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Germination behaviour of *Avena sterilis* subsp. *ludoviciana* under a range of light and temperature regimes

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ABSTRACT

Context. *Avena sterilis* subsp. *ludoviciana* (wild oats) is one of the major winter weeds of the Northern Grains Region of Australia. The abundance of this weed increased dramatically after the adoption of no-tillage conservation agriculture (NTCA). However, information is lacking on the germination characteristics of the two types of seed (i.e. primary and secondary) that it produces. **Aims.** We aimed to determine the light and temperature requirements for germination and the time to germination of primary and secondary seeds of *A. ludoviciana*, in order to find ways to manage this weed effectively under NTCA systems. **Methods.** Primary and secondary seeds and caryopses from two southern and two northern biotypes were exposed to a range of temperature and light regimes in the glasshouse, and germination was assessed. **Key results.** All biotypes had ~25% higher germination from primary than secondary seeds. Removing the hull increased caryopsis germination by ~70%. The use of a light/dark photoperiod stimulated germination of both types of seed and caryopses compared with continuous darkness. Based on data for caryopses, 7°C and 9°C were found to be optimal germination temperatures for southern and northern biotypes, respectively. At optimum germination temperature, primary caryopses germinated 7–20 days earlier than secondary caryopses. In addition, a light/dark environment resulted in germination 2–6 days earlier than continuous darkness. **Conclusions.** In the Northern Grains Region, seeds retained on or close to the soil surface (i.e. in NTCA systems) can undergo maximum germination during May–June (late autumn–winter), when long-term average temperatures match optimum germination temperatures. This coincides with winter crop plantings. **Implications.** The seasonal timing of germination and the difference in germination timing between primary and secondary seeds, which help to stagger emergence of this weed, are major issues that need to be addressed in NTCA systems.

Keywords: conservation agriculture, germination, light, no-tillage, primary seed, secondary seed, seed burial, soil surface, temperature, wild oats.

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Introduction

Wild oats (*Avena fatua* L. and *Avena sterilis* L. subsp. *ludoviciana* (Durieu) Nyman) are two of the most economically important weeds within the Australian Northern Grains Region (NGR, a region comprising parts of Queensland and all of New South Wales) (Llewellyn *et al.* 2016). Of the cropping land in the NGR, ~0.6 Mha is infested by these two species, costing growers ~AU$4.5 million in annual revenue through lost crop yield (Llewellyn *et al.* 2016). *Avena sterilis* subsp. *ludoviciana* (hereafter *A. ludoviciana*) is the more abundant species within the NGR (Nugent *et al.* 1999). Effective management of *A. ludoviciana* remains a key challenge for grain growers in the region, particularly following the adoption of no-tillage conservation agriculture (NTCA; Dang *et al.* 2015).

After physiological maturity, the primary and secondary (and occasionally tertiary) seeds of *A. ludoviciana* shed together as a unit, remaining attached as a single spikelet. The minor soil disturbance in NTCA systems leaves most of these shattered spikelets in at 0–2 cm depth in the soil, allowing a persistent seedbank to develop in that layer (Widderick and McLean 2017).

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Considering that most *A. ludoviciana* seeds are typically present on or near the soil surface, it is possible that germination of this species is stimulated by light. By contrast, several reports have shown that *A. fatua* prefers darkened conditions for germination (Leighty 1956; Cumming and Hay 1958; Hsiao and Simpson 1971; Sharma *et al.* 1976). Consequently, most germination tests with *A. fatua* have been conducted in the dark (Quail and Carter 1969; Peters 1982; Sawhney and Naylor 1982; Adkins *et al.* 1986, 1987; O'Donnell and Adkins 2001).

Seeds of *A. ludoviciana* germinate in a temperature range of 2–30°C, with the optimum at 10°C (Quail and Carter 1968; Üremiş and Uygur 1999). However, it is not known whether differences in germination exist between primary and secondary seeds in response to atmospheric temperature variation. Such information will be important for determining how germination of this weed can be impacted by the prevailing climatic conditions of the NGR.

We conducted a germination study across two consecutive years under a range of incubation temperature and light conditions, using primary and secondary seeds and caryopses from four *A. ludoviciana* biotypes from the NGR. The objectives were: (*i*) to determine the optimal light conditions for germination of primary and secondary seeds and caryopses of the four biotypes; (*ii*) to identify incubation temperatures that can maximise germination of primary and secondary seeds and caryopses; and (*iii*) to determine the germination rate (speed) of primary and secondary caryopses when incubated under either a photoperiod or continuous darkness at their optimal germination temperature. Information on the light and temperature requirements for germination of *A. ludoviciana* will facilitate future in-depth studies on the germination biology of this species. In addition, investigation on the differences in germination rates between primary and secondary seeds will aid understanding of the timing of germination from spikelets retained on the soil surface or buried within the soil, which is critical information required for improving the management of this weed.

Materials and methods

Biotypes

Spikelets of four biotypes of *A. ludoviciana* were collected from four locations in the NGR. Two were in the northern zone: Biloela 1 (−24.3547, 150.4977) and Biloela 2 (−24.3504, 150.4977); and two were in the southern zone: Toobeah (−28.3679, 149.5219) and Jandowae (−26.6672, 151.0246). The collection sites were fields where NTCA had been practised for >30 years and that have primarily been used for wheat (*Triticum aestivum* L.) production.

The four biotypes provided a good geographic coverage of the area over which *A. ludoviciana* populations are found in the NGR (Quail and Carter 1968; Whalley and Burfitt 1972; Nugent *et al.* 1999). After harvest, spikelets were placed into paper bags and stored in a dedicated seed store in the dark at 15°C (±2°C), 15% (±5%) relative humidity (RH) until used for experimental seed production 6 months later.

A spikelet typically consists of two florets: a larger primary floret and a smaller secondary floret. Each floret consists of a caryopsis covered by the lemma (carrying an awn) and palea, which together comprise the hull of the grain. Hereafter, the primary or secondary floret is referred to as a seed. A seed with a well-developed caryopsis is counted as filled, whereas a seed without a caryopsis is counted as empty.

Plant establishment and maintenance

After removal from storage, the primary seed from each spikelet was separated from the secondary seed and dehulled. In total, 120 primary caryopses were germinated from each biotype, and three healthy seedlings were transplanted to each pot (20 cm diameter, 19 cm height), containing 4.5 kg Black Vertosol soil (50% clay, pH 7.3). The pots were maintained at a gravimetric plant available water content (Soil Survey Staff 2014) of 100% throughout the trial. Soil water content was determined by weighing each pot every 2 days. Plant available water content of each pot was maintained according to the weight of the pot.

From planting until maturity, the plants were kept in a greenhouse clad with single-skin plastic film, with roof and side wall ventilation, at The University of Queensland Gatton Campus (−27.5540, 152.3390). Plants were maintained under ambient conditions of 23°C/12°C (±3°C) day/night temperature and 60% (±5%) RH, determined by TGP-4520 Tinytag Plus 2 loggers (Gemini Data Loggers, Chichester, UK). AzaMax insecticide (11.82 g L^{-1} of azadirachtin A and B present as 29.55 g L^{-1} of *Azadirachta indica* A. Juss. extract; Organic Crop Protectants, Sydney, NSW) was applied twice (at 50 and 65 days after planting) in a spray volume of 250 L ha^{-1} at the rate of 1.5 mL AzaMax L^{-1} water to control aphids (*Aphis* spp.). Pot positions within the greenhouse were randomised every 2 days.

Spikelet collection and storage

Spikelets were collected by hand from the plants at physiological maturity (when 50% of spikelets coming from a plant were ready to be shed naturally), placed in paper bags and stored in a seed store in the dark at 15°C (±2°C) and 15% (±5%) RH until used for the germination studies 6 months later. Seed storage under these conditions for 6 months started the after-ripening process and reduced the intensity of the innate dormancy system(s) present in *A. ludoviciana* seed at the time of harvest. The after-ripening process therefore allowed seeds to overcome dormancy,

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meaning that analysis of the various germination treatments could be made.

Germination test

A thermogradient-bar germination chamber (T-bar; Lindner and May Industries, Brisbane, Qld) was used to determine the germination capacity of the primary and secondary seeds and the caryopses from each biotype. Filled primary and secondary seeds were randomly isolated from the spikelet lots of each biotype. Half of these lots were dehulled to produce primary and secondary caryopses. All seeds and caryopses were surface-sterilised by shaking in 2% (v/v) sodium hypochlorite solution (NaOCl; Pental, Shepparton, Vic.) containing two drops of Tween 20 (Bio-Rad Laboratories, Hercules, CA, USA), for 5 min at a rate of 40 mL NaOCl per 100 seeds. After surface-sterilisation, all seed and caryopsis lots were rinsed four times with sterilised water before being blotted dry on sterile filter paper and used in the germination tests.

The surface-sterilised seeds and caryopses, in lots of 20, were placed into 9-cm-diameter Petri dishes on two layers of Whatman No. 1 filter paper wetted with 5 mL sterile water containing Previcur fungicide (600 g L^{-1} of propamocarb present as the monohydrochloride; Bayer CropScience, Melbourne, Vic.) at the rate of 2 mL Previcur L^{-1} water. Seeds/caryopses were incubated under constant temperatures of 4°C, 6°C, 9°C, 12°C or 15°C (±1°C) under a 12 h light/12 h dark photoperiod or constant darkness created by wrapping the Petri dishes with three layers of aluminium foil. Illumination over the T-bar was created by cool white fluorescent light producing a daytime photosynthetic photon flux density (PPFD) of ~100 μmol m^{-2} s^{-1} at the level of Petri dish incubation. Germination counts were done at 5-day intervals over 45 days. Germination was defined as the protrusion of coleorhiza through the husk or through the pericarp, for seeds and caryopses, respectively. The germinated seeds/caryopses were removed from the Petri dishes after each counting session. Seeds/caryopses germinated under constant darkness were observed in a darkened room, where the Petri dishes were opened under a green safety light (PPFD ~0.14 μmol m^{-2} s^{-1}; RS Components, Sydney, NSW). After germinated seedlings were counted and removed, the Petri dishes were again covered with three layers of aluminium foil and placed back into the appropriate cell on the T-bar.

After 45 days of imbibition, non-germinated seeds or caryopses were examined for viability. Non-germinated seeds were dehulled by hand, then the caryopses of both seed types were pierced mid-way along their dorsal surface with a sharp, sterile needle and re-imbibed in fresh Petri dishes containing two Whatman No. 1 filter papers and 5 mL gibberellic acid solution (10 μM GA_3; Sigma-Aldrich, St. Louis, MO, USA; Adkins *et al.* 1986). These germination-stimulated caryopses were then incubated for another 21 days under their initial temperature and light conditions. Caryopses that germinated after this additional treatment were counted as viable but initially dormant. All seeds and caryopses used in this study were found to be viable.

Experimental design and statistical analyses

For the first year of testing, seed multiplication was done during June–October 2018 and germination tests were conducted during April–May 2019. For the second year of testing, seed multiplication work and germination tests were done during the same months in 2019 and 2020, respectively. For the germination test, 20 primary and 20 secondary seeds or their caryopses of each biotype were used per replication, and there were three replications for each test. Because biotypes were collected from a wide range of locations within the NGR, we expected that their temperature requirement for germination might differ; hence, analysis was done separately for each biotype. The data from the 2 years of germination testing were pooled before analysis because the effect of the repeat was non-significant ($P \geq 0.05$) for both primary and secondary seeds/caryopses. Pooled data were tested for normality (Anderson–Darling test) and homoscedasticity (residuals vs fits) before being subjected to analysis of variance (ANOVA). Analyses were performed in Minitab for Windows version 18 (Minitab Software, State College, PA, USA). A two-way factorial ANOVA was conducted on the total germination percentage of primary and secondary seeds or caryopses of each biotype, and for each experimental factor (seed/caryopsis types, and light and temperature regimes). Means were separated by using Tukey's honestly significant difference (HSD) test at $P \leq 0.05$. The standard error of the total germination percentage for each experimental factor was calculated and plotted using SigmaPlot for Windows version 13 (Systat Software, San Jose, CA, USA). The optimum incubation temperature was then estimated via a nonlinear regression analysis. To do this, the significant ($P \leq 0.05$) regression equation with the highest coefficients of determination (R^2) that best explained the relationship between the incubation temperature and total germination percentage was plotted, and the optimum incubation temperature was determined by fitting a three-parameter peak Gaussian model:

$$\text{Germination } (\%) = a \times e^{\left(\frac{-0.5(x-x_o)}{b}\right)^2}$$

where a is maximum germination (percentage), b is the standard deviation of the rate of germination, x is the maximum incubation temperature (°C), and x_o is the optimum incubation temperature.

In order to understand the germination rate of the primary or secondary caryopses of each biotype when incubated under a light/dark photoperiod or continuous darkness, we used the cumulative germination percentage data obtained from their

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optimum germination temperature: Biloela 1 and 2 at 9°C (±1°C), Toobeah and Jandowae at 7°C (±1°C). The standard error of the values was calculated, and the number of days taken to reach 50% germination (G_{50}) was estimated via a nonlinear regression analysis using SigmaPlot. A significant ($P \leq 0.05$) regression equation with the highest R^2 that best explained the relationship between the incubation time (days) and cumulative germination percentage of the caryopses was plotted and the G_{50} value was determined through fitting a three-parameter sigmoid model:

$$\text{Cumulative germination of caryopses } (\%) = \frac{a}{1 + e^{\frac{-(x - x_0)}{b}}}$$

where a is fitted maximum cumulative germination (percentage), b is the rate of germination increase in the rapidly growing section of the curve, x is the accumulated time in the test (in days), and x_o is the G_{50} value.

Results

Germination behaviour of biotypes

A significant difference ($P \leq 0.001$) between the primary and secondary seeds or caryopses was observed for germination of all biotypes (Tables 1 and 2). Light regime (LR) or temperature regime (TR) alone also significantly influenced seed or caryopsis germination of all biotypes except in the case of caryopses of Biloela 1 under light regimes (Tables 1 and 2). All two-way interaction effects LR × TR, types of seed (TS) × LR, and TS × TR, and the three-way interaction effect TS × LR × TR, were significant on the germination of seeds of all biotypes, except for LR × TR and TS ×LR × TR for Biloela 2 (Table 1). On the other hand, all interaction effects were significant on the germination of caryopses of all biotypes, except for LR × TR and type of caryopsis (TC) × LR for Biloela 1 and LR × TR for Jandowae (Table 2).

Both primary and secondary seed and caryopses of all biotypes showed significantly ($P \leq 0.001$) greater germination under light/dark conditions than continuous darkness, except for Biloela 1 caryopses ($P = 0.133$) (Tables 1 and 2; Figs 1–4). Seed germination of the northern biotypes (Biloela 1 and 2) was greatest when they were incubated at ~9°C (Figs 1 and 2), whereas the southern biotypes (Toobeah and Jandowae) had maximum germination when the incubation temperature was ~7°C (Figs 3 and 4). At the optimum incubation temperature, there was ~25% more germination of primary than secondary seeds (55% vs 30%) of all biotypes when seeds were incubated under light/dark conditions ($P = 0.001$; Figs 1–4). Germination of both types of seeds was decreased by increasing incubation temperature

Table 1. Analysis of variance on germination percentage of primary or secondary seeds of *Avena sterilis* subsp. *ludoviciana* biotypes Biloela 1, Biloela 2, Toobeah and Jandowae.

Biotype		Type of seed (TS)	Light regime (LR)	Temperature regime (TR)	TS × LR	TS × TR	LR × TR	TS × LR × TR
Biloela 1	d.f.	1	1	4	1	4	4	4
	P-value	<0.001	<0.001	<0.001	<0.001	0.003	<0.001	0.003
	F-value	240.47	93.52	46.71	13	4.33	19.7	4.25
	R^2			86.61%				
Biloela 2	d.f.	1	1	4	1	4	4	4
	P-value	<0.001	<0.001	<0.001	<0.001	0.033	0.654	0.672
	F-value	67.46	42.43	32.59	16.48	2.73	0.39	0.90
	R^2			72.21%				
Toobeah	d.f.	1	1	4	1	4	4	4
	P-value	<0.001	<0.001	<0.001	<0.001	0.004	<0.001	0.037
	F-value	186.45	172.47	94.72	57.25	4.1	7.1	2.66
	R^2			89.48%				
Jandowae	d.f.	1	1	4	1	4	4	4
	P-value	<0.001	<0.001	<0.001	<0.001	0.001	0.001	<0.001
	F-value	600.07	117.88	59.09	72.67	4.82	4.84	7.29
	R^2			91.63%				

$P \leq 0.05$ is significant; R^2 value explains the relationship between experimental factors and seed germination (%). Seeds were produced under ambient greenhouse conditions (23°C/12°C (±3°C) day/night temperature and relative humidity 60% (±5%)) with soil-water content maintained at 100% of gravimetric plant available water.

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Table 2. Analysis of variance on germination percentage of primary or secondary caryopses of *Avena sterilis* subsp. *ludoviciana* biotypes Biloela 1, Biloela 2, Toobeah and Jandowae.

Biotype		Type of caryopsis (TC)	Light regime (LR)	Temperature regime (TR)	TC × LR	TC × TR	LR × TR	TC × LR × TR
Biloela 1	d.f.	1	1	4	1	4	4	4
	P-value	<0.001	0.133	<0.001	0.250	0.001	0.065	0.023
	F-value	59.07	2.59	26.37	1.15	4.7	2.33	2.93
	R^2			67.54%				
Biloela 2	d.f.	1	1	4	1	4	4	4
	P-value	<0.001	<0.001	<0.001	0.001	<0.001	0.001	0.005
	F-value	1763.78	25.26	71.32	12.2	10.68	4.96	3.98
	R^2			95.59%				
Toobeah	d.f.	1	1	4	1	4	4	4
	P-value	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
	F-value	123.90	67.57	62.60	56.77	15.34	13.22	12.77
	R^2			86.79%				
Jandowae	d.f.	1	1	4	1	4	4	4
	P-value	<0.001	<0.001	<0.001	0.001	<0.001	0.709	0.016
	F-value	224.66	45.65	101.21	11.15	13.93	0.54	3.19
	R^2			88.33%				

$P \leq 0.05$ is significant; R^2 value explains the relationship between experimental factors and seed germination (%). Caryopses were obtained by dehulling the seeds. Caryopses were produced under ambient greenhouse conditions (23°C/12°C (±3°C) day/night temperature and relative humidity 60% (±5%)) with soil-water content maintained at 100% of gravimetric plant available water.

to ≥12°C, or by decreasing incubation temperature to ≤4°C. Removing the seed hull significantly increased germination of primary and secondary caryopses under all treatments (Figs 1–4). At least 70% of primary and 30% of secondary caryopses of all biotypes were able to germinate under any incubation temperature whether under light/dark or continuous darkness. Among biotypes, Biloela 1 produced the highest number of seedlings, followed by Toobeah, Jandowae and Biloela 2 (Figs 1–4). Temperature and light incubation conditions and type of seeds were all found to be determinant factors of whether the biotypes would express their hull-imposed dormancy or embryo dormancy.

Germination rate of primary and secondary caryopsis of four biotypes

The germination rate of primary caryopses was significantly ($P \leq 0.001$) higher than of secondary caryopses (Fig. 5), and this was observed for all biotypes. For the Biloela 1 and Toobeah biotypes, primary caryopses reached the G_{50} value 7 days earlier than secondary caryopses, whereas primary caryopses of Jandowae reached the G_{50} value 10 days earlier than secondary caryopses (Fig. 5). For Biloela 2, there was a 20-day gap between primary and secondary caryopses reaching the G_{50} value (Fig. 5). Light/dark photoperiod significantly ($P \leq 0.001$) increased the rate of caryopses germination compared with incubation under continuous darkness (Fig. 5). Light/dark photoperiod sped the germination rate of both types of caryopsis for all biotypes by 2–6 days compared with continuous darkness (Fig. 5).

Discussion

Light conditions

Seed germination was higher under a photoperiod than under constant dark incubation (Figs 1–4). Overall, 40% of primary seeds were able to germinate under a photoperiod, a significant ($P \leq 0.001$) 20% increase on germination under dark incubation. Similarly, 15% of secondary seeds germinated under a photoperiod compared with 10% under dark incubation (Biloela 1, $P = 0.014$; Toobeah, $P = 0.030$). This preference for a light period during germination supports the observation that, in NTCA systems, *A. ludoviciana* seeds germinate more readily when retained on or near the soil surface (Walsh *et al.* 2017). Comparing seed types, a greater percentage of primary seeds responded under photoperiod conditions than secondary seeds (Figs 1–4). This result suggests that although these two types of seed remain attached together in a spikelet retained on or near the soil surface, a greater number of the primary seeds of the pair will germinate first. Therefore, early infestation of

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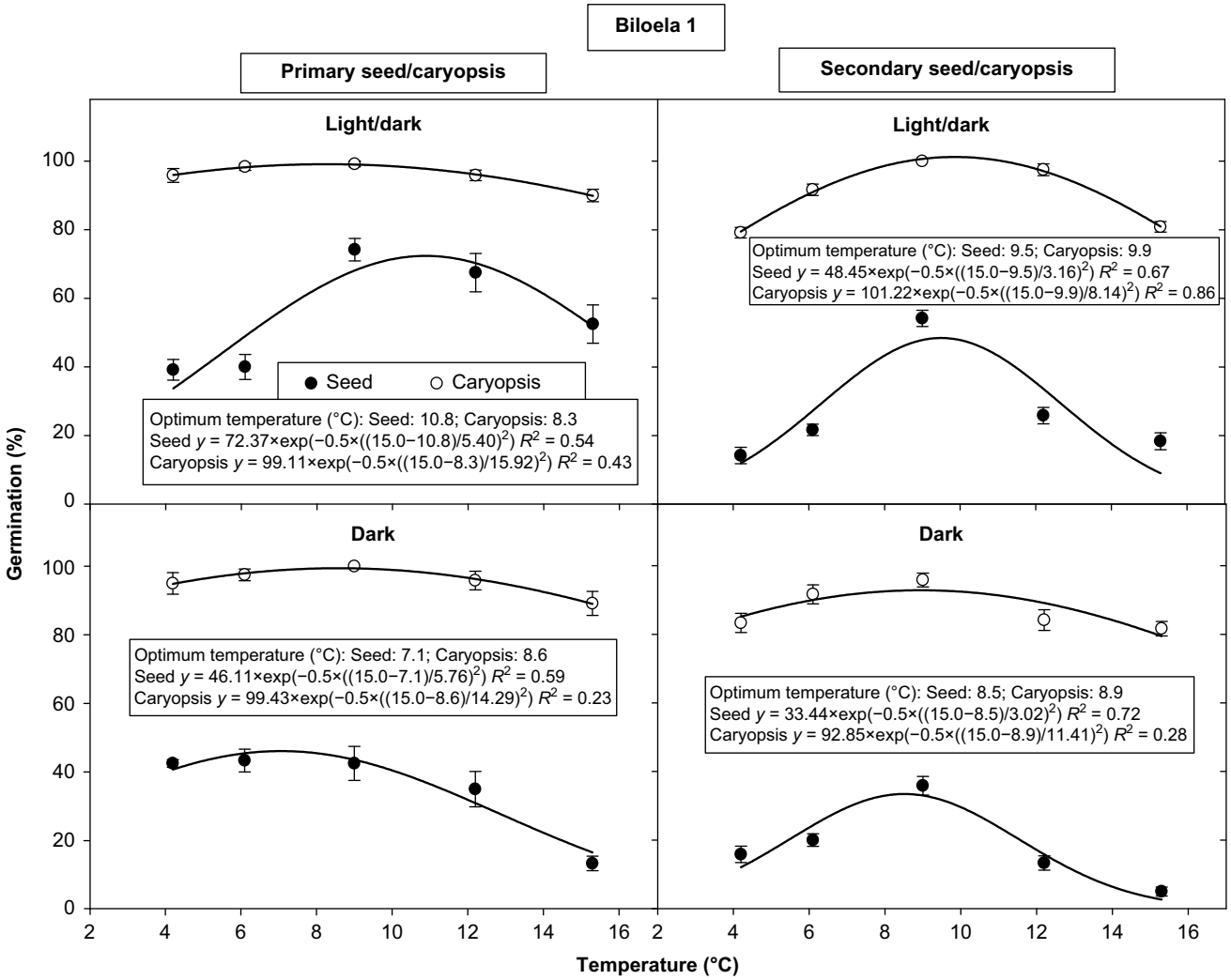

Fig. 1. Effect of light and temperature on germination percentage of primary or secondary seeds (solid symbols) or caryopses (open symbols) from biotype Biloela 1. Seeds/caryopses were produced under ambient greenhouse conditions (23°C/12°C (±3°C) day/night temperature and relative humidity 60% (±5%)) with soil-water content maintained at 100% of gravimetric plant available water. Error bars represent standard errors of the mean of six replicate samples consisting of 20 primary or secondary seeds or caryopses. Data are a pooled set from two experimental runs. Curves represent three-parameter peak Gaussian model fitted to the final germination percentage data.

A. ludoviciana seedlings in the next cropping season is likely to be produced from primary seeds, whereas later infestations may be from secondary seeds. This finding suggests that secondary seeds have the potential to facilitate avoidance of herbicide applications.

As expected, when the seeds were dehulled, a greater proportion of both primary and secondary seeds germinated, a result of removal of the hull-imposed dormancy. Approximately 90% of primary caryopses and 70% of secondary caryopses were able to produce seedlings, irrespective of the light conditions (Figs 1–4). This result indicates that, when the hull is naturally lost in the soil, greater infestations in the cropping environment can result whether the caryopses have been retained on the ground or buried at depth (e.g. >2 cm). Natural hull breakdown and loss is known to occur in *Avena* species over a period of 12–24 months. This is due to microbial and invertebrate action, as well as fluctuating temperature and water conditions within the soil, which are greatest in surface soil layers but attenuate deeper into the soil profile (Walsh *et al.* 2019).

Primary caryopses were found to germinate at a faster rate than secondary caryopses, and the rate of germination was faster when the caryopses were incubated under a light/dark photoperiod (germinating 2–6 days earlier) than under continuous darkness (Fig. 5). Depending on biotype, the G_{50} value for primary caryopses was reached 7–20 days earlier than for secondary caryopses. The inherent dormancy behaviour differences between primary and secondary seeds

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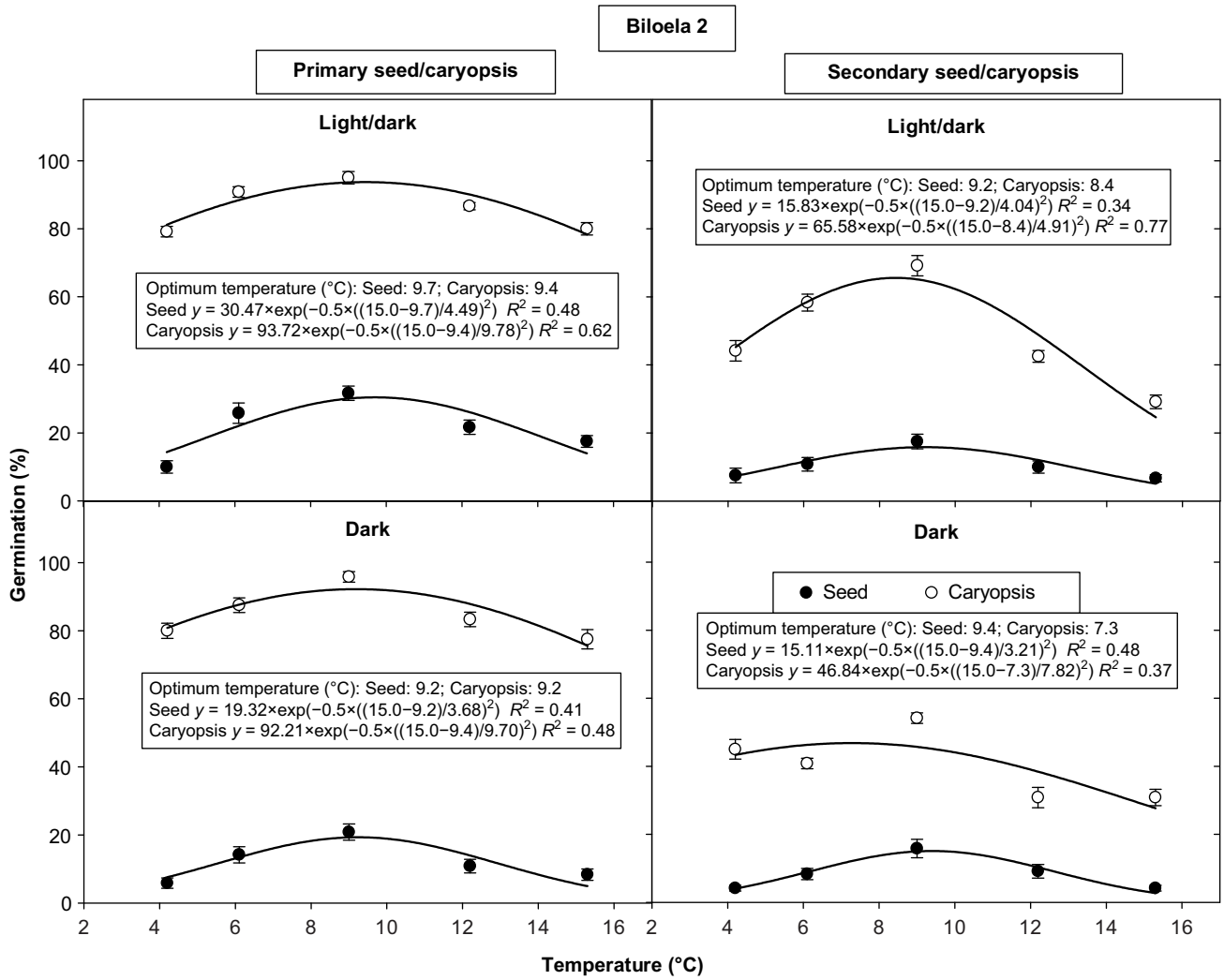

Fig. 2. Effect of light and temperature on germination percentage of primary or secondary seeds (solid symbols) or caryopses (open symbols) from biotype Biloela 2. Seeds/caryopses were produced under ambient greenhouse conditions (23°C/12°C (±3°C) day/night temperature and relative humidity 60% (±5%)) with soil-water content maintained at 100% gravimetric plant available water. Error bars represent standard errors of the mean of six replicate samples consisting of 20 primary or secondary seeds or caryopses. Data are a pooled set from two experimental runs. Curves represent three-parameter peak Gaussian model fitted to the final germination percentage data.

might be the reason for this variation in germination rate, as has been reported for *A. fatua* (Quail and Carter 1968; Adkins *et al.* 1987). This result also suggests that secondary seeds have an adaptive mechanism for avoidance of herbicide applications, potentially allowing them to germinate and emerge after herbicide is applied.

Incubation temperatures

Seed incubation temperature was also found to have a significant impact on the germination response of *A. ludoviciana* (Figs 1–4). The optimum temperature differed among biotypes and also differed depending on whether seeds or caryopses were used for germination. In general, the optimum temperature requirement for the southern biotypes was about 2°C lower than for the northern biotypes. Although the precise optimum temperature requirement for germination of seeds or caryopses was inconsistent across the biotypes, all biotypes had highest germination in the range 6–10°C (Figs 1–4). This is similar to the range discovered previously for *A. ludoviciana* biotypes in Australia (Quail and Carter 1968) and Turkey (Üremiş and Uygur 1999). The germination of seeds at cooler temperatures probably happened through the breaking down of the seed's conditional dormancy, during which time seeds can germinate only over a narrow range of conditions (Baskin and Baskin 2014), in this case a 6–10°C temperature range. Based on caryopsis germination,

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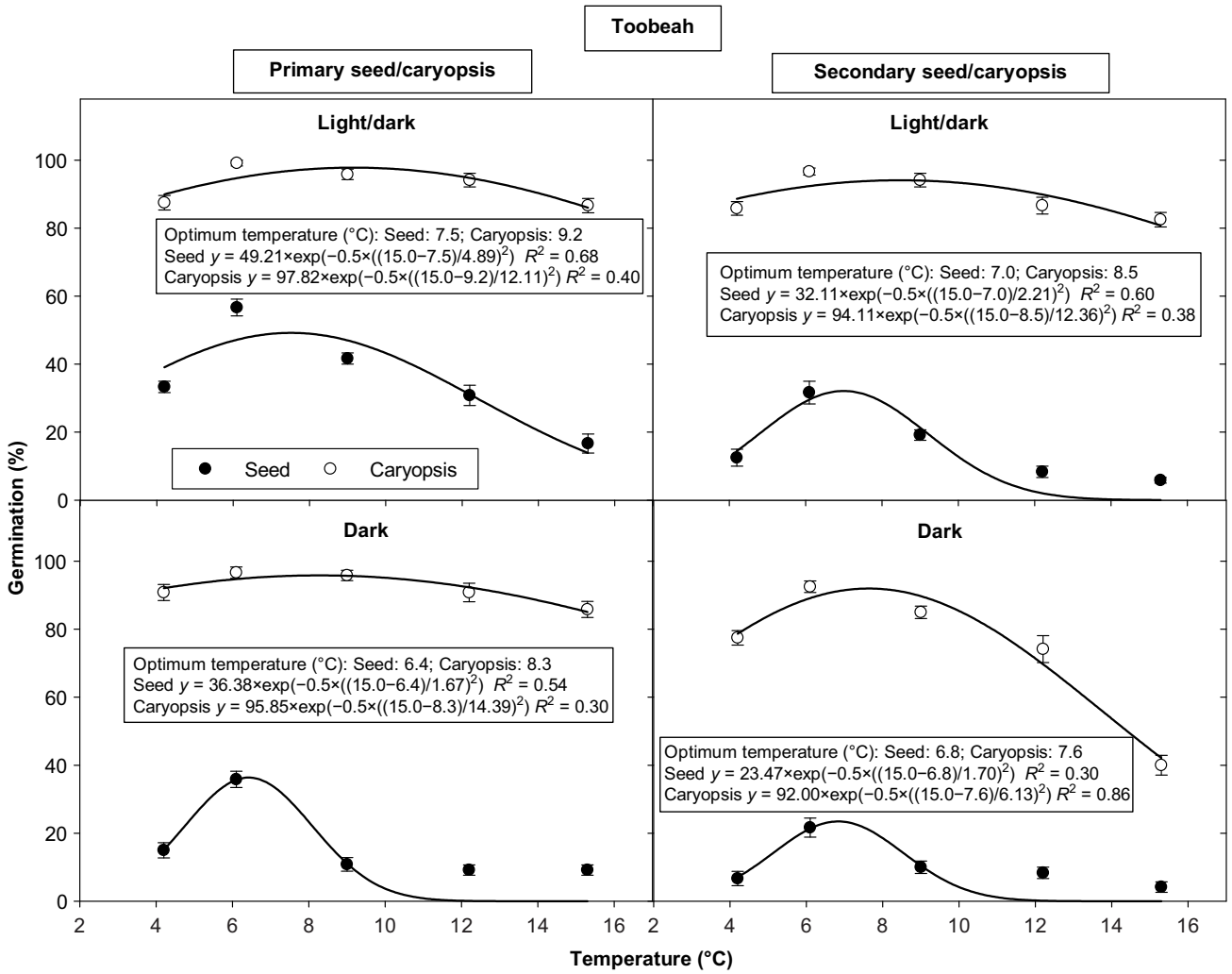

Fig. 3. Effect of light and temperature on germination percentage of primary or secondary seeds (solid symbols) or caryopses (open symbols) from biotype Toobeah. Seeds/caryopses were produced under ambient greenhouse conditions (23°C/12°C (±3°C) day/night temperature and relative humidity 60% (±5%)) with soil-water content maintained at 100% gravimetric plant available water. Error bars represent standard errors of the mean of six replicate samples consisting of 20 primary or secondary seeds or caryopses. Data are a pooled set from two experimental runs. Curves represent three-parameter peak Gaussian model fitted to the final germination percentage data.

the optimum temperature for the northern zone biotypes was ~9°C, whereas it was ~7°C for the southern zone biotypes. At these optimum temperatures, 45% of the primary seeds and 25% of the secondary seeds of all biotypes were able to germinate. These results suggest that primary seeds would be able to contribute more than secondary seeds to the population density of *A. ludoviciana* infesting a crop at the early growth stage. The findings also suggest that seedling emergence of *A. ludoviciana* in the NGR is expected to be greatest under the cooler climatic conditions experienced in late autumn–early winter (i.e. May–June), at a time when a winter crop is being planted.

As expected, seed germination was greatly increased when the seeds were dehulled (Figs 1–4). Approximately 80–95% of primary caryopses and 60–90% of secondary caryopses were able to germinate in a temperature range of 4–15°C. A higher germination percentage from caryopses than from seeds under all temperature regimes indicates that the germination window could be increased when the hull of the seeds has naturally broken down. However, the results (Figs 1–4) also indicate that the germination of primary caryopses were usually higher than secondary caryopses. The variation in germination behaviour between primary and secondary seed/caryopsis among different biotypes may be attributed to differences in their genetics. Genetic diversity within populations and between primary and secondary seed/caryopsis of *A. ludoviciana* (Quail and Carter 1968), or *A. fatua* (Peters 1986; Adkins *et al.* 1987), can play an important part in determining their seedling emergence times.

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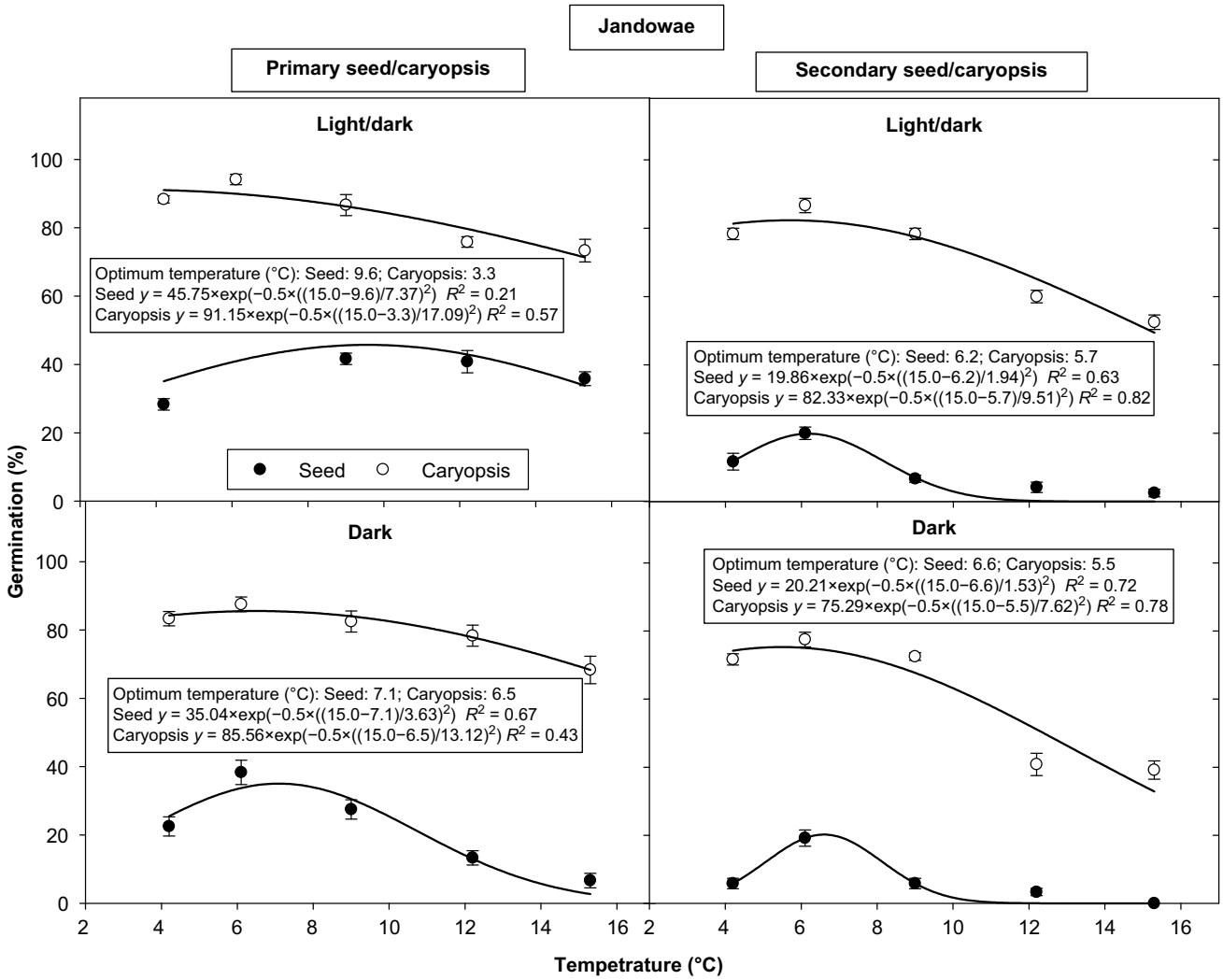

Fig. 4. Effect of light and temperature on germination percentage of primary or secondary seeds (solid symbols) or caryopses (open symbols) from biotype Jandowae. Seeds/caryopses were produced under ambient greenhouse conditions (23°C/12°C (±3°C) day/night temperature and relative humidity 60% (±5%)) with soil-water content maintained at 100% gravimetric plant available water. Error bars represent standard errors of the mean of six replicate samples consisting of 20 primary or secondary seeds or caryopses. Data are a pooled set from two experimental runs. Curves represent three-parameter peak Gaussian model fitted to the final germination percentage data.

Conclusion

Avena ludoviciana was found to germinate under both light or dark conditions to varying degrees, and under a range of incubation temperatures from 4°C to 15°C. Both primary and secondary seeds showed higher germination under a light/dark photoperiod but could still germinate in continuous darkness. This means that seeds can germinate either from the soil surface or if buried within soil, which indicates the adaptation of this weed to either no-till or reduced-tillage conservation agriculture systems. Germination was higher when the incubation temperature was in the range 6–10°C, with an optimum of 7°C for the southern biotypes and 9°C for the northern biotypes. These results show that *A. ludoviciana* is a typical winter-germinating species regardless of the latitude of the NGR from which it originates. The findings indicate that, in the field, *A. ludoviciana* seeds are likely to experience favourable germination conditions coinciding with winter crop plantings (i.e. May–June in the NGR). However, germination is likely to be staggered owing to differences between primary and secondary seeds and the effects of hull-imposed dormancy, which may have important implications for weed management. Data on the rate of hull deterioration in the soil environment are needed to improve understanding of the longevity of both types of seed in the soil seedbank. In addition, further research is required into the seed biology of this weed under a variable changing climate, which is

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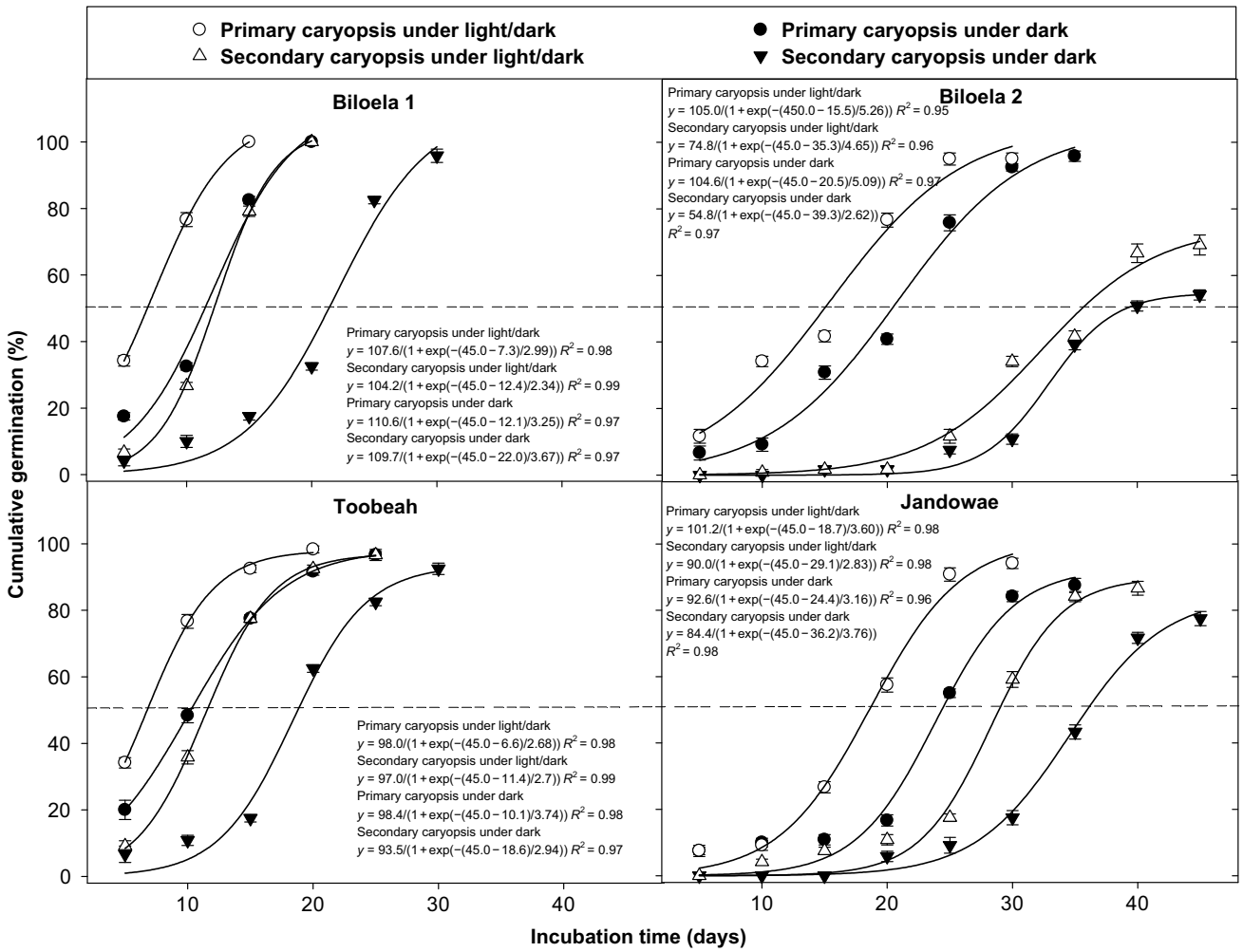

Fig. 5. Cumulative germination percentage of primary caryopses (circle symbols) and secondary caryopses (triangle symbols) incubated under light/dark (open symbols) or dark (solid symbols) conditions over time (days) at their optimum germination temperatures (Biloela 1 and 2, 9°C (±1°C); Toobeah and Jandowae, 7°C (±1°C)). Caryopses were produced under ambient greenhouse conditions (23°C/12°C (±3°C) day/night temperature and relative humidity 60% (±5%)) with soil-water content maintained at 100% of gravimetric plant available water. Error bars represent standard errors of the mean of six replicate samples consisting of 20 primary or secondary caryopses. Data are a pooled set from two experimental runs. Time to 50% germination (G_{50}) is indicated by the intersection of the curve with the dashed line.

becoming warmer and drier during August–October in the NGR (BOM and CSIRO 2020), at the time when seeds of this weed and crops mature.

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Data availability. The data that support this study will be shared upon reasonable request to the corresponding author.

Conflicts of interest. The authors declare no conflicts of interest.

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