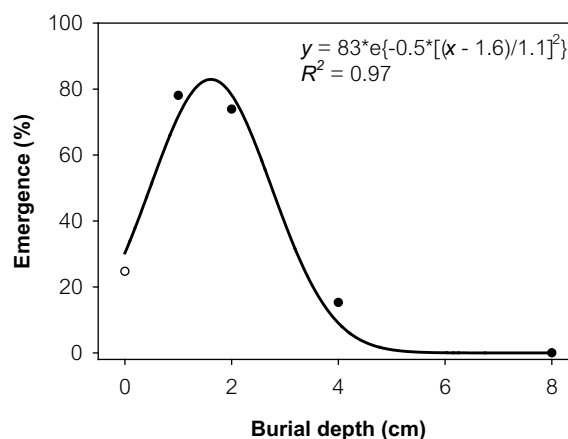
Figure 6. Effect of burial depth on the seedling emergence of the two Australian populations (Gatton and Ingham) of *Eleusine indica*. The lines represent a gaussian model fit to the emergence data obtained at different seed burial depths.

study, ion toxicity or osmotic stress might have caused germination suppression at the greatest salt concentration.

Compared with the Gatton population, the Ingham population was more resilient to the effects of salt stress, which indicates that *E. indica* plants have acclimated to a variety of soil and climatic conditions to develop seeds that can combat different environmental restrictions. These results imply that it is crucial to evaluate *E. indica* populations across various locations in future research. The results of this investigation suggest that *E. indica* can colonize locations that are salt affected and may further impact crop production.

Effect of Osmotic Stress on Germination

The interaction between *E. indica* populations and varying osmotic potentials affected the seed germination of this weed (Figure 5). In the control treatment (no stress), both populations exhibited maximum germination, which then declined with decreasing osmotic potential. Greater germination was observed for the Ingham population at –0.2, –0.4, and –0.8 MPa compared with the Gatton population. Germination of both populations was similar at other osmotic potentials.

The highest germination rate observed in the no-water stress treatment suggests that the uniform distribution of rainfall throughout the year in eastern Australia, coupled with irrigated cropping systems, may contribute to the proliferation of this weed (BOM 2023). Osmotic potential below –0.2 MPa significantly reduced germination, indicating that a moist environment is preferred by *E. indica* for germination. Hence, after rainfall, a substantial number of *E. indica* seedlings might emerge. This situation could arise early in the growing season, posing challenges to crop production. Similar results of a sharp decrease in the germination of *E. indica* seeds due to a decrease in osmotic potential beyond –0.2 MPa were observed in the Philippines (Chauhan and Johnson 2008).

In the current study, none of the populations germinated at –1.6 MPa. The sigmoid model estimated that osmotic potentials that could cause a 50% reduction in germination were –0.27 MPa for the Gatton population and –0.53 MPa for the Ingham population. Sharpe and Boyd (2019) also reported that seed germination of *E. indica* occurred at osmotic potentials as low as –0.5 MPa. These results suggest that high osmotic stress (–0.8 MPa) can be tolerated

by the Ingham population, giving it the ability to adapt to situations that are water stressed. The ability of the Ingham population to germinate under relatively dry conditions confirms that it can survive in dryland agriculture systems, although its germination would be favored by additional soil moisture conditions prevailing in conservation agriculture systems (Oryokot et al. 1997; Singh et al. 1998).

These findings suggest that *E. indica* may germinate vigorously under conditions of relatively high soil moisture. When compared with the Gatton population, the Ingham population was found to be comparatively more tolerant of water-stress situations. The ability of the Ingham population to tolerate high water stress may be increased by maintaining seed dormancy until optimum moisture conditions are present for effective germination (Fernando et al. 2016). The germination behavior of both populations in response to water stress differed, particularly at lower osmotic potential concentrations. Similarly, two populations (glyphosate-resistant and glyphosate-susceptible biotypes) of *E. indica* also showed differential germination behavior in response to varying osmotic stress (Ismail et al. 2002).

Effect of Burial Depth on Emergence

When sown at various seed burial depths, both populations of *E. indica* exhibited similar emergence behavior; therefore, data were averaged across populations, and the emergence data were fit with a gaussian model (Figure 6). When seeds were positioned on the surface (0-cm depth), only 29% of *E. indica* plants emerged. The emergence increased from 29% to 71% with the increase in burial depth from 0 cm to 1 cm. The gaussian model calculated that the highest (peak) seedling emergence (83%) of *E. indica* was at a burial depth of 1.6 cm, (Figure 6). At a depth of 2 cm, 79% of seedlings of *E. indica* emerged; after that, emergence declined rapidly, reaching 8% from the 4-cm depth and no emergence from the 8-cm depth.

Similarly, Ismail et al. (2002) reported that only 21% of the seeds of one *E. indica* biotype emerged from the soil's surface. However, contradictory to this in a previous study in the Philippines, the maximum seedling emergence (82%) of *E. indica* was observed for the seeds placed on the soil surface, and emergence thereafter decreased with increasing burial depth, with only 4% emerging from a depth of 6 cm (Chauhan and Johnson 2008). Boyd and Van Acker (2003) also reported that seedling emergence in several weed

species decreased due to increased burial depth. Different experimental conditions, genetic variation, or adaptation to localized climatic conditions could be the cause of the disparate results in the two investigations (Dehnavi et al. 2020).

The size of seeds plays a very important role in emergence from various burial depths. Larger seeds can emerge from greater burial depths due to their greater carbohydrate reserves (Baskin and Baskin 1998). However, weeds with small seeds, like *E. indica*, may not emerge from deep burial, because they may not have enough energy to support hypocotyl elongation. Mahajan et al. (2018) and Singh et al. (2021) also reported that as soil depth increased, the emergence of many small-seeded weed seedlings decreased. Our results indicate that *E. indica* could be a problematic weed in no-till or shallow-tillage situations. The findings of our study indicate that *E. indica* would emerge more frequently under farming practices that achieve a shallow burial of weed seeds; however, deep tillage (>6 cm) could reduce its emergence. Therefore, to bury the weed seeds below 6 cm, deep inversion tillage could be used as a weed management approach.

In this study, the application of postemergence herbicides, such as butroxydim, clethodim, glufosinate, glyphosate, haloxyfop, and propaquizafop, effectively controlled both populations of *E. indica*, whereas the application of paraquat failed to control the Ingham population. Compares with the Ingham population, the Gatton population required a paraquat dose 21 to 30 times higher to achieve a 50% drop in survival, spike number, and plant biomass. Farmers should rotate different postemergence herbicides to control this weed and adopt integrated weed management strategies to delay the evolution of resistance. The seed germination of both populations of *E. indica* was greater at 30/20 and 35/25 C alternating temperatures than at 25/15 and 20/10 C, which can be expected for a tropical weed. Both populations' germination rates were comparable (>90%) in light/dark regimes; however, with the total absence of light, significantly higher germination of the Ingham population (45%) was observed as compared with the Gatton population (35%). The Ingham population was more tolerant to salt- and water-stress conditions compared with the Gatton population. Seedling emergence of *E. indica* was found to be maximum for seeds buried at the 2-cm depth, and no emergence was recorded from the 8-cm depth. These results indicate that *E. indica* could be a problematic weed in no-till systems, but deep tillage (>6 cm) could reduce its emergence.

The findings of our study underscore critical factors that contribute to the widespread and problematic nature of *E. indica* as a weed in humid tropical regions. The insights derived from this research can be harnessed to craft successful strategies for managing *E. indica* across diverse agroecological settings. However, it is essential to acknowledge that our study examined only one population from each environment. Consequently, further investigations encompassing a diverse spectrum of populations from various environments are imperative to foster the development of comprehensive and effective management methodologies. It is important to highlight that the observed germination disparities between the populations may not necessarily correlate with the paraquat resistance status of the two populations. Considering that the two populations were collected from regions separated by a distance of 1,500 km, these differences could likely stem from genetic variations.

References

Baskin CC, Baskin JM (1998) Seeds: Ecology, Biogeography, and Evolution of Dormancy and Germination. San Diego, CA: Academic Press. 627 p

Bendixen LE (1986) Weed hosts of Meloidogyne, the root-knot nematodes. Pages 101–172 in K. Noda and B. L. Mercado, eds. Weeds and the Environment in the Tropics. Chiang Mai, Thailand: Asian-Pacific Weed Science Society

Bliss RD, Plattaloia KA, Thomson WW (1986) Osmotic sensitivity in relation to salt sensitivity in germinating barley seeds. Plant Cell Environ 9:721–725

Boyd NS, Van Acker RC (2003) The effects of depth and fluctuating soil moisture on the emergence of eight annual and six perennial plant species. Weed Sci 51:725–730

Buhler DD (1991) Influence of tillage systems on weed population dynamics and control in the northern Corn Belt of the United States. Adv Agron 1:51–60

Buker RS, Steed T, Stall WM (2002) Confirmation and control of paraquat-tolerant goosegrass (*Eleusine indica*) biotype. Weed Technol 16:309–313

[BOM] Bureau of Meteorology, Australia (2023) Historical weather observations and statistics. http://www.bom.gov.au/climate/data-services/station-data.shtml. Accessed: February 9, 2023

Chauhan BS, Congreve M, Mahajan G (2021) Management options for large plants of glyphosate-resistant feather fingergrass (*Chloris virgata*) in Australian fallow conditions. PLoS ONE 16:e0261788

Chauhan BS, Gill G, Preston C (2006a) African mustard (*Brassica tournefortii*) germination in Southern Australian. Weed Sci 54:891–897

Chauhan BS, Gill G, Preston C (2006b) Influence of tillage systems on vertical distribution, seedling recruitment, and persistence of rigid ryegrass (*Lolium rigidum*) seed bank. Weed Sci 54:669–676

Chauhan BS, Johnson DE (2008) Germination ecology of goosegrass (*Eleusine indica*): an important grass weed of rainfed rice. Weed Sci 56:699–706

Chauhan BS, Johnson DE (2010) The role of seed ecology in improving weed management strategies in the tropics. Adv Agron 105:221–262

Chauhan BS, Manalil S, Florentine S, Jha P (2018) Germination ecology of *Chloris truncata* and its implication for weed management. PLoS ONE 13: e0199949

Chin HF (1979) Weed seed—a potential source of danger. Pages 115–119 in L. T. Kwee, ed. Proceedings of the Plant Protection Seminar. Kuala Lumpur: Malaysian Plant Protection Society

Coble HD, Schroeder J (2016) Call to action on herbicide resistance management. Weed Sci 64(S1):661–666

Deng C Li J, Liu S, Zhu X, Chen Y, Shen X (2019) Effects of spermidine and salinity stress on growth and biochemical response of paraquat-susceptible and -resistant goosegrass (*Eleusine indica* L.). Weed Biol Manag 19:75–84

Dehnavi AR, Zahedi M, Ludwiczak A, Perez SC, Piernik A (2020) Effect of salinity on seed germination and seedling development of sorghum (*Sorghum bicolor* (L.) Moench) genotypes. Agronomy 10:859–874

Di Bella L, Zahmel M, van Zwieten L, Rose TJ (2021) Weed suppression, biomass and nitrogen accumulation in mixed-species and single-species cover crops in a tropical sugarcane fallow. Agriculture 11:640

Fernando N, Humphries T, Florentine SK, Chauhan BS (2016) Factors affecting seed germination of feather fingergrass (*Chloris virgata*). Weed Sci 64: 605–612

Fuerst EP, Vaughn KC (1990) Mechanisms of paraquat resistance. Weed Technol 4:50–156

Gupta B, Huang B (2014) Mechanism of salinity tolerance in plants: physiological, biochemical and molecular characterization. Int J Genomics 39:1–18

Hawkes TR (2014) Mechanisms of resistance to paraquat in plants. Pest Manag Sci 70:1316–1323

Heap I (2023) The International Herbicide-Resistant Weed Database. www.weedscience.org. Accessed: March 27, 2023

Holm LG, Plucknett DL, Pancho JV, Herberger JP (1977) The World's Worst Weeds: Distribution and Biology. Honolulu: University of Hawaii Press. 609 p

Ismail BS, Chuah TS, Salmijah S, Teng YT, Schumacher RW (2002) Germination and seedling emergence of glyphosate-resistant and susceptible

biotypes of goosegrass (*Eleusine indica* [L.] Gaertn.). Weed Biol Manag 2:177–185

Li J, Zhang Z, Lei Q, Lu B, Jin C, Liu X, Wang Y, Bai L (2022) Multiple herbicide resistance in *Eleusine indica* from sugarcane fields in China, Pesticide Biochem Physiology 182:105040

Li J, Mu J, Bai J, Fu F, Zou T, An F (2013) PARAQUAT RESISTANT1, a Golgi-localized putative transporter protein, is involved in intracellular transport of paraquat. Plant Physiol 162:470–483

Llewellyn RS, Ronning D, Ouzman J, Walker S, Mayfield A, Clarke M (2016) Impact of Weeds on Australian Grain Production: The Cost of Weeds to Australian Grain Growers and the Adoption of Weed Management and Tillage Practices. Report for GRDC. Canberra, Australia: CSIRO, 112 p

Maathuis FJM, Ahmad I, Patishtan J (2014) Regulation of Na$^+$ fluxes in plants. Front Plant Sci 124:451–467

Mahajan G, Matloob A, Walsh M, Chauhan BS (2018) Germination ecology of two Australian populations of African turnipweed (*Sisymbrium thellungii*). Weed Sci 66:752–757

Manalil S, Mobli A, Chauhan BS (2020) Competitiveness of windmill grass (*Chloris truncata*) and feathertop Rhodes grass (*Chloris virgata*) in mungbean (*Vigna radiata*). Crop Pasture Sci 71:916–923

Martinson K, Durgan B, Forcella F, Wiersma J, Spokas K, Archer D (2007) An emergence model for wild oat (*Avena fatua*). Weed Sci 55:584–591

Michel BE, Radcliffe D (1995) A computer program relating solute potential to solution composition for five solutes. Agron J 87:126–130

Nonogaki H (2014) Seed dormancy and germination-emerging mechanisms and new hypotheses. Front Plant Sci 5:233.

Nonogaki H (2017) Seed biology updates—highlights and new discoveries in seed dormancy and germination research. Front Plant Sci 8:524

Oryokot J, Murphy SD, Swanton CJ (1997) Effect of tillage and corn on pigweed (*Amaranthus* spp.) seedling emergence and density. Weed Sci 45:120–126

Preston AL (2019) Integrated Weed Management in Australian Cropping Systems—A Reference Manual for Grains Research and Development Corporation (GRDC). Canberra, Australia: CSIRO. 314 p

Qian H, Chen W, Sun L, Jin Y, Liu W, Fu Z (2009) Inhibitory effects of paraquat on photosynthesis and the response to oxidative stress in *chlorella vulgaris*. Ecotoxicology 18:537–543

[QDPIF] Queensland Department of Primary Industries and Fisheries (2011) Special Edition of Environmental Weeds of Australia for Biosecurity Queensland. Brisbane, Australia: University of Queensland and Department of Primary Industries and Fisheries. https://keyserver.lucidcentral.org/weeds/data/media/Html/eleusine_indica.htm. Accessed: May 2, 2023

Rengasamy P (2002) Transient salinity and subsoil constraints to dryland farming in Australian sodic soils: an overview. Aust J Exp Agric 42:351–361

Ryan GF (1970) Resistance of common groundsel to simazine and atrazine. Weed Sci 18:614–616

Schutte BJ, Regnier EE, Harrison SK, Schmoll JT, Spokas K, Forcella F (2008) A hydrothermal seedling emergence model for giant ragweed (*Ambrosia trifida*). Weed Sci 56:555–560

Sharpe S, Boyd N (2019) Germination ecology for Florida populations of carpetweed (*Mollugo verticillata*), Carolina geranium (*Geranium carolinianum*), eclipta (*Eclipta prostrata*), and goosegrass (*Eleusine indica*). Weed Sci 67:1–8

Singh A, Mahajan G, Chauhan BS (2022) Germination ecology of wild mustard (*Sinapis arvensis*) and its implications for weed management. Weed Sci 70:103–111

Singh B, Chanasyk DS, McGill WB (1998) Soil water regime under barley with long-term tillage-residue systems. Soil Till Res 45:59–74

Singh S, Mahajan G, Singh R, and Chauhan BS (2021) Germination ecology of four African mustard (*Brassica tournefortii* Gouan.) populations in the eastern region of Australia. Weed Sci 69:461–467

Switzer CM (1957) The existence of 2,4-D resistant strains of wild carrot. Proc Northeast Weed Control Conf 11:315–318

Tahmasebi BK, Alcántara-de la Cruz R, Alcántara E, Torra J, Domínguez-Valenzuela JA, Cruz-Hipólito HE, Rojano-Delgado AM, De Prado R (2018) Multiple resistance evolution in bipyridylium-resistant *Epilobium ciliatum* after recurrent selection. Front Plant Sci 9:1–11

Teasdale JR, Beste CE, Potts WE (1991) Response of weeds to tillage and cover crop residue. Weed Sci 39:195–199

Thiam M, Champion A, Diouf D, Ourye M (2013) NaCl effects on in vitro germination and growth of some Senegalese cowpea (*Vigna unguiculata* (L) Walp.) cultivars. Biotechnol J 2013:1–11

Travlos I, Gazoulis I, Kanatas P, Tsekoura A, Zannopoulos S, Papastylianou P (2020) Key factors affecting weed seeds' germination, weed emergence, and their possible role for the efficacy of false seedbed technique as weed management practice. Front Agron 2:1–9

Walsh M, Newman P, Powles S (2013) Targeting weed seeds in-crop: a new weed control paradigm for global agriculture. Weed Technol 27:431–436

Walsh MJ, Broster JC, Schwartz-Lazaro LM, Norsworthy JK, Davis AS, Tidemann BD, Beckie HJ, Lyon DJ, Soni N, Neve P, Bagavathiannan MV (2018) Opportunities and challenges for harvest weed seed control in global cropping systems. Pest Manag Sci 74:2235–2245