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Growth, Development, and Seed Biology of Feather Fingergrass (*Chloris virgata*) in Southern Australia

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Feather fingergrass is a major weed in agricultural systems in northern Australia and has now spread to southern Australia. To better understand the biology of this emerging weed species, its growth, development, and seed biology were examined. Under field conditions in South Australia, seedlings that emerged after summer rainfall events required 1,200 growing degree days from emergence to mature seed production and produced 700 g m^{-2} shoot biomass. Plants produced up to 1,000 seeds $panicle^{-1}$ and more than 40,000 seeds $plant^{-1}$, with seed weight ranging from 0.36 to 0.46 mg. Harvested seeds were dormant for a period of about 2 mo and required 5 mo of after-ripening to reach 50% germination. Freshly harvested seed could be released from dormancy by pretreatment with 564 mM sodium hypochlorite for 30 min. Light significantly increased germination. Seed could germinate over a wide temperature range (10 to 40 C), with maximum germination at 15 to 25 C. At 20 to 25 C, 50% germination was reached within 2.7 to 3.3 d, and the predicted base temperature to germinate was 2.1 to 3.0 C. The osmotic potential and NaCl concentration required to inhibit germination by 50% were −0.16 to −0.20 MPa and 90 to 124 mM, respectively. Seedling emergence was highest (76%) for seeds present on soil surface and was significantly reduced by burial at 1 (57%), 2 (49%), and 5 cm (9%). Under field conditions, seeds buried in the soil persisted longer than those left on the soil surface, and low spring–summer rainfall increased seed persistence. This study provides important information on growth, development, and seed biology of feather fingergrass that will contribute to the development of a more effective management program for this weed species in Australia.

Nomenclature: Feather fingergrass, *Chloris virgata* Sw.

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

Feather fingergrass is a warm-season, C_4, annual grass that is widely distributed globally. It generally grows throughout tropical, subtropical, and warm temperate regions, extending well into temperate regions in areas where hot summers are typical (Anderson 1974). In Australia, this grass has been a major weed in cotton (*Gossypium hirsutum* L.) and grain crops in the subtropical region for many years (Werth et al. 2013). In a survey of the northern subtropical grain region of Australia in 2008 and 2010, feather fingergrass was ranked in the top 20 weeds, and it would be expected to further increase in dominance in a glyphosate-based system (Werth et al. 2013). It was the third most common weed found (50% of paddocks) in a summer fallow survey in 2012 (Widderick et al. 2014). This grass was a weed of vineyards and orchards in the state of South Australia and in parts of the grain region in the state of Western Australia (Osten 2012). More recently, this species has been ranked in the top 10 (national ranking) and top four (northern regional ranking) residual weeds in all crops in Australia (Llewellyn et al. 2016). Overreliance on glyphosate in reduced tillage systems has favored feather fingergrass, which tends to have a higher level of tolerance to this herbicide relative to other weeds present in the region (Werth et al. 2013; Widderick et al. 2014).

The timing of germination and emergence is critical for the survival of annual plants (Saatkamp et al. 2009), with temperature and light among the most important environmental signals that regulate germination and emergence of a plant species (Baskin and Baskin 1998; Schutte et al. 2014). For seeds in the soil, temperature and light are important cues for initiating germination by providing a sense of their position in the soil profile and the occurrence of soil disturbance (Batlla and Benech-Arnold 2014). There have been several studies of the effect of temperature on seed germination of feather fingergrass in China, Qatar, and Australia (Bhatt et al. 2016; Fernando et al. 2016; Zhang et al. 2012, 2015). However, there

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is currently no information on the base temperature required for germination in Australia.

Seed germination, a process regulated by several environmental factors such as moisture and soil salinity, is a key event determining the success of a weed in an agroecosystem (Chachalis and Reddy 2000; Koger et al. 2004). Seeds that respond to environmental conditions and alter their germination behavior are more likely to survive and successfully establish themselves. The influence of seed age on dormancy release and the effect of burial depth on germination of feather fingergrass in southern Australia is poorly understood. The effect of osmotic stress (Fernando et al. 2016) and salinity (Fernando et al. 2016; Zhang et al. 2012) on germination of feather fingergrass was studied in China and Queensland, Australia. In China, this grass is considered as a halophyte (salt-tolerant) species and as a potentially useful grass species for saline areas (Zhang et al. 2012).

To effectively manage a weed, an understanding of its basic biology is critical. This includes germination conditions, dormancy, seedbank dynamics, growth, and development (Bhowmik 1997; Cousens and Mortimer 1995; Mennan and Ngouajio 2006). An understanding of the particular seed-dormancy mechanisms involved is vital 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 capability to germinate, but dormancy is due to the embryo-covering structures. The mechanisms within the covering structures may involve permeability (preventing water uptake or gaseous exchange) and mechanical (preventing embryo expansion) and chemical barriers to germination (Adkins et al. 2002). It is also important to manage the soil seedbank of weed populations that have developed herbicide resistance (Kleemann et al. 2016) or other difficult to manage weeds. Persistence of the soil seedbank determines the length of time management strategies are required to reduce the population to minimal levels (Matthews 1994). Preliminary reports showed that feather fingergrass seed had short field persistence (10 to 12 mo) in the northern cropping region of Australia (Osten 2012; Widderick et al. 2014). However, seedbank persistence in cooler Mediterranean conditions of the southern and western grain regions of Australia has not been reported.

Most seed biology studies on feather fingergrass so far have been undertaken in China, India, Qatar, Honduras (Bhatt et al. 2016; Li et al. 2006; Zelaya et al. 1997), and northern Australia (Fernando et al. 2016). There is little information on growth, development, and seed biology of feather fingergrass in southern Australia. Therefore, the objectives of this study were to determine (1) growth and development under field conditions, particularly time required to reach flowering and seed production; (2) seed dormancy and mechanism; (3) effect of physical environmental factors (temperature, light, osmotic stress, salt stress, and burial depth) on seed germination and seedling emergence; and (4) seedbank persistence under field conditions.

Materials and Methods

Seed Sources. Mature seeds of feather fingergrass populations were collected from Monash (namely *Chloris virgata* (CV) 1 in June 2013), Hectorville (CV4 in June 2013), Mildura (CV5 in March 2013), and Vintners (CV14 in April 2014) in South Australia; and Emerald (CV12 in January 2011) in Queensland, Australia. Harvested seeds were cleaned and stored in paper bags at room temperature (~20 C). Seeds of these populations were collected from plants grown at a common site (Waite Campus, University of Adelaide, South Australia, Australia), and this seed was used for further studies.

Growth, Development, Seedling Emergence, and Survival

Growth and Development under Irrigated and Rainfed Conditions. A total of 200 seeds each of CV5 and CV12 were sown on January 24, 2014, in 1 m^2 plots with four replicates in randomized complete blocks in a field at Roseworthy, South Australia (−34.524807, 138.686362). The field soil was a clay loam. Before this experiment was conducted, feather fingergrass 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. The time taken to reach tillering, panicle emergence and seed production, and panicle number per plant and square meter were recorded. Four panicles of each population were sampled from each replicate and dried at 25 C for 4 wk to calculate seed weight (g 100 $seeds^{-1}$) and number of seeds per panicle and square meter. Shoot biomass at flowering was determined from a quadrat (0.5 by 1 m) with each of four replicates, dried in an oven at 70 C for 48 h. Remaining plants were allowed to mature and set seed from April to June 2014. Naturally shed seed germinated after rainfall on November 21 to November 23, 2014, and

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January 8 to January 13, 2015. Time taken to reach tillering, panicle emergence, and seed production were determined.

Seedling Emergence and Survival. Field plots with seeds produced from April to June 2014 were used to examine seedling emergence and survival. Four quadrats (0.3 by 0.3 m) were established in the field to investigate the mortality of seedlings that emerged after the rainfall events from January 8 to January 13, 2015 in both low-density (fewer than 1,700 seedlings m^{-2}) and high density (more than 6,200 seedlings m^{-2}) areas of the field. The mortality data were recorded every 2 wk until panicle emergence.

General Germination Test Protocols. Germination was evaluated by evenly placing 25 (or 50) seeds of each population in a 15-cm-diameter petri dish containing two layers of Whatman No. 1 filter paper and moistened with 9 ml of distilled water or a treatment solution (gibberellic acid, polyethylene glycol, and salt). There were four replicates of each population of each treatment. Dishes were sealed within parafilm and placed in an incubator set at 25 C, the temperature previously determined to be in the optimum range for germination of feather fingergrass (Bhatt et al. 2016; Zhang et al. 2012, 2015). The photoperiod was set at 12 h with fluorescent lamps used to produce light intensity of 43 μmol m^{-2} s^{-1}. Seed germination was determined under 12 h alternating light/dark conditions, and germinated seeds (emerged coleoptile, radical >5 mm long) were counted every 2 d for 14 d.

Seed Dormancy. Germination tests began soon after harvest and were repeated at approximately monthly intervals for 11 mo. Previous research had shown that a tetrazolium viability test was ineffective in a closely related small-seeded species, windmill grass (*Chloris truncata* R. Br.) (Farley et al. 2013), which could be due to small seed size and dark seed color. Therefore, maximum germination at 25 C during the after-ripening period was used as the indicator of seed viability. The experiment was conducted with original field-collected seeds of CV1 and CV4 (25 seeds per replicate). As feather fingergrass can produce seeds over several weeks, the experiment was also conducted with freshly harvested seeds of CV1 and CV4 (50 seeds per replicate) grown at the Waite Campus, University of Adelaide, South Australia, Australia, to determine the influence of the timing of seed maturity on the expression of seed dormancy. Seeds that matured in February, March, and April 2015 were collected and stored, and germination was assessed using the general germination test.

Seed Germination with a Pretreatment of NaOCl. Preliminary experiments were conducted to determine a suitable treatment time (30 min) for fresh seed in 564 mM sodium hypochlorite (NaOCl) (White King Premium Bleach; Pental Products, Victoria, Australia). Four replicates of 50 seeds each were used in four different treatments to break dormancy: (1) incubation in 300 ml of 564 mM NaOCl for 30 min followed by rinsing for 30 min in running water and incubation in water; (2) incubation in 300 ml of 564 mM NaOCl for 30 min followed by rinsing for 30 min in running water and incubation in 0.5 mM gibberellic acid (GA_3); (3) incubation in 0.5 mM GA_3; and (4) incubation in water. Freshly harvested seeds of CV12 were used for this experiment, and the experiment was conducted three times with 15-, 30-, and 45-d-old seeds.

Effect of Temperature on Germination. Nondormant (12-mo-old) seeds (25) of each replicate of CV4 and CV5 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 for the estimation of base temperature. Germination tests were terminated when no further germination occurred for 7 d, and 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 nondormant (more than 7 mo old, 50 seeds per replicate) seeds of CV4 and CV5 was examined. 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 conducted twice.

Effect of Osmotic Stress on Germination. Four replicates of 50 nondormant (12-mo-old) seeds each of CV4 and CV5 were used to investigate the effect of osmotic stress on germination. 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 8,000 (BioUltra, 8,000; Sigma-Aldrich Pty. Ltd., Castle Hill, NSW, Australia) in distilled water as described by Michel (1983). The tests were terminated

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when no further germination occurred for 7 d. The experiment was conducted twice.

Effect of Salt Stress on Germination. Salt-stress treatments were applied by using sodium chloride (NaCl) solutions of 0, 20, 40, 80, 160, 250, 320, and 500 mM. This range represents the level of salinity occurring in some soils in southern Australia (Chauhan et al. 2006). Seed source and other methods were similar to those described in "Effect of Osmotic Stress on Germination."

Seedling Emergence from Different Burial Depths. The pot experiment was conducted by placing seed at 0, 1, 2, and 5 cm below the soil surface to assess the impact of seed burial on emergence. Four replicates of 50 seeds (CV4 and CV5) each were placed at the selected depths in pots (15-cm deep by 12-cm diameter). The pots were filled with field soil (clay loam) 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 feather fingergrass seeds in the test soil. The number of emerged seedlings were counted after 2 wk and were expressed as the percentage of total seed input. The experiment was conducted twice: in a glasshouse with natural light and temperature of 25 C and in a growth room set at 12 h photoperiod at 708 μmol m^{-2} s^{-1} and temperature of 25 C.

Seedbank Persistence under Field Conditions. A split-plot design was used for this field experiment at Roseworthy, South Australia, Australia. Main plot treatments (seeds at the soil surface or buried at 5-cm depth) were randomly assigned among the four replicates. Within each main plot, subplots (populations) were randomly assigned. A total of 25 (or 50) seeds from each population (at least 7 mo old) were mixed with soil and placed in a permeable nylon bag (10 by 5 cm).

Seed packages were removed at 0, 2, 4, 6, 8, 10, and 12 mo, and seeds were germinated in an incubator for 14 d. In addition, seeds of the same populations stored in the lab were germinated at the same time as the seeds removed from the field. Seed viability (%) was expressed as germination count of seeds removed from 0 or 5 cm in the field relative to the maximum germination count (as maximum viability) of seeds stored in the lab. The experiment was conducted three times in late July 2013 with CV5, in late August 2014 with CV5 and CV14 (25 seeds per replicate), and in early April 2015 with CV1 and CV4 (50 seeds per replicate).

Statistical Analyses

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

$$Y = 100/\left\{1+10\hat{}\left[\left(\log T_{50}-X\right)^{*}\text{HillSlope}\right]\right\} \quad [1]$$

where Y is the percentage of cumulative germination, X is the time (in hours), 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 germination rates of the four replicates against incubation temperature. The base temperature (T_b) was estimated as the intercept of the specific regression line with the temperature axis. As G_{max} of both CV4 and CV5 decreased by more than 50% at 40 C as compared with the optimum temperature, the T_{50} value of this temperature was excluded from the estimation of T_b.

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:

$$\text{GDD}(\text{degree days, Cd}) = \sum\left[\left(T_{max}+T_{min}\right)/2-T_b\right] \quad [2]$$

where Cd is degree days, T_{max} is the daily maximum air temperature, T_{min} is the daily minimum air temperature, and T_b is the base temperature.

As there was no experiment (or population) by treatment interaction, data from two experiments (osmotic and salt stress), two experiments and two populations (burial depth), and two populations (seedbank persistence) were combined for analysis.

Exponential models (one-phase decay) were selected as the best fit for survival of emerged seedlings, germination at different concentrations of osmotic potential, and changes in viable seeds (seedbank persistence). A logistic function provided the best fit for germination of seeds after harvest (dormancy) and germination at different concentrations of NaCl.

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Table 1. Growth and development under field conditions.

			Thermal time and days from emergence to:[a]					
			Tillering		Panicle emergence		First mature seed	
Condition	Emergence date	Population	Cd	d	Cd	d	Cd	d
Irrigated	January 24, 2014	CV5	261 ± 37ab	12 ± 1.3a	816 ± 61a	45 ± 2.3a	1,145 ± 63a	67 ± 2.4a
		CV12	309 ± 9bc	14 ± 0.3a	1,000 ± 33b	57 ± 1.5b	1,256 ± 33a	77 ± 1.5b
Rainfed	November 23, 2014	CV5	247 ± 29a	14 ± 1.9a	1,741 ± 31c	96 ± 1.7c	2,095 ± 19b	118 ± 1.4c
	January 10, 2015	CV12	330 ± 30c	19 ± 3.2a	1,813 ± 33c	117 ± 3.5d	—	—

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

The Shapiro-Wilk test for normality was used to examine the residuals of the original percentage data. If the residuals failed to meet the assumptions ($P < 0.05$), the original percentage values (response to NaOCl, effect of light) were arcsine transformed before ANOVA. Otherwise, the original percentage values (effect of temperature: G_{max}) were used for ANOVA. 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

Growth, Development, Seedling Emergence, and Survival

Growth and Development. Under field conditions, it took 260 to 330 degree days (12 to 19 d) from seedling emergence to tillering, and this value was similar for both irrigated and rainfed environments. Plants growing under irrigated conditions required 816 to 1,000 Cd and 1,145 to 1,256 Cd to reach panicle and seed maturity stages, respectively (Table 1). This thermal time to panicle emergence of feather fingergrass is similar to that of shattercane [*Sorghum bicolor* (L.) Moench ssp. *arundinaceum* (Desv.) de Wet & Harlan] in a well-watered environment with 861 to 1,126 Cd (Donatelli et al. 1992), but is much greater than that of southern sandbur (*Cenchrus echinatus* L.) with 518 Cd (Machado et al. 2014). However, almost double the thermal time was required to reach the panicle (1,740 to 1,810 Cd) and seed maturity (2,095 Cd) stages in rainfed compared with irrigated conditions (Table 1). This delay in plant development under rainfed conditions may be associated with water stress due to extremely low rainfall over the summer months in 2014 to 2015 (Figure 1). A previous study also found that the thermal time to flowering in shattercane increased with an increase in water

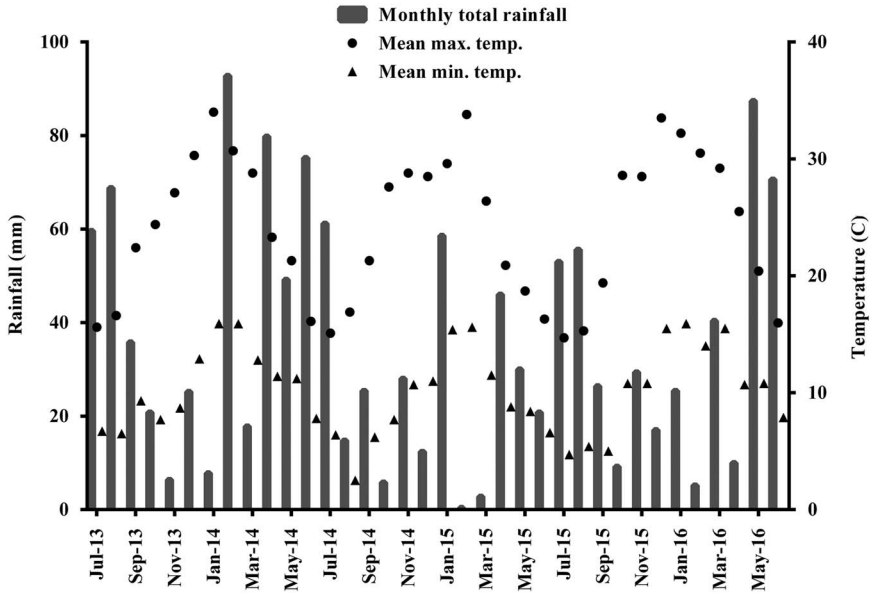

Figure 1. Monthly total rainfall and mean maximum and minimum temperatures from July 2013 to May 2016 at Roseworthy, South Australia, Australia (http://www.bom.gov.au).

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Table 2. Biomass, panicle density, and seed production in an irrigated field.

Population	Biomass	Panicle plant^{-1}	Seed panicle^{-1}	Seed m^{-2}	Seed weight
	g m^{-2}	panicle	seed	1,000 seed	mg
CV5	619 ± 53	37.4 ± 6.6	1,071 ± 64	573 ± 43	0.360 ± 0.017
CV12	730 ± 89	42.7 ± 6.7	1,244 ± 72	468 ± 120	0.455 ± 0.020
P[a]	0.223	0.425	0.090	0.202	0.009

[a] P: probability of *t*-test of null hypothesis that mean ± SE of CV5 is equal to mean ± SE of CV12.

stress when transpiration was reduced to 0.5 or less of that in irrigated controls (Donatelli et al. 1992). The delay in flowering due to severe drought stress could be a result of abscisic acid accumulation under water deficit (Blum 1996).

Under irrigation, feather fingergrass produced 468,000 to 573,000 seeds m^{-2}, with an average seed weight of 0.4 to 0.5 mg (67 to 77 d after sowing) and 619 to 730 g of dry biomass m^{-2} (89 d after sowing) (Table 2). The mean seed weight obtained was lower than that reported (0.63 mg) in north-eastern China (Zhang et al. 2015). The dry biomass and seed production values of feather fingergrass were much higher than those of naturally occurring windmill grass (146 g m^{-2} and 61,000 seeds m^{-2}) in Merredin, Western Australia (Borger et al. 2011). If these large amounts of feather fingergrass seeds were dispersed into cropping fields and successfully established, this summer weed would reduce the potential yield of winter crops by utilizing moisture and nutrients that would otherwise be available to the crop and would delay sowing due to the time needed for weed control in the autumn (Osten et al. 2006).

Seedling Emergence and Survival. Large numbers of seedlings emerged after the rainfall events from January 8 to January 13, 2015, and seedling survival of this cohort was investigated. Exponential (one-phase decay) models fitted well to seedling density over time in both low- and high-density plots (Figure 2). At 10 d after seedling emergence started, seedling density in the high-density plots was 3.6-fold higher than those in the low-density area. Seedling density decreased rapidly by 50% in both low- and high-density plots at 10 to 12 d (half-life) after emergence. Self-thinning of seedlings reduced the difference between the high- and low-density patches with time, particularly beyond 50 d after emergence (Figure 2). This self-thinning is likely to be mainly due to drought stress, as there was little rain from February to March 2015 (Figure 1). Drought was also the major cause of mortality in seedling populations of 20 other species establishing under natural conditions (Moles and Westoby 2004). The self-thinning of feather fingergrass in this study provides additional evidence for the operation of density-dependent population regulation in plants (Weller 1987; Yoda et al. 1963). Plants that survived until April 5, 2015, received rainfall from April 6 to April 27, 2015 with a total of 45.6 mm (Figure 1), which allowed them to produce seeds. Results of this study provide evidence for the adaptation of feather fingergrass to the dry summer conditions of South Australia, where despite these conditions, plants were able to emerge, survive, and produce a large amount of seed to complete their life cycles.

Seed Dormancy. Germination response to time after harvest fitted well to a logistic model (R^2 = 0.90 to 0.98). Under room storage conditions, freshly harvested seeds did not germinate until they had after-ripened for about 2 mo (Figure 3). The dormancy pattern was not affected by the times of seed maturation. Seeds that had matured in February, March, and April 2015 had very similar

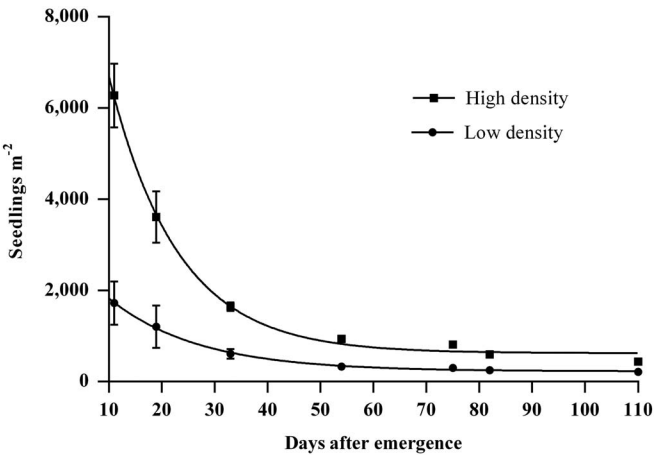

Figure 2. Survival of seedlings following rainfall January 8 – 13, 2015. The fitted lines represent one-phase decay exponential model: $Y = 2891.2*\exp(-0.05805*X) + 225.8$ ($R^2 = 0.59$) for low-density; and $Y = 13188.7*\exp(-0.07738*X) + 623.3$ ($R^2 = 0.92$) for high-density plots. Each data point represents the mean of four replicates, and the vertical bars are SE of the mean.

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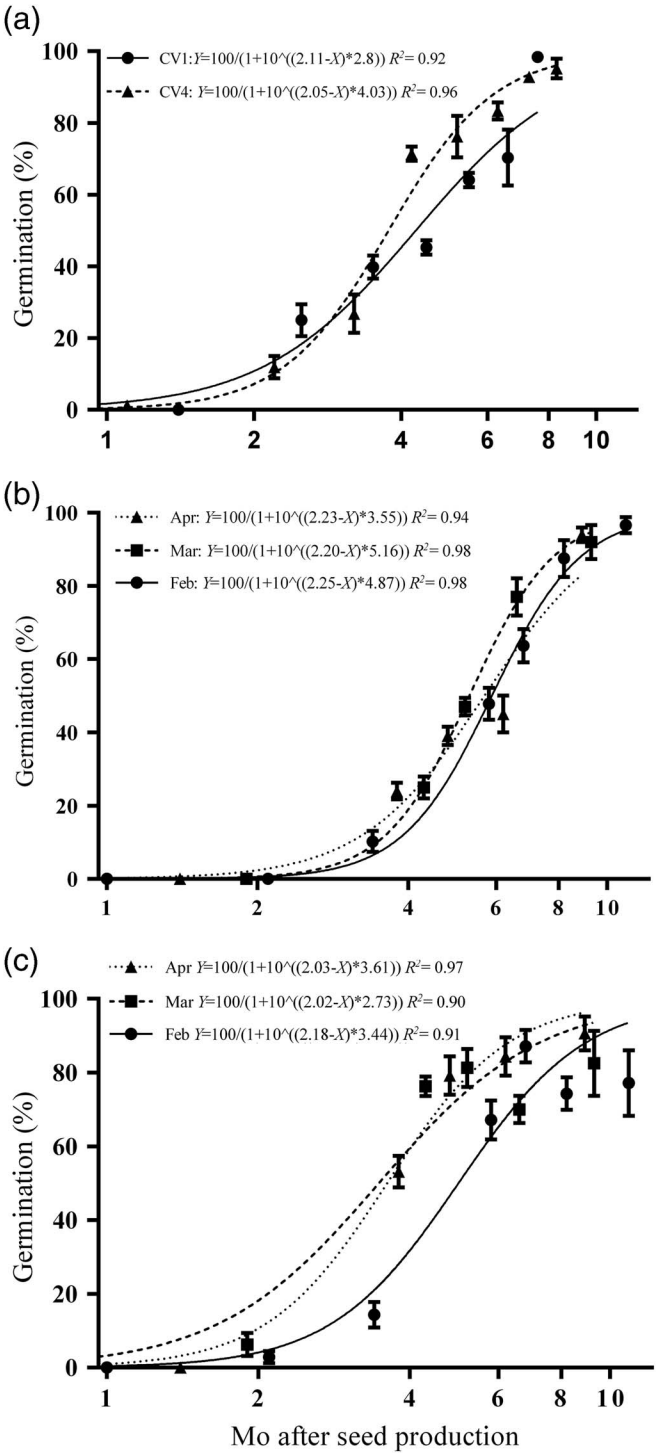

Figure 3. Dormancy pattern of CV1 and CV4 collected in June 2013 (a); CV1 (b) and CV4 (c) matured in February, March, and April 2015. Each data point represents the mean of four replicates, and the vertical bars are SE of the mean.

dormancy patterns (Figure 3b and c). Germination of fresh seed was nil. Seeds required about 5 mo after maturity to achieve more than 50% germination. Germination reached a maximum at 8 to 9 mo after maturity (Figure 3). Feather fingergrass in Central Queensland also required an after-ripening period of 6 to 10 wk to germinate (Osten 2012); however, 39%, 50%, and 98% of fresh seeds collected in Honduras, Qatar, and northern China, respectively, could germinate (Bhatt et al. 2016; Li et al. 2006; Zelaya et al. 1997). The differences in level of dormancy among studies may be due to the wide geographic and climatic range of this species, which could have selected for different levels of dormancy and dormancy mechanisms in different regions (Loch et al. 2004).

Response of Dormant Seeds to NaOCl. Germination of fresh dormant seeds was significantly ($P \leq 0.01$) increased by treatment with NaOCl. NaOCl increased germination of fresh seeds (15, 30, and 45 d old) by 10-fold, whereas GA_3 alone could not overcome the dormancy in feather fingergrass. Furthermore, treatment with NaOCl followed by GA_3 did not increase seed germination as compared with NaOCl alone (Table 3). Hsiao and Quick suggested two major roles for NaOCl in the termination of dormancy (Hsiao 1979, 1980; Hsiao and Quick 1984). First, NaOCl may modify the properties of the hull and seed coat membranes in such a way as to increase water uptake by the embryo, leading to the release from dormancy. Second, NaOCl could act as oxidant on vital pregermination processes within the caryopsis. The prevention of water uptake is not a common dormancy mechanism found in grass species. However, the capacity for gaseous exchange might be limited by the tissues surrounding the embryo (Adkins et al. 2002). The dormancy mechanism of feather fingergrass in this study could be based on embryo-covering structures of the seed.

Effect of Temperature on Germination. 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 (unpublished data). Based on G_{max}, germination was significantly inhibited at 40 C. Previously, it was reported that feather fingergrass could germinate across temperatures of 5 to 40 C (Zhang et al. 2012, 2015), and germination was similar among three temperature regimes 15/25, 20/30, and 25/35 C (Bhatt et al. 2016).

Seed germinated faster as temperature increased (Figure 4). The optimum temperatures for both G_{max} and germination rate (T_{50}) were 20 to 25 C. It required about 2.7 to 3.3 d for 50% germination at 20 to 25 C. Our results are consistent with previous studies in China, which reported 1 to 3 d to reach

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Table 3. Germination response of freshly harvested seeds to NaOCl and GA_3 treatments.

Treatment	Germination (%) of seeds of different age[a]		
	15 d	30 d	45 d
H_2O	5.0 ± 1.3a	4.0 ± 1.4a	4.5 ± 2.5a
0.5 mM GA_3	6.5 ± 3.3a	10.5 ± 2.2a	4.0 ± 1.4a
564 mM NaOCl for 30 min → H_2O	54.0 ± 3.6b	56.5 ± 5.7b	74.5 ± 5.7b
564 mM NaOCl for 30 min → 0.5 mM GA_3	61.5 ± 4.6b	48.5 ± 1.5b	67.5 ± 2.2b

[a] Values (mean ± SE) within a column followed by different letters are significantly different (Fisher's protected LSD test: $P \leq 0.01$).

half of the maximum germination (Li et al. 2006; Liu et al. 2003).

By plotting temperature against the inverse of time to 50% germination, the base temperature (T_b) for germination was estimated to be 2.1 to 3.0 C (Figure 5). This estimate of T_b is consistent with the findings of Zhang et al. (2015), who reported that more than 80% of feather fingergrass seed could germinate at 5 C, which is difficult to reconcile with their estimate of 7.0 C for T_b. Our estimated T_b value for feather fingergrass is much lower than those of four other annual summer grass weeds, namely green foxtail [*Setaria viridis* (L.) Beauv.], yellow foxtail [*Setaria pumila* (Poir.)], large crabgrass [*Digitaria sanguinalis* (L.) Scop.], and goosegrass [*Eleusine indica* (L.) Gaertn.] with T_b for germination of 6.1, 8.3, 8.4, and 12.6, respectively (Masin et al. 2005). With rapid germination and a low base temperature, feather fingergrass can germinate and emerge under field conditions after rainfall events in South Australia that would maintain adequate soil moisture for a few days only in spring. Within this study period, suitable conditions for seed germination and seedling establishment were created by rainfall events in summer in 2014 (November 21 to 23) and summer (January 8 to 13) and autumn (April 6 to 8) of 2015 (Table 1 and Figure 1; emergence data in April 2015 not shown).

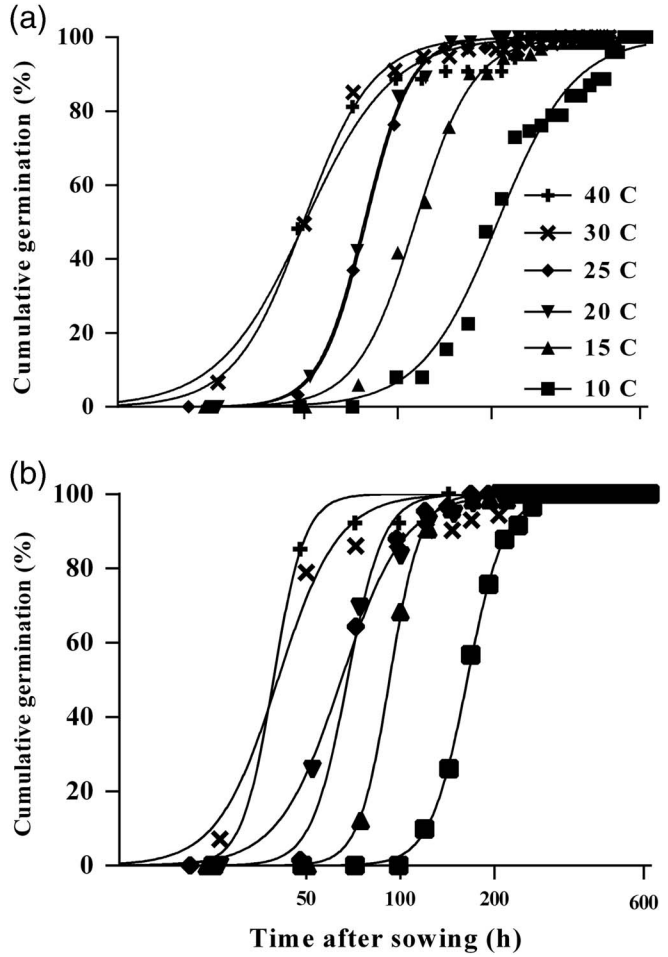

Figure 4. Cumulative germination of CV4 (a) and CV5 (b) at different temperatures. Each data point represents the mean of four replicates, and curves were fitted using Equation 1. R^2 of the fitted curves for both CV4 and CV5 ranged from 0.92 to 0.99.

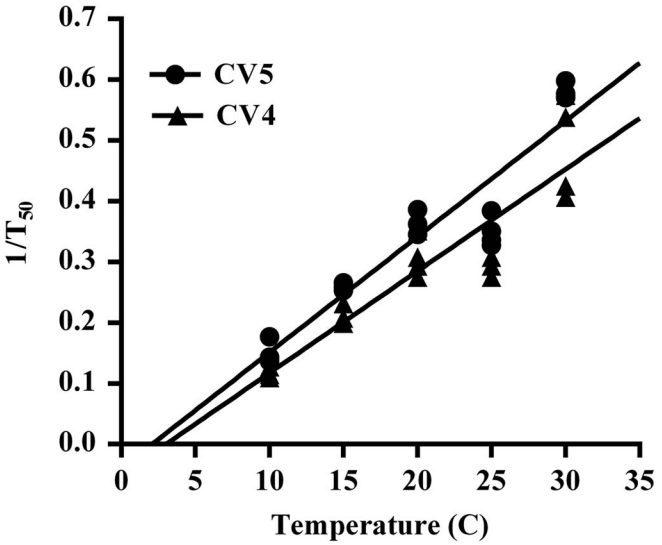

Figure 5. Base temperature (T_b) estimation of CV4: $Y = 0.01678*X - 0.05059$ ($R^2 = 0.93$); and CV5: $Y = 0.01906*X - 0.03959$ ($R^2 = 0.90$). Each data point represents a replicate.

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Table 4. Effect of light on germination.[a]

Year	Population	Germination (%)	
		24 h dark	12 h light/dark
2014	CV4	35.0 ± 3.4b	78.0 ± 1.2cd
	CV5	17.0 ± 5.3a	72.0 ± 6.5c
2015	CV4	2.3 ± 1.6a	84.7 ± 4.0d
	CV5	33.0 ± 2.1b	70.0 ± 2.5c

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

Effect of Light on Germination. Germination was significantly stimulated by light, but the light effect was variable across populations and years (Table 4). In 2014 germination increased from 17% to 35% in the dark to 72% to 78% in the light. Similarly, in 2015 germination increased from 2% to 33% in the dark to 70% to 85% when exposed to light (Table 4). Similar results were also found in feather fingergrass in Queensland, Australia (Fernando et al. 2016). 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 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 close to the soil surface (Adkins et al. 2002; Milberg et al. 2000), which would enhance the probability of seedling survival of such small-seeded weed species.

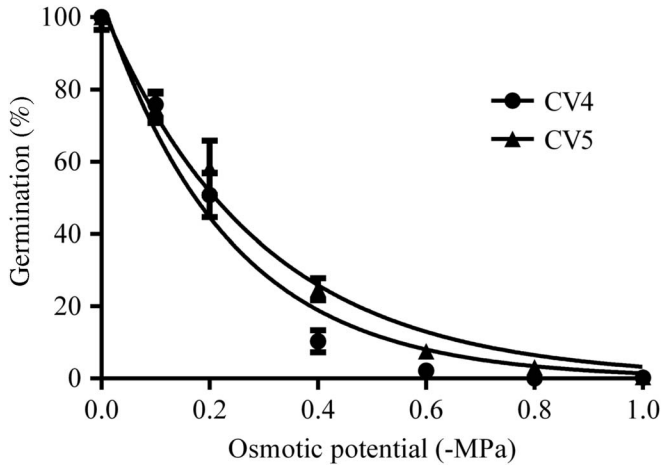

Figure 6. Effect of osmotic potential (MPa) on germination at 25 C and 12 h alternating fluorescent light/dark. The fitted line represents an exponential model: $Y = 105.2*\exp(-4.286 *X)$ ($R^2 = 0.93$) for CV4; and $Y = 103.2*\exp(-3.459*X)$ ($R^2 = 0.92$) for CV5. Each data point represents the mean of two experiments pooled with four replicates. Vertical bars are SE of the mean.

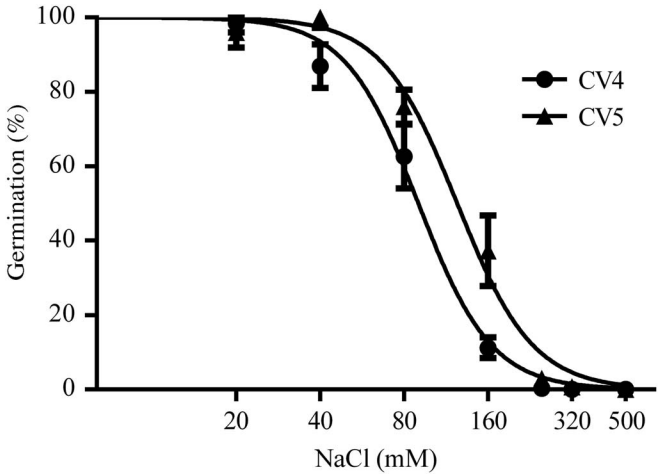

Figure 7. Effect of salt stress (NaCl) on germination at 25 C and 12 h alternating fluorescent light/dark. The fitted line represents a logistic response equation: $Y = 100/\{1 + 10\text{^}[(1.954 - X)* - 3.298]\}$ ($R^2 = 0.94$) for CV4; and $Y = 100/\{1 + 10\text{^}[(2.094 - X)* - 3.193]\}$ ($R^2 = 0.92$) for CV5. Each data point represents the mean of two experiments pooled with four replicates. Vertical bars are SE of the mean.

Effect of Osmotic Stress on Germination. Germination decreased exponentially with increased osmotic potential and was completely inhibited at −1.0 MPa (Figure 6). Similarly, for other annual summer grasses, the base water potentials for germination of yellow foxtail, green foxtail, large crabgrass, and goosegrass were −0.7, −0.7, −0.8, and −1.2 MPa, respectively (Masin et al. 2005). In another study, base water potential for rigid ryegrass (*Lolium rigidum* Gaudin) in South Australia was −1.2 MPa (Chauhan et al. 2006). The osmotic potential required for 50% inhibition of the maximum germination was −0.16 to −0.20 MPa (Figure 6), which was higher than that of feather fingergrass (−0.09 MPa) in Queensland, Australia (Fernando et al. 2016). This means feather fingergrass has a similar base water potential to other grass weed species, is not drought tolerant at germination, and only germinates when there is adequate soil moisture (osmotic potential less than −1.0 MPa).

Effect of Salt Stress on Germination. Germination response to NaCl stress fitted well to a logistic model ($R^2 = 0.92$ to 0.94). Germination was not inhibited below 40 mM NaCl. The concentration of NaCl required to inhibit germination by 50% was estimated to range from 90 to 120 mM, which was much higher than that of feather fingergrass (less than 50 mM) in Queensland, Australia (Fernando et al. 2016). Seed germination was completely inhibited at 320 to 500 mM NaCl (Figure 7). At 250 mM NaCl, there

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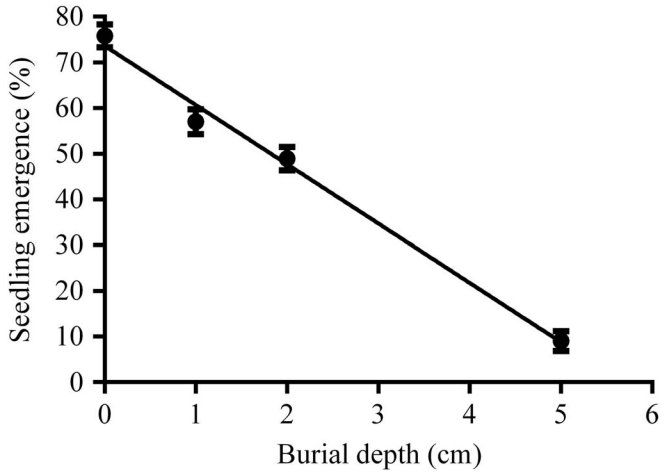

Figure 8. Linear relation between seedling emergence (CV4 and CV5) and burial depths. Each data point represents the mean of two experiments and two populations pooled with four replicates. Vertical bars are SE of the mean. Estimated equation for regression line $Y = -12.97*X + 73.63$ ($R^2 = 0.99$).

was less than 3% germination in this study (Figure 7), which is much lower than that of a population (more than 80%) from the Songnen Grassland in China at this level of salt stress (Zhang et al. 2012). These differences between studies could reflect adaptation of ecotypes in China to soil salinity.

Seedling Emergence from Different Burial Depths. Seedling emergence response to different burial depths was linear ($R^2 = 0.99$), decreasing significantly as the depth of seed burial increased (Figure 8). Similarly, 2-cm depth of seed burial had a significant impact on the emergence of feather fingergrass in Queensland (McLean et al. 2014). Seedling emergence was highest for seeds on the soil surface (76%), but reduced significantly to 57%, 49%, and 9% for seeds buried at 1, 2, and 5 cm, respectively (Figure 8). This reduction in seedling emergence is consistent with the stimulation of seed germination by exposure to light observed in this study (Table 4). Ability of some seeds of this species to germinate and emerge in the dark at shallow burial depth (1 and 2 cm) could be an advantage in fields used for crop production where seeds are likely to be buried by tillage or a seed drill at planting time. In fact, seeds buried at shallow depth could have a higher probability to germinate and emerge, because after each rainfall event, the soil is likely to remain moist for longer at depth than on the surface. Therefore, weed seeds present on the soil surface over hot summer months are likely to desiccate faster than seeds buried at shallow depths.

Deep burial (5 cm) significantly reduced seedling emergence (9%) compared with seeds on the soil surface (76%). As seeds are small (0.3 to 0.4 mg), they are unlikely to have sufficient energy reserves or coleoptile length to emerge from deep burial. Therefore, emergence in fields where deep tillage was applied was likely to be much lower than in fields where crops were grown with zero- or no-till systems (McLean

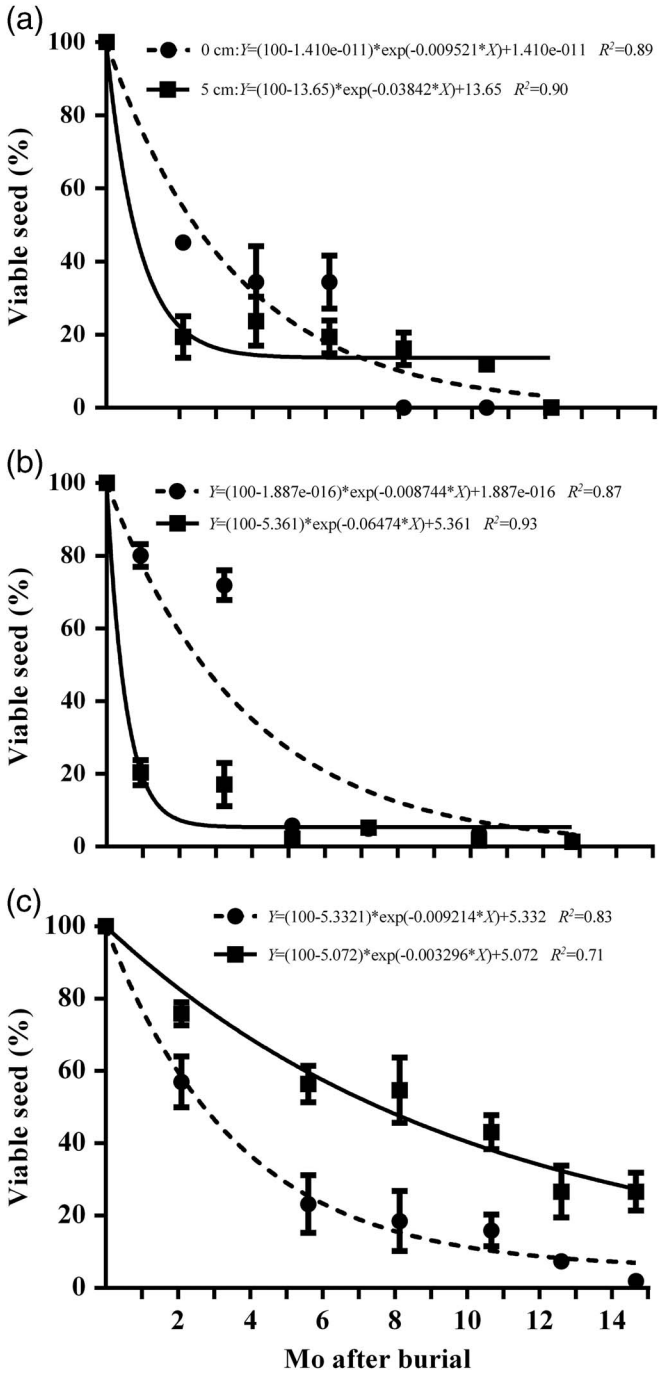

Figure 9. Changes in viability of seeds at the soil surface compared with seeds at 5-cm burial depth, conducted in July 2013 for CV5 (a), in August 2014 for CV5 and CV14 (b), and in April 2015 for CV1 and CV4 (c). Each data point represents the mean of four replicates (a) or two populations pooled with four replicates (b and c). Vertical bars are SE of the mean.

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et al. 2014; Widderick et al. 2014). Widespread adoption of no-till cropping systems in Australia is likely to favor invasion by feather fingergrass.

Seedbank Persistence under Field Conditions. Under field conditions, viability of seeds decreased exponentially with time ($R^2 = 0.71$ to 0.93), and was influenced by the amount of summer rainfall received over the 3 yr (Figure 9). In 2013 to 2014 and 2014 to 2015 experiments, seeds at 5-cm depth initially lost their viability faster than those left on the soil surface. At 2 mo after seed burial, seed viability at 5-cm depth decreased to about 20%, whereas the number of viable seeds on the soil surface remained high (50% to 75%) (Figure 9a and b). Some seeds could have germinated in the dark under more favorable moisture conditions, and this could have contributed to the faster decline of viable seeds buried at 5 cm. Seeds placed on the soil surface would have dried faster and maintained greater seed viability. Seed viability of the surface-stored seeds decreased rapidly from 34% to 0% from January to March (8 mo after burial) 2014 and from 71% to 5% from December 2014 to January 2015 (5 mo after burial) (Figure 9a and b). This rapid loss of viability in surface seeds was associated with 92 mm rainfall in February 2014 and 58 mm in January 2015 (Figure 1). After these heavy rainfall events, favorable moisture and temperature conditions could have stimulated seed germination in the field and reduced the viable seedbank.

In the 2013 to 2014 and 2014 to 2015 experiments, seed viability both on the soil surface and at depth was almost completely lost (0% to 3.4% viable seed) after 12 mo (Figure 9a and b). These results are consistent with previous reports from the northern cropping region of Australia, where seeds of feather fingergrass persisted only for 10 to 12 mo, irrespective of burial depth (Osten 2012; Widderick et al. 2014). However, seed persistence in the 2015 to 2016 experiment was much greater than in 2013 to 2014 and 2014 to 2015. In 2015 to 2016, seeds buried at 5 cm had greater viability in all assessments than those placed on the soil surface (Figure 9c). Viability of seeds removed at 8 mo after placement was 18% for those on the soil surface compared with 54% for those at 5-cm depth. After 14 mo, seed viability on the soil surface was almost completely lost (2% viable seed), whereas seeds buried at 5 cm still had 25% viability (Figure 9c). An extremely dry summer in 2015 to 2016 could have increased seed persistence compared with 2013 to 2014 and 2014 to 2015, when significant rainfall events occurred (Figure 1). These differences in seed persistence between years could be associated with greater seed germination and seed decay in wet and warm conditions than in dry and warm conditions. Our results suggest that feather fingergrass populations are unlikely to develop persistent seedbanks and could be reduced quickly if no further seeds are added to the seedbank by dispersal. Our results also indicate that an adequate seedbank can be present in spring to early summer (September to December) or over summer (September to February) for the recruitment of seedlings of this weed species in southern Australia. As shown earlier, plants can emerge, establish, and produce seeds when temperature and moisture are favorable, as was the case after spring (2014) and summer (2015) rainfall events (Table 1 and Figure 1). Plants have high fecundity, with up to 1,000 seeds panicle^{-1} and more than 40,000 seeds plant^{-1} (Table 2). Consequently, even a small seedbank can lead to successful colonization of agricultural and nonagricultural land.

Feather fingergrass has several characteristics that enable it to survive and persist in the Mediterranean environment of South Australia. It has rapid germination and a low base temperature (2.1 to 3.0 C), so it can 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 300 and 1,200 Cd from seedling emergence to tillering and mature seed stages, and high fecundity. Germination of this small-seeded species was stimulated by light, and seedling emergence was highest for seeds present on the soil surface, but declined significantly for seeds buried at 1, 2, and 5 cm. Seeds were dormant for about 2 mo after maturity; however, seeds buried at 5-cm depth remained viable for more than 14 mo, whereas seeds on the soil surface lost viability after 12 mo. Low rainfall over the 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 also make feather fingergrass ideally suited to the no-till farming systems widely adopted in southern Australia, and it is likely this species will become a problem in such production systems.

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