Weed Science 2017 65:395–405

Plant Development and Seed Biology of Windmillgrass (*Chloris truncata*) in Southern Australia

The D. Ngo, Peter Boutsalis, Christopher Preston, and Gurjeet Gill*

Windmillgrass is a major weed in agricultural systems in northern Australia, and it has now become more common in southern Australia. Because little information is available on the biology of this weed species in southern Australia, studies were conducted to investigate plant development and seed biology. Under irrigated field conditions in South Australia, windmillgrass required 748 to 786 growing degree days from emergence to mature seed production. Freshly harvested seed had low dormancy with 16% to 40% germination. Seeds required light exposure for germination and less than 2% germination was observed in complete darkness. Seed could germinate over a wide temperature range (10 to 40 C) with maximum germination at 20 to 25 C. At 25 to 30 C, 50% germination occurred within 27.3 to 45.5 h, and the predicted base temperature for germination of the two populations investigated ranged from 9.2 to 11.2 C. The sodium chloride concentration and osmotic potential required to inhibit germination by 50% were 51 to 73 mM and −0.27 MPa, respectively. Seedling emergence was completely inhibited by burial of seed, which is consistent with its absolute requirement for light exposure to begin germination. Under field conditions, there was no clear effect of burial depth on seed viability in the first 2 yr with average rainfall, and seeds were completely nonviable after 12 mo. However, in the third year, with low spring–summer rainfall, buried seeds (37% viability after 14 mo) persisted longer than those left on the soil surface (6% viability after 14 mo). This study provides important information on plant development and seed biology of windmillgrass that will contribute to the development of a management program for this weed species in southern Australia.

Nomenclature: Windmillgrass, *Chloris truncata* R. Br.

Key words: Base temperature, dormancy, emergence, germination, seedbank persistence.

Windmillgrass is a warm-season, C_4, annual or short-lived perennial grass native to Australia (Mitchell 1994; Nightingale et al. 2005). In Australia, some native grass species have the ability to establish in disturbed ecosystems that have regular cultivation, input of fertilizer, ruminant grazing, or crop competition (Kloot 1985; Michael et al. 2012a). This group includes windmillgrass, which has been a significant weed in cotton (*Gossypium hirsutum* L.) and grain crops in the subtropical region of Australia, particularly in no-till agriculture cropping systems (Werth et al. 2013). In the Western Australian grain belt, this species was found at 12% of the sites in a field survey of summer fallow sites (Michael et al. 2010a). It was projected that windmillgrass could become one of the five most threatening weed species to agriculture in the southwest of Western Australia (Michael et al. 2010b). More recently, this species has been ranked as the seventh most important weed of summer fallow by yield loss (36,871,000 kg) and revenue loss (A$9.1 million) in Australia (Llewellyn et al. 2016).

As a result of an overreliance on glyphosate for weed control, glyphosate resistance occurred in windmillgrass in chemical fallow sites and roadsides in Australia (Malone et al. 2012; Preston 2016), making control of this weed in summer fallow situations more difficult. The dominance of reduced-tillage systems combined with the overreliance on glyphosate for weed control in the fallow phase of crop rotations has also favored this grass in northern Australia (Werth et al. 2013; Widderick et al. 2014). As a summer annual grass species, windmillgrass will reduce the potential yield of winter crops by taking up moisture and nutrients that would otherwise be available for crops and will delay sowing due to the time needed for weed control in the autumn (Osten et al. 2006). For example, the absence of management of windmillgrass over summer fallow reduced yield of the following wheat (*Triticum aestivum* L.) crop in Merredin, WA, by 0.3 ton ha^{-1} (Borger et al. 2010).

DOI: 10.1017/wsc.2017.5

* First, second, third, and fourth authors: Postgraduate Student, Postdoctoral Fellow, Associate Professor, and Associate Professor, School of Agriculture, Food and Wine, University of Adelaide, PMB 1, Glen Osmond, SA 5064, Australia. Corresponding author's E-mail: ducthe.ngo@adelaide.edu.au

Seed germination, a process regulated by several environmental factors such as temperature, light, moisture, and soil salinity, is a key event determining the success of a weed species in an agroecosystem (Chachalis and Reddy 2000; Koger et al. 2004). The timing of germination and emergence is critical for the survival of annual plants, with temperature and light among the most important environmental signals that regulate germination and emergence of a plant species (Baskin and Baskin 1998; Saatkamp et al. 2009; Schutte et al. 2014). For seeds in the soil, temperature and light are important cues for initiating germination, providing a sense of position in the soil profile and reflecting the occurrence of soil disturbance (Batlla and Benech-Arnold 2014). In Australia, there have been several studies of the effect of temperature and light on germination of windmillgrass in New South Wales (Lodge and Whalley 1981; Maze et al. 1993). However, there is currently no information available on the base temperature required for germination of windmillgrass in Australia. In addition, seeds that respond to environmental conditions and alter their germination behavior are more likely to survive and establish successfully. The effect of burial depth and other factors that may impact germination of windmillgrass in southern Australia are poorly understood.

To effectively manage a weed, an understanding of its basic biology is critical. This includes germination conditions, dormancy, seedbank dynamics, and plant development (Bhowmik 1997; Cousens and Mortimer 1995; Mennan and Ngouajio 2006). An understanding of the particular seed-dormancy mechanisms involved can also be useful for the development of control strategies for weeds (Adkins et al. 2002). Simpson (1990) listed 89 species of C_4 grasses from 24 genera, including *Chloris*, as having one or more forms of dormancy. In many species, the embryo has the ability to germinate, but dormancy is caused by embryo covering structures. The mechanisms within the covering structures may involve permeability (preventing water uptake or gaseous exchange), mechanical (preventing embryo expansion), and chemical barriers to germination (Adkins et al. 2002). Furthermore, it is important to manage the soil seedbank of herbicide-resistant weed populations such as windmillgrass (Kleemann et al. 2016). Persistence of the soil seedbank determines the length of time management strategies are required to reduce the population to minimal levels (Matthews 1994). A preliminary report showed that windmillgrass seed had short field persistence (12 mo) in the northern cropping region of Australia (Widderick et al. 2014). However, the seedbank persistence of windmillgrass in cooler Mediterranean conditions of the southern and western grain regions of Australia has not been reported.

The objectives of this study were to determine (1) plant development under field and controlled conditions (time required to reach panicle emergence and seed maturity); (2) seed dormancy; (3) effect of physical environmental factors (temperature, light, salt stress, osmotic potential and burial depth) on germination and seedling emergence; and (4) seedbank persistence under field conditions.

Materials and Methods

Seed Sources. Mature seeds were collected in June 2013 from two windmillgrass populations in Buchfelde (CT2) and Smithfield (CT3) in South Australia, Australia. Harvested seeds were cleaned and stored in paper bags at room temperature (~20 C). Seeds of these populations were grown at a common site (Waite Campus, University of Adelaide, SA, Australia), and the seeds collected from these plants were used for further studies.

Plant Development in an Irrigated Field and Pots. A total of 200 seeds (more than 6 mo old, average germination of 77% for lab tests) from each of the CT2 and CT3 populations were mixed with sand and surface scattered in 1-m^2 plots with four replicates in randomized complete blocks at Roseworthy, SA, Australia (34.524807°S, 138.686362°E), on January 24, 2014. The field soil was a clay loam. Before this experiment was conducted, windmillgrass had never been observed at the experimental site, which is regularly used for crop production. After sowing, irrigation was applied weekly to prevent water stress. Ten tagged seedlings in each replicate were used to assess the time taken to reach tillering, panicle emergence, and seed production.

Field-collected seeds of CT2 and CT3 populations were germinated in an incubator set at 25 C to produce seedlings. These windmillgrass seedlings were transplanted into pots eight different times at 3- to 4-week intervals from October 3, 2013, to March 8, 2014, to determine the influence of growing season on the timing of panicle emergence. Ten seedlings (1-leaf) of each population (CT2 and CT3) were grown in four pots (25-cm deep by 18-cm diameter) containing standard potting mix (Boutsalis et al. 2012) and kept outdoors at Waite

Campus, University of Adelaide, SA, Australia (34.970302°S, 138.639700°E). Plants were watered as required to maintain adequate soil moisture. The time taken to reach panicle emergence was recorded.

Standard Germination Test Protocols. Effects of seed dormancy, temperature, light, and salt or osmotic potential on seed germination were evaluated. Germination was evaluated by evenly placing seeds of each population in a 15-cm-diameter petri dish containing two layers of Whatman No. 1 filter paper moistened with 9 ml of distilled water or a treatment solution (e.g., polyethylene glycol and salt). There were four replicates of each treatment. Dishes were sealed with parafilm and placed in an incubator (cat. no. R1235D, ser. no. SO 17, S.E.M., Magill, SA, Australia) set at 25 C, the temperature previously determined to be in the optimum range for germination of windmillgrass (Lodge and Whalley 1981; Maze et al. 1993; Michael et al. 2012b). The photoperiod was set at 12 h with fluorescent lamps used to produce light intensity of 43 μmol m^{-2} s^{-1}. Germinated seeds (emerged coleoptile, radical >5-mm long) were counted every 2 d for 14 d.

Seed Dormancy. Covering structures (lemma and palea) of windmillgrass seeds turn black at maturation. Mature seeds were collected, and experiments were started within a week after seed collection and repeated at approximately monthly intervals for 12 mo. The tetrazolium seed viability test is considered unreliable for windmillgrass (Farley et al. 2013) and was not used in this study. Germination was calculated as a percentage of total seeds used in each test. The experiment was conducted with the original field-collected seeds of CT2 and CT3 in June 2013 (25 seeds each replicate). As windmillgrass can produce seeds over several weeks, the experiment was also conducted with seeds that were freshly harvested in November and December 2014 to determine the influence of the timing of seed maturity on germination response.

Effect of Temperature on Germination. Seeds (9 mo old, 25 seeds each replicate) of CT2 and CT3 populations were used to examine the effect of temperature on germination. Seeds were incubated at six different constant temperature regimes (10, 15, 20, 25, 30, and 40 C). Germinated seeds were counted and recorded daily, and germination tests were terminated when no further germination occurred for 7 d. The maximum germination (G_{max}) was expressed as the percentage of total seeds used.

Effect of Light on Germination. The effect of two light regimes (12-h alternating light/dark and 24-h dark) on germination of CT2 and CT3 populations (5 to 7 mo old, 50 seeds each replicate) was investigated in an incubator set at 25 C. The 24-h dark treatment was achieved by wrapping each petri dish in two layers of aluminum foil. The petri dishes of both treatments were only opened after 14 d, and the number of germinated seeds were counted. The experiment was repeated.

Effect of Salt Stress and Osmotic Potential on Germination. Four replicates of 50 seeds (≥8 mo old) each of CT2 and CT3 were used to investigate the effect of salt stress (or osmotic potential) on germination. Salt-stress treatments were applied by using sodium chloride (NaCl) solutions of 0, 20, 40, 80, 160, 250, and 320 mM. This selected range represents the level of salinity occurring in some soils in southern Australia (Chauhan et al. 2006b). Solutions with osmotic potentials of 0, −0.1, −0.2, −0.4, −0.6, −0.8, and −1.0 MPa were prepared by dissolving polyethylene glycol 8000 (BioUltra, 8,000, Sigma-Aldrich, Castle Hill, NSW, Australia) in distilled water as described by Michel (1983). The tests were terminated when no further germination occurred for 7 d. The experiments were repeated.

Seedling Emergence from Different Burial Depths. A pot experiment was conducted by placing seed 0, 1, 2, and 5 cm below the soil surface to assess the impact of seed burial on emergence. Fifty seeds of each population (CT2 and CT3) were placed at a single depth in each pot (15-cm deep by 12-cm diameter) with four replicates. The pots were filled with field soil (clay loam) sieved through a 2-mm-diameter sieve to 1.5 cm below the rim and randomly placed on a bench. The pots were lightly watered as needed to maintain adequate soil moisture. Four pots without seeds were used as controls to check whether there was any contamination of the test soil with seeds of this grass species. There was no emergence of windmillgrass from the control pots during the course of the experiment, confirming that there was no contamination. The number of emerged seedlings was counted after 14 d and was expressed as the percentage of total seed input. The experiment was conducted in a greenhouse with natural light and a temperature of 25 C and was repeated in a growth room set at a 12-h photoperiod at 708 µmol m^{-2} s^{-1} and a temperature of 25 C.

Seedbank Persistence under Field Conditions. A field experiment was conducted at Roseworthy, SA, Australia (34.525252°S, 138.686388°E), to determine seedbank persistence of windmillgrass. The experiment was a split-plot design with main plot treatments (two burial depths at 0 and 5 cm) randomly assigned among the four replicates. Within each main plot, subplots (populations) were randomly assigned. A total of 25 (Experiment 1: July 2013 to July 2014; Experiment 2: August 2014 to September 2015) or 50 (Experiment 3: April 2015 to June 2016) seeds from each population were mixed with soil (clay loam) and placed in a permeable nylon bag (10 by 5 cm). As previously described, there was no contamination of the test soil with windmillgrass seeds.

Seed bags from two burial depths in four replicates were removed at 0, 2, 4, 6, 8, 10, and 12 mo following burial. The exhumed seeds were germinated in an incubator set at 25 C, 12 h photoperiod cycle for 14 d. In addition, seeds of the same populations stored in the lab were germinated at the same time as the seeds exhumed from the field. Seed viability (%) was expressed as germination count of exhumed seeds buried at 0 or 5 cm in the field relative to the maximum germination count (as maximum viability) of seeds stored in the lab during the course of the experiment. The experiment was conducted three times in time and space.

Statistical Analyses. Estimation of Base Temperature. Among several methods used to estimate the minimum temperature thresholds for seed germination, the reciprocal time to 50% of germination has been shown to be the most statistically robust and biologically relevant method (Steinmaus et al. 2000). A logistic function was used to analyze germination response of each replicate (GraphPad Prism v. 6.00, La Jolla, CA):

$$Y = 100/\left\{1 + 10^{[(\log \mathrm{T}_{50} - X) * \mathrm{HillSlope}]}\right\} \qquad [1]$$

where Y is the percentage of cumulative germination, X is the time (h), germination rate (T_{50}) is the time required for the germination of half the total germinated seeds, and HillSlope describes the steepness of the family of curves.

A linear regression was performed with the reciprocal of the T_{50} against incubation temperature. The base temperature (T_b) was estimated as the intercept of the specific regression line with the temperature axis.

The estimated T_b value was used to calculate the growing degree days (GDD) to tillering, panicle emergence, and seed production by the following equation:

$$\mathrm{GDD} = \sum [(\mathrm{T}_{\max} + \mathrm{T}_{\min})/2 - \mathrm{T}_b] \qquad [2]$$

where GDD is degree days (Cd), T_{max} is the daily maximum air temperature, T_{min} is the daily minimum air temperature, and T_b is the estimated base temperature for seed germination of each population.

There was no population by treatment interaction for the plant development (pot study), seed dormancy, and seedbank persistence experiments, so data were pooled across populations. There was no experiment by treatment interaction for the salt-stress experiments, so data were pooled across experiments. There was no experiment and population by treatment interaction for the osmotic potential experiments, so data were pooled across experiments and populations. Logistic models were fit to data of germination at different concentrations of NaCl and different osmotic potentials (GraphPad Prism v. 6.00, La Jolla, CA).

The Shapiro-Wilk test for normality was conducted to investigate the distribution of percentage data. As the percentage data (effect of temperature: G_{max} and effect of light) was not normally distributed ($P < 0.05$), the original percentage values were arcsine transformed before ANOVA analysis. Fisher's protected LSD multiple comparisons were employed to differentiate between predicted means, and means were presented as back-transformed data (GenStat 17, VSN International, Herts, UK).

Results and Discussion

Plant Development in an Irrigated Field and Pots. Under irrigated field conditions, windmillgrass required 272 (21 to 23), 518 to 522 (43 to 45), and 748 to 786 growing degree days (Cd) (74 to 75 d) from seedling emergence to reach tillering, panicle emergence, and mature seed stages, respectively (Table 1). The thermal time to panicle emergence of windmillgrass is similar to that of southern sandbur (*Cenchrus echinatus* L.) in a well-watered environment with 518 Cd (Machado et al. 2014). However, windmillgrass in another study conducted in Merredin, WA, Australia, under greenhouse conditions required a greater thermal

Table 1. Growing degree days and days from emergence to tillering, panicle emergence, and first mature seed of two windmillgrass populations (CT2 and CT3) in an irrigated field (2014).

	Tillering		Panicle emergence		First mature seed	
	Cd	d	Cd	d	Cd	d
CT2	272.3 ± 5.9	22.8 ± 0.8	521.9 ± 6.6	43.3 ± 0.5	786.1 ± 34.0	73.8 ± 2.5
CT3	272.0 ± 10.0	21.0 ± 1.1	518.4 ± 19.7	44.5 ± 1.6	747.5 ± 18.8	75.3 ± 1.8
P[a]	0.978	0.232	0.873	0.471	0.359	0.640

[a] P, probability of *t*-test of null hypothesis that mean ± SE of CT2 is equal to mean ± SE of CT3.

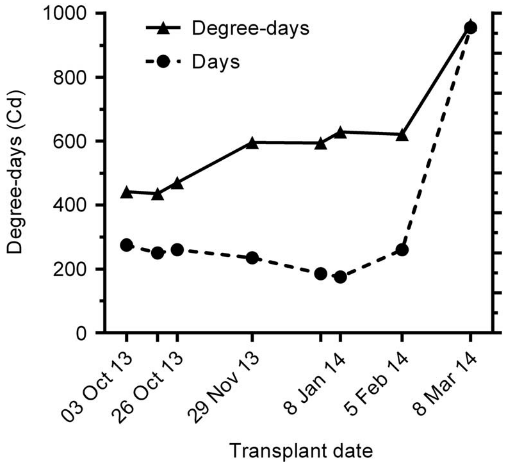

Figure 1. Growing degree days and number of days from 1-leaf stage to panicle emergence of windmillgrass populations at different transplant dates.

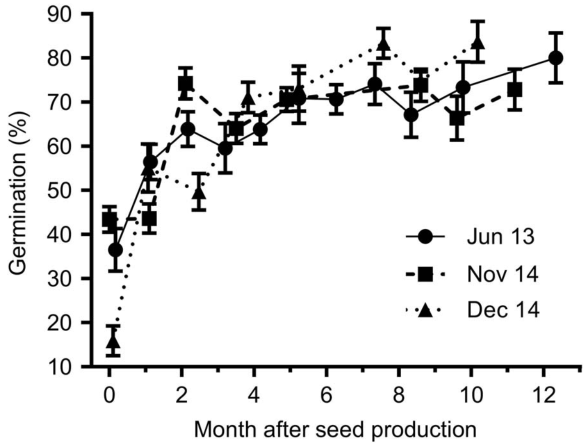

Figure 2. Germination response of CT2 and CT3 populations of windmillgrass from matured seed collected in June 2013, November 2014, and December 2014. Each data point represents the mean of two populations pooled with four replicates. Vertical bars are SE of the mean.

time from emergence to the start of seed production (970 Cd) (Michael et al. 2012b) than did the CT2 and CT3 populations in this study. The observed differences between the two studies may be related to the differences between populations or environments for this parameter.

In the pot studies, the thermal time to panicle emergence increased from 442 Cd for plants transplanted on October 3, 2013, to 629 Cd for plants transplanted on January 8, 2014, whereas the number of days to panicle emergence decreased from 55 to 35 d over this period (Figure 1). However, the thermal time to panicle emergence increased from 621 to 964 Cd for plants transplanted from February 5 to March 8, 2014 with a corresponding increase in days to panicle emergence from 52 to 191 over this period. Plants transplanted on March 8, 2014, when day length was less than 12 h and temperatures were cooler, remained vegetative over the winter and did not produce panicles until September 15, 2014 (the following spring). This indicates that windmillgrass can behave as an annual or a short-lived perennial in South Australia.

Seed Dormancy. Freshly harvested seed had low dormancy, with 16% to 40% germination at the optimum temperature (Figure 2). Lower germination (9%) was observed for freshly harvested seed in a study of windmillgrass in New South Wales, Australia (Lodge and Whalley 1981). In the present study, germination response was not affected by the timing of seed maturity. Seeds that had matured in June 2013, November 2014, and December 2014 had similar germination patterns. Seed required approximately 1 mo after maturity to achieve 43% to 56% germination. Germination reached a maximum (73% to 83%) at 5 to 7 mo after maturity (Figure 2). Other windmillgrass populations in Western Australia and New South Wales, Australia also took more than 6 mo after seed production to achieve a maximum germination of 70% and 80%, respectively (Borger et al. 2011; Maze et al. 1993). These findings indicate that windmillgrass can germinate soon after seed maturity whenever temperature and moisture are suitable, but some seed will not germinate for several months, allowing it to avoid complete depletion of the seedbank in adverse summer conditions.

Table 2. Effect of temperature on germination rate (T_{50}, R^2 from Equation 1) and maximum germination (G_{max}) of CT2 and CT3 populations of windmillgrass under 12 h alternating light/dark conditions.

	CT2[a]			CT3[a]		
Temp	T_{50}	R^2	G_{max}	T_{50}	R^2	G_{max}
C	(h)		(%)	(h)		(%)
10	—	—	5.0 ± 1.0 a	—	—	0.0 ± 0.0 a
15	99.0 ± 2.2 b	0.99	62.0 ± 1.2 cd	228.3 ± 10.1 c	0.97	95.0 ± 1.9 cd
20	52.1 ± 1.9 ab	0.98	67.0 ± 2.5 de	99.2 ± 4.9 b	0.98	98.0 ± 2.0 cd
25	40.4 ± 3.0 a	0.99	70.0 ± 1.2 e	47.3 ± 3.1 a	0.97	99.0 ± 1.0 d
30	27.3 ± 0.6 a	0.98	58.0 ± 3.5 c	45.5 ± 1.3 a	0.99	92.0 ± 3.7 bc
40	49.2 ± 1.8 ab	0.96	13.0 ± 1.0 b	60 ± 0.7 a	0.98	85.0 ± 1.0 b

[a] Values (mean ± SE) within a column followed by different letters are significantly different (Fisher's protected LSD test: $P \leq 0.05$).

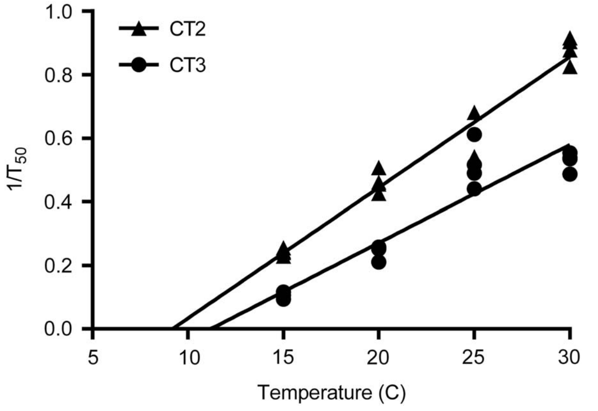

Figure 3. Base temperature (T_b) estimation for windmillgrass seed germination. The lines are: CT2: $Y = 0.041*X - 0.378$ ($R^2 = 0.98$), and CT3: $Y = 0.031*X - 0.344$ ($R^2 = 0.92$). Each data point represents a replicate.

Effect of Temperature on Germination. Windmillgrass seed could germinate across a wide range of temperatures from 10 to 40 C. The optimum temperatures for maximum germination (G_{max}) ranged from 15 to 30 C, with highest G_{max} of 70% (CT2) and 99% (CT3) at 25 C. G_{max} was significantly inhibited to 0% (CT3) and 5% (CT2) at 10 C, and to 13% (CT2) at 40 C (Table 2). This is consistent with previous studies that reported the optimum range for germination of windmillgrass was 15 to 35 C (Lodge and Whalley 1981; Maze et al. 1993; Michael et al. 2012b). Our results also show large variation in the tolerance of some populations (CT3) to germinate under high-temperature conditions (G_{max} of 85% at 40 C) (Table 2).

Windmillgrass germinated more rapidly as temperature increased. The optimum temperatures for both G_{max} and germination rate (T_{50}) of windmillgrass were 25 to 30 C. It required about 27.3 to 45.5 h for 50% germination at 25 to 30 C. (Table 2). By plotting temperature against the inverse of time to 50% germination, the base temperature (T_b) for germination was estimated to be 9.2 to 11.2 C (Figure 3). This estimated T_b value is consistent with previous findings that windmillgrass germination was near zero at 5 to 10 C (Lodge and Whalley 1981; Maze et al. 1993). The estimated T_b value of windmillgrass is similar to that of three other annual summer grass weeds: yellow foxtail [*Setaria pumila* (Poir.) Roemer & J. A. Schultes.], large crabgrass [*Digitaria sanguinalis* (L.) Scop.], and goosegrass [*Eleusine indica* (L.) Gaertn.], with T_b for germination of 8.3, 8.4, and 12.6 C, respectively; however, it is higher than that of green foxtail [*Setaria viridis* (L.) Beauv.], which has a T_b of 6.1 C (Masin et al. 2005). With its rapid germination (T_{50} = 27.3 to 45.5 h) and T_b of 9.2 to 11.2 C, windmillgrass is likely to germinate and emerge under field conditions after rainfall events that would maintain adequate soil moisture for only a few days in spring (6 to 29 C), summer (12 to 34 C), and autumn (9 to 29 C) (Figure 4) in South Australia. Germination in spring would make weed control difficult, as cereal crops are still growing in the fields at this time (Borger et al. 2011).

Effect of Light on Germination. Germination was strongly stimulated by light. In 2014, germination increased from 2% in the dark to 44% to 77% when seeds were exposed to light; and in 2015, germination increased from 0% to 0.5% in the dark to 63% to 83% in the light (Table 3). Maze et al. (1993) also reported that less than 5% of windmillgrass seeds germinated in the dark, while there was more than 80% germination in the light. Light requirement for germination is common among small-seeded species and warm-season grasses (Adkins et al. 2002; Grime et al. 1981; Milberg et al. 2000). Light may stimulate germination by altering the balance of germination promoters and

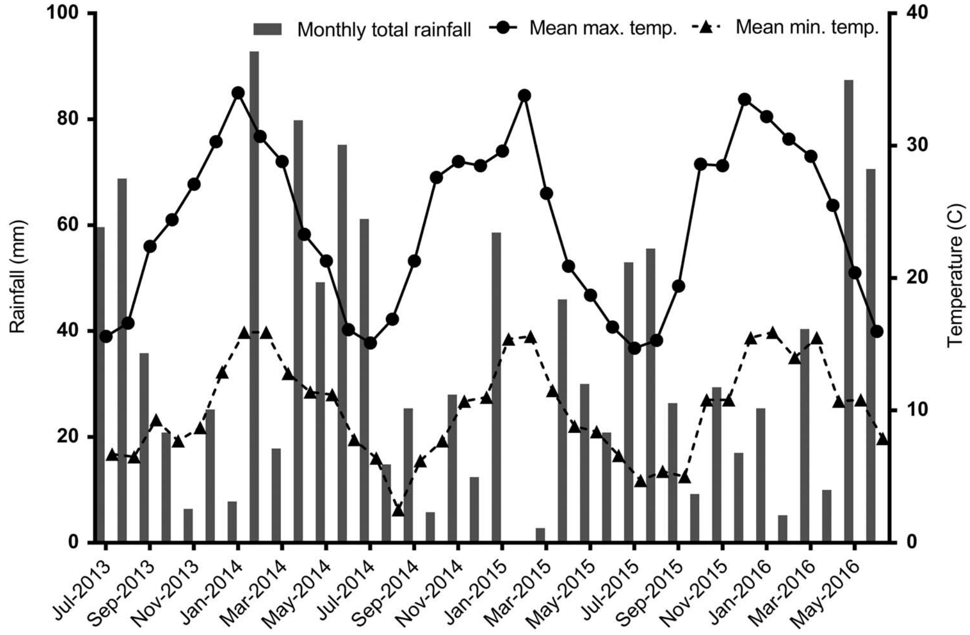

Figure 4. Monthly total rainfall and mean maximum and minimum temperatures from July 2013 to May 2016 at Roseworthy, SA, Australia, the period covered by the field experiments (http://www.bom.gov.au).

Table 3. Effect of light on germination of CT2 and CT3 populations of windmillgrass at 25 C.

		Germination (%)[ab]	
Year	Population	24 h dark	12 h light/dark
2014	CT2	2.0 ± 1.2 a	44.0 ± 3.7 b
	CT3	2.0 ± 1.2 a	77.0 ± 3.0 d
2015	CT2	0.0 ± 0.0 a	63.0 ± 3.6 c
	CT3	0.5 ± 0.5 a	83.7 ± 3.6 e

[a] Values (mean ± SE) followed by different letters are significantly different (Fisher's protected LSD test: $P \leq 0.05$).

inhibitors in the embryo (Adkins et al. 2002). The light requirement can ensure that germination takes place away from other vegetation and only on or near the soil surface (Adkins et al. 2002; Milberg et al. 2000), which would enhance the probability of seedling survival for small-seeded weed species such windmillgrass, which had average seed mass of 0.31 to 0.33 mg $seed^{-1}$ in the present study. Management practices such as tillage (or use of a seed drill at planting time), narrow crop row spacing, and use of cover crops could reduce germination and emergence of windmillgrass under field conditions.

Effect of Salt Stress and Osmotic Potential on Germination. A logistic model was fit to germination response to NaCl concentration ($R^2 = 0.94$ to 0.95). Seed germination was greater than 50% up to a NaCl concentration of 40 mM. The concentration of NaCl required to inhibit germination by 50% was estimated to range from 51 to 73 mM (Figure 5). The NaCl concentration that completely inhibited germination of windmillgrass was 250 mM NaCl, similar to that of annual sowthistle (*Sonchus oleraceus* L.) (Chauhan et al. 2006a) but slightly lower than that of rigid ryegrass in South Australia (*Lolium rigidum* Gaudin), which required 320 mM for complete inhibition of germination (Chauhan et al. 2006b).

A logistic model was fit to the germination response to osmotic potential of the germination medium ($R^2 = 0.95$). Germination was inhibited by 50% at −0.27 MPa and completely at −0.8 MPa (Figure 6). Similarly, the base water potentials for germination of yellow foxtail, green foxtail, and large crabgrass were −0.7, −0.7, and −0.8 MPa, respectively (Masin et al. 2005). This indicates that windmillgrass has a base water potential similar to other summer grass weed species, is not drought tolerant at germination, and will only germinate when there is adequate soil moisture (osmotic potential less than −0.8 MPa).

Seedling Emergence from Different Burial Depths. Seedling emergence was completely inhibited by burial regardless of depth. Emergence of seedlings from seeds on the soil surface was 57.3 ± 5.7% to 69.8 ± 4.3% for CT2 and 66.5 ± 8.5% to 78.4 ± 2.6% for CT3, while seedling emergence was zero for all seeds buried at depths of 0.5, 1, 2, or 5 cm (unpublished data). The

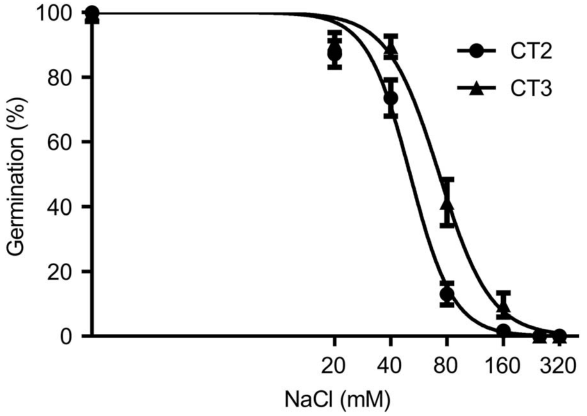

Figure 5. Effect of salt stress (NaCl) on germination of CT2 and CT3 populations of windmillgrass at 25 C and 12-h alternating fluorescent light/dark. Each data point represents the mean of two experiments pooled with four replicates. Vertical bars are SE of the mean. The fitted line represents a logistic response equation: $Y = 100/\{1 + 10^{[(1.704 - X)*- 3.750]}\}$ ($R^2 = 0.95$) for CT2; and $Y = 100/\{1 + 10^{[(1.861 - X)*- 3.150]}\}$ ($R^2 = 0.94$) for CT3.

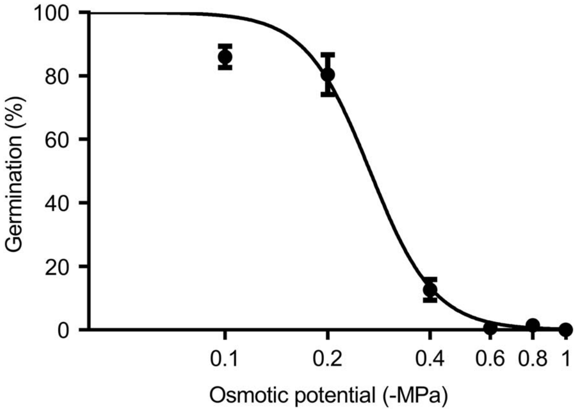

Figure 6. Effect of osmotic potential on germination of pooled populations of windmillgrass (CT2 and CT3) at 25 C and 12-h alternating light/dark. Each data point represents the mean of four replicates from two experiments and two populations pooled. Vertical bars are SE of mean. The fitted line represents a logistic response equation: $Y = 100/\{1 + 10^{[(2.425 - X)* -4.587]}\}$ ($R^2 = 0.95$), where X is log(osmotic potential) in kilopascals.

lack of seedling emergence with burial is consistent with other findings in this study that windmillgrass seed required light for germination (Table 3). Light can penetrate only a few millimeters in soil (Benvenuti 1995; Cussans et al. 1996), so there would be no light to stimulate germination of buried seed; therefore, seedling emergence was not observed, even at the shallowest burial depth (0.5 cm). Tillage that buries seed is likely to inhibit germination, and widespread adoption of no-till cropping in Australia is likely to favor windmillgrass invasion. These results are consistent with a previous study in which all types of tillage treatments reduced emergence of windmillgrass compared with the no-till treatment (Widderick et al. 2014).

Seedbank Persistence under Field Conditions. Under field conditions, seed viability was reduced with time (Figure 7) and was influenced by the amount of summer rainfall received over the 3 yr (Figure 4). In Experiment 1 (July 2013 to July 2014), viability of seeds on the soil surface and at 5-cm depth decreased by 50% after 6 mo, and was completely lost after 12 mo (Figure 7a). Seeds in Experiment 2 (August 2014 to September 2015) initially lost viability faster than those in Experiment 1. After 2 mo, seeds on the soil surface and at 5-cm depth lost 50% of viability in Experiment 2. In this year, viability of buried seed was lost completely after 12 mo, while there was 8% viable seed remaining on the soil surface (Figure 7b). Widderick et al. (2014) also found that less than 1% of windmillgrass seed persisted up to 12 mo after burial at 2 cm and 10 cm in the northern cropping region of Australia. As the windmillgrass seedbank was found to only persist for 12 mo, prevention of seed set in windmillgrass populations with herbicides, tillage, or mowing could deplete their seedbanks rapidly.

Conversely, seedbank persistence in Experiment 3 (April 2015 to June 2016) was much greater than that in Experiment 1 and Experiment 2. Seeds buried at 5 cm in Experiment 3 had greater viability in all assessments than those placed on the soil surface. Viability of seeds exhumed at 8 mo after burial was 70% for those at 5-cm depth as compared with 56% for those on the soil surface. After 14 mo, buried seed still had 37% viability, whereas seed viability on the soil surface was almost completely lost (6% viable seed) (Figure 7c). An extremely dry spring and summer in 2015 to 2016 could have increased seedbank persistence compared with 2013 to 2014 and 2014 to 2015, when significant rainfall events occurred (Figure 4). These differences in seedbank persistence between years could be associated with less seed germination and less seed decay in dry and hot conditions than would occur in wet and warm conditions. Our results show that an adequate surface seedbank can be present in spring to summer (September to February) for seedling recruitment of this weed species in most seasons in southern Australia.

Windmillgrass has several characteristics that enable it to survive and persist in the Mediterranean environment of South Australia. It has rapid germination (27.3 to 45.5 h for 50% germination) and a base temperature of 9.2 to 11.2 C, so it can

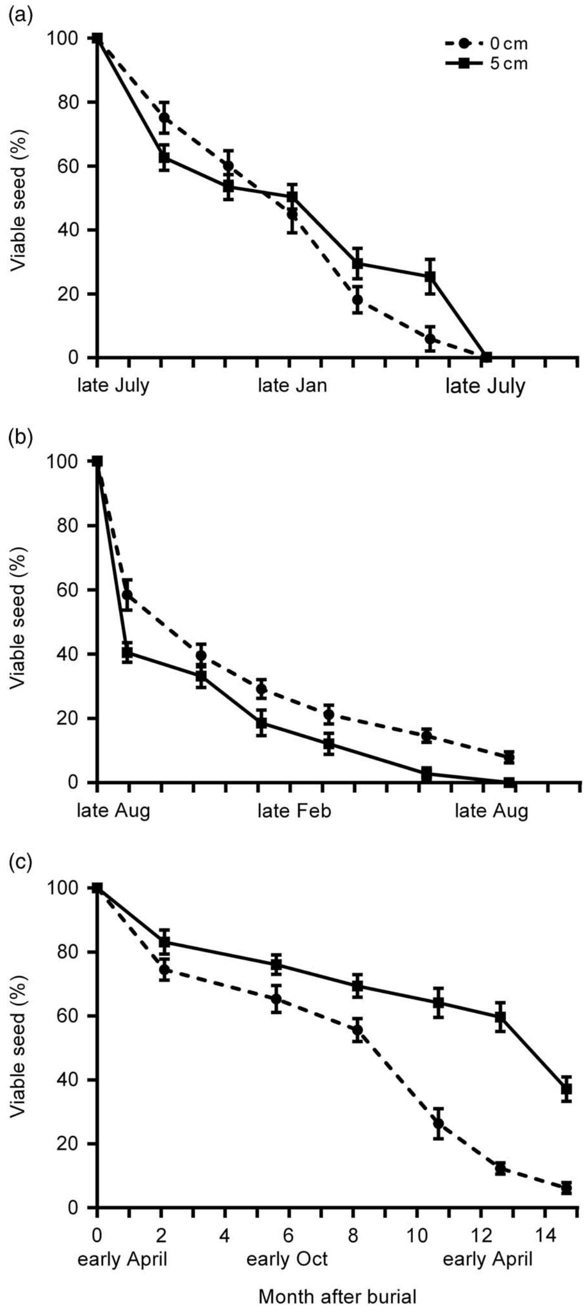

Figure 7. Changes in viability of seeds of CT2 and CT3 populations of windmillgrass at the soil surface compared with seeds at 5-cm burial depth. Experiment 1 (a): July 2013 to July 2014; Experiment 2 (b): August 2014 to September 2015; and Experiment 3 (c): April 2015 to June 2016. Each data point represents the mean of two populations pooled with four replicates. Vertical bars are SE of the mean.

germinate and emerge under field conditions after rainfall events in spring, summer, and autumn in South Australia. It has a short period to maturity, requiring 780 Cd from emergence to mature seed stage. Germination of this small-seeded species required light, so seedling emergence occurred only for seeds present on the soil surface. Seed has low dormancy; however, seeds on the soil surface and buried at 5-cm depth remained viable for more than 11 mo. Low rainfall over spring and summer in the third year of this study extended seedbank persistence beyond 14 mo, especially for the seeds buried at 5-cm depth. These characteristics make this grass species ideally suited to the no-till farming system widely adopted in southern Australia, and it is likely this species will become a problem in such production systems. The demonstration that windmillgrass seeds persist for about 12 mo in an average season offers the opportunity to eradicate this weed species from a field, provided there is no further seed invasion. Control of new seed production for a period of 12 mo or more should exhaust the soil seedbank. Windmillgrass seed requires soil temperatures above 9 C and sufficient moisture to germinate. This allows a focus on periods during the year when seedlings may establish and need to be controlled. Finally, seed germination in windmillgrass has an absolute requirement for light. Therefore, burial to depths greater than 0.5 cm, through strategic inversion tillage, for example, could completely inhibit germination.

Acknowledgments

This research was supported by the Grains Research and Development Corporation (project UA00149) and a Ph.D scholarship from the Vietnam Government and the University of Adelaide.

Literature Cited

Adkins S, Bellairs S, Loch D (2002) Seed dormancy mechanisms in warm season grass species. Euphytica 126:13–20

Baskin CC, Baskin JM (1998). Seeds: Ecology, Biogeography, and Evolution of Dormancy and Germination (2nd edn, Tokyo: Elsevier. 666 p

Batlla D, Benech-Arnold RL (2014) Weed seed germination and the light environment: implications for weed management. Weed Biol Manag 14:77–87

Benvenuti S (1995) Soil light penetration and dormancy of jimsonweed (*Datura stramonium*) seeds. Weed Sci 43:389–393

Bhowmik PC (1997) Weed biology: importance to weed management. Weed Sci 45:349–356

Borger CPD, Riethmuller G, Hashem A (2010) Control of windmill grass over the summer fallow increases wheat yield. Pages 48–51 *in* Zydenbos SM, ed. 17th Australasian Weeds Conference: New Frontiers in New Zealand: Together We Can Beat the Weeds. September 26–30, 2010. Christchurch, New Zealand: New Zealand Plant Protection Society

Borger CPD, Riethmuller GP, Hashem A (2011) Emergence, survival, biomass production, and seed production of *Chloris truncata* (windmill grass) in the Western Australian wheatbelt. Crop Pasture Sci 62:678–685

Boutsalis P, Gill GS, Preston C (2012) Incidence of herbicide resistance in rigid ryegrass (*Lolium rigidum*) across southeastern Australia. Weed Technol 26:391–398

Chachalis D, Reddy KN (2000) Factors affecting *Campsis radicans* seed germination and seedling emergence. Weed Sci 48:212–216

Chauhan BS, Gill G, Preston C (2006a) Factors affecting seed germination of annual sowthistle (*Sonchus oleraceus*) in southern Australia. Weed Sci 54:854–860

Chauhan BS, Gill G, Preston C (2006b) Influence of environmental factors on seed germination and seedling emergence of rigid ryegrass (*Lolium rigidum*). Weed Sci 54:1004–1012

Cousens R, Mortimer M (1995) Dynamics of Weed Populations. Cambridge, UK: Cambridge University Press. 332 p

Cussans G, Raudonius S, Brain P, Cumberworth S (1996) Effects of depth of seed burial and soil aggregate size on seedling emergence of *Alopecurus myosuroides*, *Galium aparine*, *Stellaria media* and wheat. Weed Res 36:133–141

Farley GJ, Bellairs SM, Adkins SW (2013) Germination of selected Australian native grass species, with potential for minesite rehabilitation. Aust J Bot 61:283–290

Grime J, Mason G, Curtis A, Rodman J, Band S (1981) A comparative study of germination characteristics in a local flora. J Ecol 69:1017–1059

Kleemann SGL, Preston C, Gill GS (2016) Influence of management on long-term seedbank dynamics of rigid ryegrass (*Lolium rigidum*) in cropping systems of southern Australia. Weed Sci 64:303–311

Kloot PM (1985) The spread of native Australian plants as weeds in South Australia and in other Mediterranean regions. J Adel Bot Gard 7:145–157

Koger CH, Reddy KN, Poston DH (2004) Factors affecting seed germination, seedling emergence, and survival of texasweed (*Caperonia palustris*). Weed Sci 52:989–995

Llewellyn R, 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. Kingston, ACT, Australia: Grains Research and Development Corporation (GRDC). 112 p

Lodge G, Whalley R (1981) Establishment of warm- and cool-season native perennial grasses on the north-west slopes of New South Wales. I. dormancy and germination. Aust J Bot 29:111–119

Machado ECR, Lima RSO, Silva APP, Marques BS, Goncalves MF, Carvalho SJP (2014) Initial growth and development of southern sandbur based on thermal units. Planta Daninha 32:335–343

Malone J, Cook A, Wu H, Hashem A, Preston C (2012) Management of glyphosate resistant weeds in non-agricultural areas. Developing solutions to evolving weed problems. 18th Australasian Weeds Conference. October 8–11, 2012. Melbourne, VIC, Australia

Masin R, Zuin MC, Archer DW, Forcella F, Zanin G (2005) Weedturf: a predictive model to aid control of annual summer weeds in turf. Weed Sci 53:193–201

Matthews J (1994) Management of herbicide resistant weed populations. Pages 317–335 *in* Powles S & Holtum J eds, Herbicide Resistance in Plants: Biology and Biochemistry. Boca Raton, FL: CRC

Maze KM, Koen TB, Watt LA (1993) Factors influencing the germination of six perennial grasses of central New South Wales. Aust J Bot 41:79–90

Mennan H, Ngouajio M (2006) Seasonal cycles in germination and seedling emergence of summer and winter populations of catchweed bedstraw (*Galium aparine*) and wild mustard (*Brassica kaber*). Weed Sci 54:114–120

Michael PJ, Borger CP, MacLeod WJ, Payne PL (2010a) Occurrence of summer fallow weeds within the grain belt region of southwestern Australia. Weed Technol 24:562–568

Michael PJ, Yeoh PB, Scott JK (2010b) Potential climate change impacts on agricultural weeds in the northern agricultural region of Western Australia. Pages 74–75 *in* Zydenbos SM, ed. 17th Australasian Weeds Conference: New Frontiers in New Zealand: Together We Can Beat the Weeds. September 26–30, 2010. Christchurch, New Zealand: New Zealand Plant Protection Society

Michael PJ, Yeoh PB, Scott JK (2012a) The current and future projected distribution of *Solanum hoplopetalum* (Solanaceae): an indigenous weed of the south-western Australian grain belt. Aust J Bot 60:128–135

Michael PJ, Yeoh PB, Scott JK (2012b) Potential distribution of the Australian native *Chloris truncata* based on modelling both the successful and failed global introductions. PLoS One 7:e42140

Michel BE (1983) Evaluation of the water potentials of solutions of polyethylene glycol 8000 both in the absence and presence of other solutes. Plant Physiol 72:66–70

Milberg P, Andersson L, Thompson K (2000) Large-seeded spices are less dependent on light for germination than small-seeded ones. Seed Sci Res 10:99–104

Mitchell M (1994) Native Grasses: An Identification Handbook for Temperate Australia. Collingwood, VIC, Australia: Landlinks. 41 p

Nightingale ME, Lazarides M, Weiller CM (2005) Flora of Australia Vol. 44B, Poaceae 3, Melbourne: ABRS/CSIRO

Osten V, Hashem A, Koetz E, Lemerle D, Pathan S, Wright G (2006) Impacts of summer fallow weeds on soil nitrogen and wheat in the southern, western and northern Australian grain regions. Pages 395–398 *in* Preston C, Watts JH, Crossman ND, eds. 15th Australian Weeds Conference: Managing Weeds in a Changing Climate. Adelaide, SA, Australia: Weed Management Society of South Australia

Preston C (2016) Glyphosate Resistant Weeds in Australia. http://glyphosateresistance.org.au/register_summary.html. Accessed: October 20, 2016

Saatkamp A, Affre L, Dutoit T, Poschlod P (2009) The seed bank longevity index revisited: limited reliability evident from a burial experiment and database analyses. Ann Bot 104: 715–724

Schutte B, Tomasek B, Davis A, Andersson L, Benoit D, Cirujeda A, Dekker J, Forcella F, Gonzalez-Andujar J, Graziani F (2014) An investigation to enhance understanding of the stimulation of weed seedling emergence by soil disturbance. Weed Res 54:1–12

Simpson GM (1990) The occurrence of dormancy in the Gramineae (Pages 3–59 in Seed Dormancy in Grasses, New York: Cambridge University Press

Steinmaus SJ, Prather TS, Holt JS (2000) Estimation of base temperatures for nine weed species. J Exp Bot 51:275–286

Werth J, Boucher L, Thornby D, Walker S, Charles G (2013) Changes in weed species since the introduction of glyphosate-resistant cotton. Crop Pasture Sci 64:791–798

Widderick M, Cook T, McLean A, Churchett J, Keenan M, Miller B, Davidson B (2014) Improved management of key northern region weeds: diverse problems, diverse solutions. Pages 312–315 *in* Baker M, ed. 19th Australasian Weeds Conference: Science, Community and Food Security: The Weed Challenge. Hobart, TAS, Australia: Tasmanian Weed Society

Received November 21, 2016, and approved February 19, 2017.

Associate Editor for this paper: J. Anita Dille, Kansas State University.