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Elevated Temperature Affects *Avena sterilis* ssp. *ludoviciana* Reproductive Biology

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Abstract: The weed *Avena sterilis* ssp. *ludoviciana* has a high economic impact in the winter cereal crop production systems of Australia's northern grains region (NGR). In the NGR, the frequency of high-temperature periods at the end of winter is increasing. This shift in climate may modify this weed's maturity time and reproductive biology, and thereby impact on crop production. This study examined the reproductive biology of four *A. ludoviciana* biotypes in relation to elevated temperature when applied at different times during their seed development. Plants of all four *A. ludoviciana* biotypes were grown in an ambient temperature glasshouse (23/14 °C day/night). At panicle initiation, a portion of the plants were transferred to an elevated temperature glasshouse (29/23 °C day/night) and remained there until maturity. This process of plant movement was repeated on three further occasions with separate batches of plants, each 10 days apart. The remaining plants were kept under ambient conditions for their whole lifespan. Plants exposed to elevated temperature from panicle initiation to maturity, matured 18 days earlier than plants kept under ambient conditions, had 30% fewer filled seeds, 37% lower seed mass, and 40% less seed dormancy. Depending on the time and duration of plants exposed to elevated temperature, predicted seed longevity was ranged from 1 to 4 years in the soil seedbank. All reproductive traits were less affected when plants were exposed to elevated temperature at a later stage of development. If the frequency of high-temperature periods continues to increase, then it may lead to the development of less dormant populations of this weed that would be ready to germinate and re-infest the next winter crops under no-tillage conservation agriculture (that does not bury seeds deep in the soil profile). However, the seasonal climatic variability of the NGR in addition to the weed's natural genetic variability may contribute to a seedbank of both dormant and less dormant seeds—making this species an even more difficult-to-control weed.

Keywords: changing climate; elevated temperature; no-tillage conservation agriculture; wild oat maturity; seed dormancy; seed longevity

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Citation: Ali, M.; Williams, A.; Widderick, M.; Adkins, S. Elevated Temperature Affects *Avena sterilis* ssp. *ludoviciana* Reproductive Biology. *Agronomy* **2023**, *13*, 474. https://doi.org/10.3390/agronomy13020474

Academic Editors: Jose L. Gonzalez-Andujar and Guillermo R. Chantre

Received: 23 December 2022
Revised: 27 January 2023
Accepted: 31 January 2023
Published: 6 February 2023

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1. Introduction

Wild oat (*Avena sterilis* (L.) spp. *ludoviciana* (Durieu) Nyman; hereafter *A. ludoviciana*) is one of the most economically important weeds within the northern grains region (NGR, comprising parts of Queensland and all of New South Wales) of Australia [1]. This weed was problematic across the NGR at an earlier time, when the approach of conventional agriculture was commonly used, and has maintained its importance over the past 40 to 50 years during the adoption of conservation agriculture (CA) [2–4]. This weed also has the potential to spread further within the NGR with the increasing adoption of no-tillage CA (NTCA) [5]. However, the persistence mechanism of this weed has not been studied much in the NGR or around the globe, especially under the context of a changing climate.

It has been observed from previous studies [6–11] conducted on its close relative, *A. fatua* L., that the growing environment, especially atmospheric temperature, and soil

water status can manipulate the persistence mechanisms of *A. fatua*. Due to environmental stresses, *A. fatua* plants were reported to produce fewer seeds than when grown under favorable conditions [7,11,12]. However, these seeds matured earlier and shattered to the ground before the crop matured [7,8,11,12], the level of seed dormancy was reduced [6–8,11,13,14], and seed viability declined substantially [11,15,16]. Genetic factors are also reported to be responsible for impacting the persistence mechanism of *A. fatua* [17–19]. Due to genetic factors, the dormancy level present in the two kinds of seeds (the larger one referred to as the primary seed, and the smaller one referred to as the secondary seed) produced in the same spikelet, and among different biotypes can be variable [20], which all favor *A. fatua* to infest crops at different growth stages.

In the NGR, the frequency of warm and dry periods is increasing under the present changing climate scenario, especially during the late winter/early spring period [21]. However, the response of *A. ludoviciana* towards these kinds of shifts in climate is unknown. Unlike *A. fatua*, no studies have been carried out on seed characteristics (e.g., dormancy and longevity) of *A. ludoviciana* growing under a stressful environment. Although warm and dry periods often occur together, it is possible and relatively common to receive one without the other [22].

Our study focused on understanding the reproductive biology of *A. ludoviciana* in response to elevated temperature. This study was conducted across two consecutive years to evaluate the effect of the timing and duration of a late-season elevated temperature event on the reproductive biology of four NGR *A. ludoviciana* biotypes. The aims were to (1) determine the differences in plant maturity time when an elevated temperature event was imposed at different times during seed development; and (2) determine the seed production, seed mass, seed dormancy, and seed longevity in relation to the timing and duration of the imposed elevated temperature event. This knowledge is critical to understanding its ecological response and persistence mechanisms within the NGR cropping systems under rising atmospheric temperature. Knowing this information will help to determine the most effective management strategy for this weed.

2. Materials and Methods

2.1. Biotypes Used

Spikelets of four biotypes of *A. ludoviciana* were collected from four locations in the NGR viz. Biloela (northern zone of NGR; Biloela 1: −24.3547, 150.4977 and Biloela 2: −24.3504, 150.4977), Toobeah and Jandowae (southern zone of NGR; Toobeah: −28.3679, 149.5219 and Jandowae: −26.6672, 151.0246). *A. ludoviciana* infested wheat (*Triticum aestivum* L.) fields where NTCA had been practiced for >30 years. Spikelets were collected in November 2017 from mature *A. ludoviciana* plants located at least 10 m from the paddock edge along a 'W-shaped' transect with a depth of approximately 50 m. On average, 1000 spikelets were collected from each site. After collection, spikelets were air-dried under shade for 3 to 4 days, cleaned and then placed into paper bags and stored in a dedicated seed store in the dark at 15 ± 2 °C, 15 ± 5% relative humidity (RH) at the University of Queensland, Gatton (−27.5540, 152.3390), Australia, until used for pot trial (approximately 6 months later for the first-year trial and 18 months later for the second-year trial). The four biotypes provided a good geographic coverage of the area, over which *A. ludoviciana* populations are found in the NGR [20,23,24], and covered a range of temperature and rainfall conditions. Over a 20-year period (1999 to 2018), Biloela and Toobeah both experienced monthly mean maximum and minimum temperatures of 28/10 °C and average rainfall totals of 98 and 92 mm, respectively, from August to October 2021 (the time when seeds of *A. ludoviciana* usually develop and mature). At the same time of the year, Jandowae experienced monthly mean maximum and minimum temperatures of 26/9 °C and average rainfall totals of 117 mm [21]. October minimum temperatures in Biloela sometimes reached 21 °C, Toobeah 24 °C and Jandowae 20 °C [21]. The definition of the spikelet, and primary and secondary seed/caryopsis are described in Ali et al. [25].

2.2. Experimental Design and Treatment Set Up of Pot Trial

The pot trial was conducted from June to October 2018 and was repeated from June to October 2019 on both occasions using a completely randomized design with six replications. Approximately 100 spikelets from each biotype were randomly collected from the bulked seed lots that had been stored in the seed storage facility. The primary seed from each spikelet was then separated from the secondary seed and dehulled by hand. These dehulled primary seeds (i.e., primary caryopses) were germinated in a germination incubator under conditions of 15/5 °C thermoperiod with 12/12 h light/dark photoperiod and 47 ± 2% RH. Subsequently, three healthy seedlings were transplanted per experimental unit, i.e., 20 × 19 cm diameter/height plastic pot (containing 4.5 kg of a black Vertosol soil; 50% clay, pH 7.3).

In total, 30 pots were used per biotype. The pots were maintained at a gravimetric plant available water content (PAWC) [26] of 100% throughout the trial. Soil water content was determined by weighing each pot every 2 days. PAWC of each pot was maintained according to the weight of the pot. Plants were grown to panicle initiation in a greenhouse under ambient conditions of 23/12 ± 2 °C thermoperiod under a natural day/night photoperiod, and 60 ± 5% RH, determined by TGP-4520 Tinytag Plus 2 logger (Gemini Data Loggers Ltd., Chichester, UK) at the University of Queensland, Gatton, Australia.

At the time of panicle initiation i.e., Biologische Bundesanstalt, Bundessortenamt, Chemische Industrie (BBCH) code 49 [27], six pots per biotype were moved from the ambient greenhouse to a temperature-controlled glasshouse (TCG) to impose the elevated temperature treatment (29/23 ± 2 °C and 50 ± 5% RH, with a natural photoperiod), where they remained until maturity. This process of plant movement was repeated on three further occasions with separate batches of plants, each 10 days apart (Table 1). Similar to *A. fatua* [6–9], BBCH code 49 was selected to expose *A. ludoviciana* plants to the stress environment to examine their reproductive biology. In total 24 out of 30 pots per biotype were moved to the TCG. The remaining six pots were never removed from the ambient temperature glasshouse, and these pots were considered as control plants. Pot positions in both houses were rerandomized every 2 days to minimize potential microclimate effects. The selection of an elevated temperature (29/23 °C day/night temperature) was considered based on historic climate data for the NGR [21].

Table 1. The four times when *Avena sterilis* ssp. *ludoviciana* plant batches were moved from the ambient temperature greenhouse (23/12 ± 2 °C day/night temperature) to the temperature-controlled glasshouse (29/23 ± 2 °C day/night temperature) to expose them to the elevated temperature.

Elevated Temperature Treatments		at Panicle Initiation (PI)	10 Days after Panicle Initiation (10 DAPI)	20 Days after Panicle Initiation (20 DAPI)	30 Days after Panicle Initiation (30 DAPI)
Biotypes		**Days to Reach These Stages of Development**			
Northern zone	Biloela 1	58	68	78	88
	Biloela 2	58	68	78	88
Southern zone	Toobeah	63	73	83	93
	Jandowae	65	75	85	95

2.3. Data Collection and Spikelet Storage

The number of days taken to reach physiological maturity was recorded for all plants and biotypes. Physiological maturity was defined as the time when 50% of the spikelets coming from one plant were ready to be shed from the plant. The total number of spikelets was counted for all plants (in total 360 plants) of all four biotypes. Physiologically mature spikelets were collected by hand, placed into paper bags, and stored in a seed store in the dark at 15 ± 2 °C, 15 ± 5% RH. Later, the total number of filled and empty primary and secondary seeds per plant was determined by X-ray imaging (Faxitron Specimen Radiography System, Lincolnshire, IL, USA). For this, 12 lots of 25 spikelets were taken from the bulked seed lots (combined across replicates of each biotype × elevated temperature

and control treatments). The data were then converted to total numbers of filled and empty primary or secondary seeds produced per plant. The 1000-primary and 1000-secondary seed weights were determined by taking four lots of 50 filled seeds (from the seeds that were separated for determination of filled and empty primary and secondary seed production per plant) and drying them in an oven at 80 ± 5 °C for a period of 96 h. Once dry, these 200 seeds were weighed, and values were multiplied by five to reach 1000 seed weight. After about 20 days of the first lot of spikelets being collected, the dormancy and viability tests were carried out on the filled primary and secondary seeds and caryopses.

2.4. Dormancy Tests

To determine the dormancy status of the freshly harvested seeds and caryopses, 20 days after the first lot of spikelet collection, two separate germination studies were undertaken simultaneously using (1) a thermogradient-bar germination chamber (T-bar; Lindner and May Industries, Brisbane, Australia) applied to intact seeds and (2) a germination incubator (TRIL-750 Illuminated Refrigerator Incubator, Thermoline, Wetherill Park, Australia) applied to caryopses. The T-bar test provided an understanding of the degree of hull (palea and lemma)-imposed dormancy of the fresh seeds, whereas the germination incubator test provided an understanding of the degree of embryo dormancy present in the fresh caryopses. For both germination studies, (T-bar or germination incubator), spikelets were randomly collected from the bulked seed lots. Primary and secondary seeds were separated from spikelets and hand processed for the studies. Seeds/caryopses were surface sterilized using the method described by Ali et al. [25]. After surface sterilization, seeds/caryopses were rinsed four times with sterilized deionized water and then placed into Petri dishes. Each Petri dish contained two Whatman No 1 filter papers wetted with 5 mL of sterile water containing Previcur fungicide at a rate 2 mL Previcur L^{-1} of water [25].

Dormancy test of seeds in the T-bar: Three replicate Petri dishes each containing 20 primary or secondary seeds per treatment were used for this test in both years trial. Seeds were imbibed under constantly applied temperatures of either 4, 6, 9, 12 or 15 ± 1 °C using a 12/12 h light/dark photoperiod. Petri dishes were illuminated using overhead cool white fluorescent light producing a daytime photosynthetic photon flux density of about 100 µmol m^{-2} s^{-1} at the level of Petri dish incubation. Germination counts were undertaken at 2-day intervals for a total of 42 days. Germination was defined as the protrusion of coleorhiza through the husk, or through the pericarp, for seeds and caryopses, respectively. The germinated seeds were removed from the Petri dishes after each counting session. At the end of 42 days of imbibition, the non-germinated seeds were tested for viability using the method described by Ali et al. [25]. The caryopses that germinated after this additional treatment were viable but initially dormant. All seeds and caryopses used in this study in both years were found to be viable.

Dormancy test of caryopses in the germination incubator: Three replicate Petri dishes each containing 20 primary or secondary caryopses coming from panicle initiation (PI), 20 days after panicle initiation (DAPI), and control treatments were used for this test in both years' trials. The test was conducted under a previously determined optimum day/night temperature of 15/5 ± 1 °C, and with a matching 12/12 h light/dark photoperiod using cool white fluorescent light as described above. The test ran for 42 days, and after that period, both the primary and secondary non-germinated caryopses were tested for viability [25]. All caryopses used in this test were found to be viable.

2.5. Seed Longevity Determined Using Controlled Ageing Test

A laboratory-based controlled ageing test (CAT) was conducted to determine the potential seedbank longevity of primary and secondary seeds coming from PI, 20 DAPI and control treatments. For this purpose, 12 replicate glass vials each containing 20 primary or secondary caryopses coming from PI, 20 DAPI and control treatment of all four biotypes were used in both years. The CAT was conducted according to the method described by Long et al. [28] but with the following modifications: (1) 20 primary or secondary

fresh caryopses were placed into each glass vial; (2) instead of an oven, an incubator (Model: Polar 1000, Contherm Scientific Ltd., Hutt City, New Zealand) was used for the pre-equilibrium phase (7 ± 2 °C and 47 ± 2% RH for 21 days) as well as for the ageing phase (48 ± 2 °C and 60 ± 3% RH); (3) caryopses were kept in darkness in both phases; (4) Tinytag Plus 2 data loggers were used to monitor temperature and RH conditions inside the sealed boxes; (5) during the ageing phase, glass vials were removed at 0, 5, 16, 30, 39, 55, 70, 85, 100 and 118 days to examine their viability by incubating caryopses for 21 days under 15/5 ± 1 °C, 12/12 h light/dark photoperiod and with an addition of 10 µM of gibberellic acid (GA_3; Sigma-Aldrich Pty. Ltd., Macquarie Park, NSW, Australia) at a rate of 5 mL per Petri dish to overcome dormancy issue. The germinated caryopses were counted as viable and non-germinated caryopses were considered dead. The number of viable caryopses was plotted against time to determine their P_{50} value (predicted time for seed lot viability to fall to 50%).

2.6. Thermal Time Calculation

To understand the impact of elevated temperature on plant maturation, thermal time (degree days) was calculated with the following equation [29]:

Thermal time (degree days) = [(Maximum temperature + Minimum temperature)/2] − Base temperature

The base temperature was set as 0 °C [30]. Thermal time calculations began when the germinated seedlings were transplanted to the pots and continued until maturity. Thermal time data calculation considered the greenhouse temperature data until the plants exposed to the elevated temperature in the TCG and from this point forward, TCG's fixed temperature (29/23 °C) was counted to calculate the rest thermal time (until maturity as per treatment). The experiment ran for two years and therefore thermal time was calculated for 2 years, and their average was determined to interpret experimental results.

2.7. Statistical Analysis

Pot trial: The data from the two repeats of the pot trial were pooled before analysis, as the effect of the repeat trial was non-significant ($p \geq 0.05$) for all parameters measured. Plant responses to the elevated temperature treatments were analyzed using an analysis of variance (ANOVA) performed using Minitab software. Means were separated using Bonferroni's protected least significant difference (LSD) test at $p \leq 0.05$. The relationship between the time of plant maturation and seed weight was determined by plotting 1000 filled primary or secondary seed weight against plant maturation time under elevated temperature treatments using a linear regression model in SigmaPlot software 14.0. The coefficient of determination (R^2) value was used to determine the goodness of fit of the linear regression model.

Dormancy tests: The data from the two repeats of the T-bar or germination incubator tests were pooled before analysis, as the effect of the repeat experiment was non-significant ($p \geq 0.05$) for both tests. For the T-bar test, the data were analyzed against an individual germination temperature either for the primary or secondary seeds. Data for both tests (T-bar and germination incubator) were expressed as cumulative germination percentages. Data were analyzed using ANOVA, performed using Minitab software. Means were separated using Bonferroni's protected LSD test at $p \leq 0.05$.

Seed longevity tests: The average data from the two repeats of the study were pooled, as the effect of the repeat experiment was nonsignificant ($p \geq 0.05$). Caryopsis viability (expressed as a percentage of germination) was plotted against time (days) in ageing conditions. A nonlinear regression analysis was carried out using SigmaPlot to estimate P_{50} value through fitting sigmoid, three-parameter curves to the data using the following equation:

$$Caryopsis\ viability(\%) = \frac{a}{1 + e^{\frac{-(x-x0)}{b}}}$$

where a is fitted initial viability (percentage), b is the rate of viability loss in the rapidly declining section of the curve, x is the accumulated time in the CAT (in days), and $x0$ is the P_{50} value.

3. Results

3.1. Time to Plant Maturity

From the ANOVA, it was observed that the time of imposition of elevated temperature had a significant effect ($p = 0.007$; Figure 1) on the time to plant maturity of all biotypes. Plant maturity time differed between the northern and southern NGR biotypes, and due to the timing and duration of elevated temperature imposed on the plants (Figures 1 and 2). The two northern biotypes (Biloela 1 and 2) matured in around 95 days (an average of all different timing and duration of elevated temperature), 6 to 11 days earlier than southern biotypes (Toobeah and Jandowae), which matured in around 105 days (Figure 1). However, elevated temperature imposed at an early stage of seed development and continued until maturity (i.e., PI) resulted in rapid maturation compared to their control plants in all biotypes (Figure 1). Plants of all biotypes matured in 92 days under PI, i.e., 18 days earlier than their control plants (Figure 1). The rate of plant maturity varied depending on the timing and duration of elevated temperature applied during seed development (Figures 1 and 2).

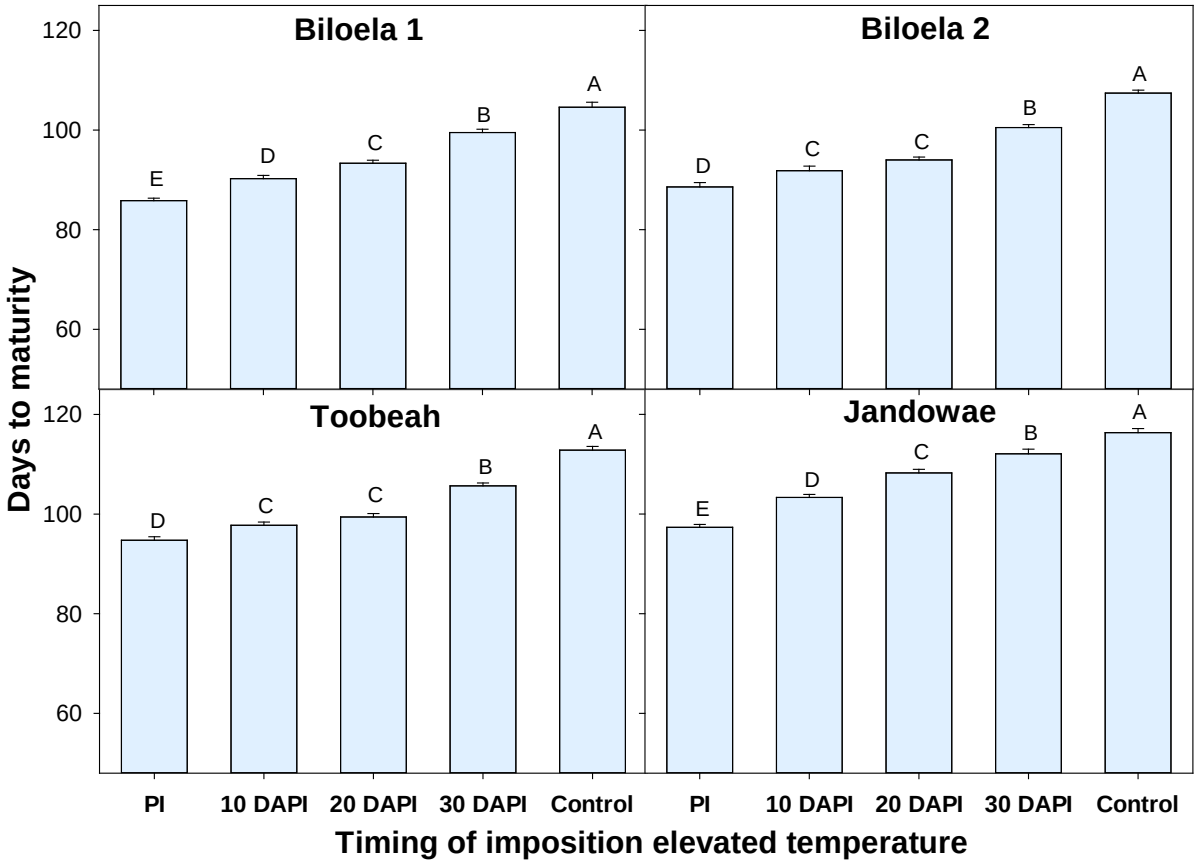

Figure 1. Effect of elevated temperature applied at panicle initiation (PI), 10 days after panicle initiation (10 DAPI), 20 DAPI or 30 DAPI, on plant maturity time of four *Avena sterilis* ssp. *ludoviciana* biotypes. Error bars represent standard errors of the mean of 12 replicates and represent pooled data from two experimental runs. Different letters within a biotype indicate significant differences among the treatments (Bonferroni test).

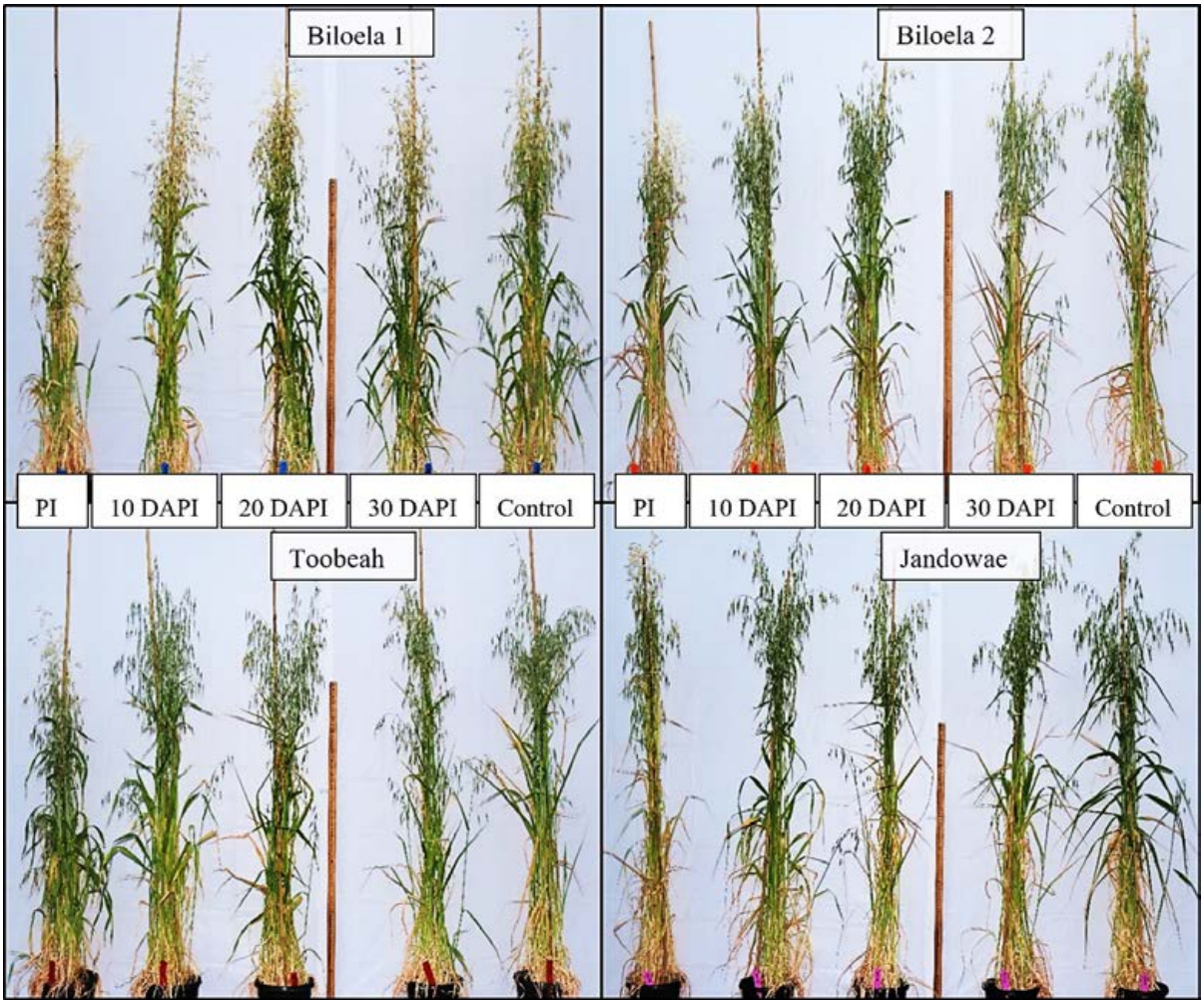

Figure 2. Effect of time of imposition of elevated temperature on the maturity of four *Avena sterilis* ssp. *ludoviciana* biotypes. Pots from left to right are randomly selected plants of elevated temperature applied at panicle initiation (PI), 10 days after panicle initiation (10 DAPI), 20 DAPI, 30 DAPI and control (no imposition of elevated temperature) treatments. Plants within a biotype matured approximately 18, 14, 11 and 6 days earlier using PI, 10 DAPI, 20 DAPI and 30 DAPI treatments compared to the control treatment. Images were taken 80 days after planting.

3.2. Seeds Produced

The time of imposition of elevated temperature had a significant effect ($p \leq 0.001$) on the production of filled and empty primary and secondary seed production of all biotypes (Figure 3). The greatest number of filled and the lowest number of empty primary and secondary seeds were produced by the control plants of each biotype, whereas the opposite occurred under the PI treatment (Figure 3). Filled primary and secondary seed production of all biotypes was reduced by 30 to 35%, and empty primary and secondary seed production was increased by three- to sixfold under PI treatment as compared to the control (Figure 3). The filled primary and secondary seed production was gradually increased, and empty primary and secondary seed production was gradually decreased when plants were exposed to an elevated temperature at later times during their development and this was observed in all biotypes. Filled primary and secondary seed production were reduced by only 5% under 30 DAPI as compared to the control.

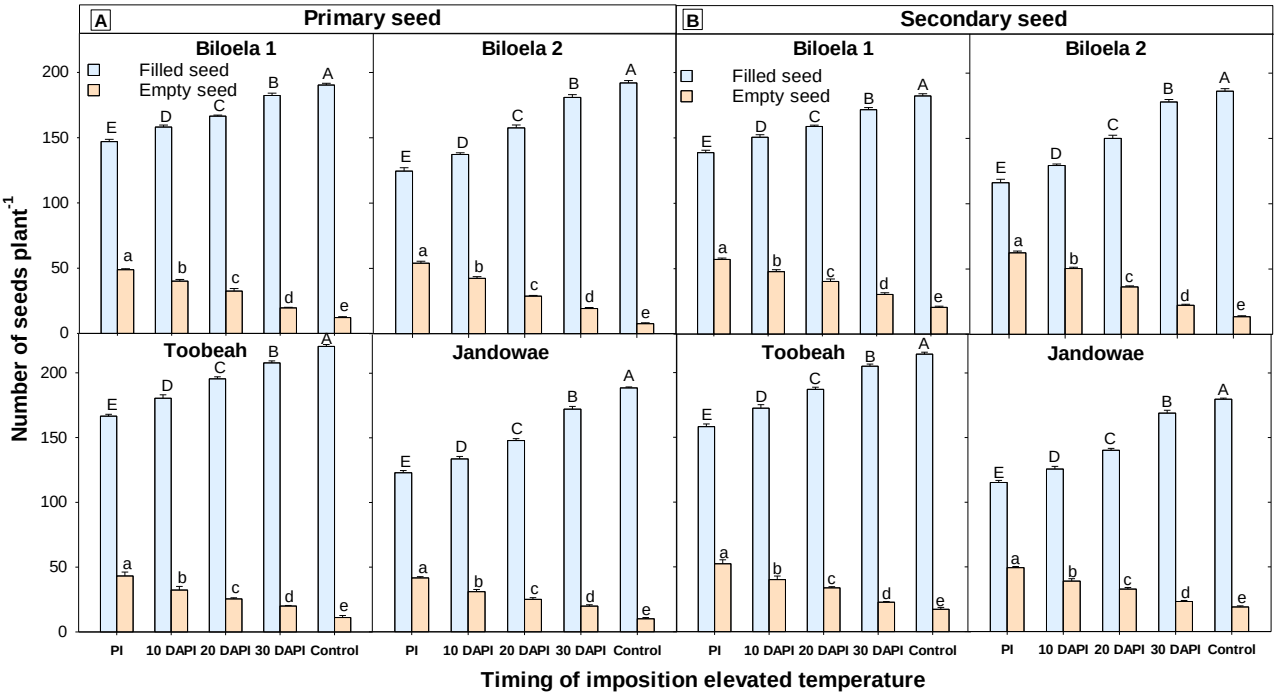

Figure 3. Effect of elevated temperature applied at panicle initiation (PI), 10 days after panicle initiation 10 DAPI, 20 DAPI or 30 DAPI, on the production of filled and empty (**A**) primary seeds, (**B**) secondary seeds plant^{-1} of four *Avena sterilis* ssp. *ludoviciana* biotypes. Error bars represent standard errors of the mean of 12 replicates and represent pooled data from two experimental runs. Letters within a biotype indicate significant differences among the treatments (Bonferroni test). Upper- and lower-case letters are used for filled and empty seeds, respectively.

3.3. 1000 Primary and Secondary Seed Weight

A significant effect ($p \leq 0.001$) of the time of imposition of elevated temperature was observed on primary seed weight of all biotypes (Figure 4). The mass of the secondary seeds was also greatly impacted due to the timing and duration of elevated temperature on all biotypes ($p \leq 0.001$; Figure 4). Among the biotypes, Jandowae produced the largest primary and secondary seeds when grown under control conditions (Figure 4); however, seed mass was reduced by 30% at PI compared to the control. The seed mass of Biloela 1 was greatly impacted by the timing and duration of imposition of elevated temperature (51% reduction in seed weight at PI, as compared to the control) (Figure 4). Interestingly, the mass of the primary seed was always twofold greater than its secondary seed mass. There was also a positive effect observed between the plant's maturity time and the seed mass of both the primary and secondary seeds (Figure 5). Seed weight of all biotypes was reduced as the time to plant maturity reduced because of the elevated temperature imposed at different times during their seed development as compared to their control plants.

3.4. Dormancy Test of Seeds in the T-Bar

The ANOVA test shows the constant incubation temperatures of 6 °C ($p = 0.040$) and 9.0 °C ($p = 0.007$) were found to significantly increase the germination of primary seed from all four biotypes produced under elevated temperature and when imposed at different times during their development (Figure 6). In addition, a constant incubation temperature of 9 °C ($p = 0.029$) was found to significantly increase germination of secondary seeds (Figure 6). Both primary and secondary seeds of the two northern biotypes provided the highest levels of germination at 9 °C whereas the two southern biotypes germinated best at 6 °C (Figure 6). Except for Biloela 2, 70% of the primary seeds and 50% of the secondary seeds of all other biotypes coming from the PI treatment were found to germinate at their optimum germination temperature, a 50% increase in germination as compared to the

seeds produced by their control plants. Biloela 2 seemed to possess a deeper dormancy as compared to the other biotypes. However, seeds of all biotypes produced under lately imposed elevated temperature were found to be less dormant than control plants but had greater dormancy than PI treatment (Figure 6).

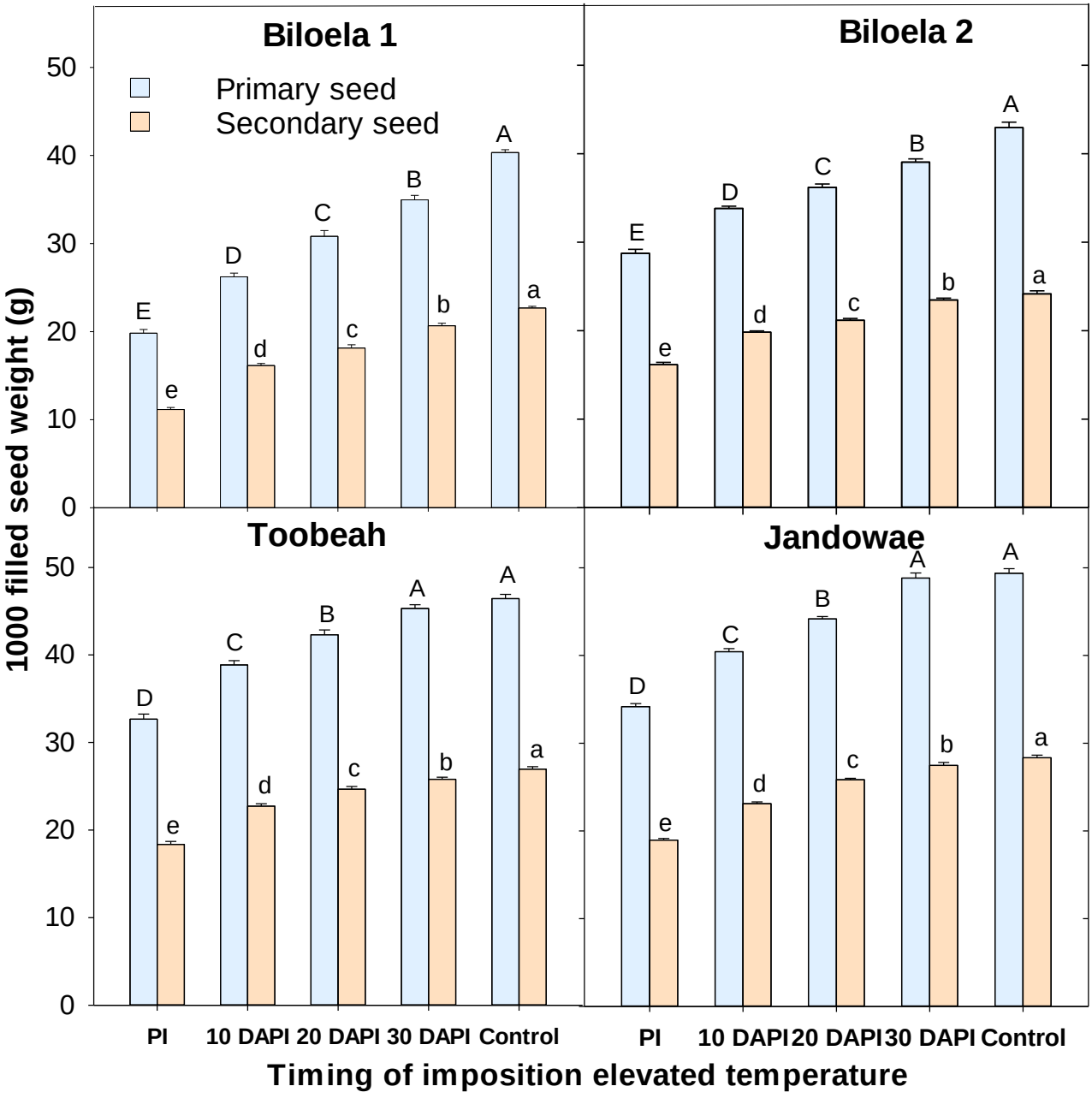

Figure 4. Effect of elevated temperature applied at panicle initiation (PI), 10 days after panicle initiation 10 DAPI, 20 DAPI or 30 DAPI, on the 1000 filled seed weight of both primary and secondary seeds from four *Avena sterilis* ssp. *ludoviciana* biotypes. Error bars represent standard errors of the mean of 12 replicates and represent pooled data from two experimental runs. Letters within a biotype indicate significant differences among the treatments (Bonferroni test). Upper- and lower-case letters are used for 1000 primary and 1000 secondary filled seed weight, respectively.

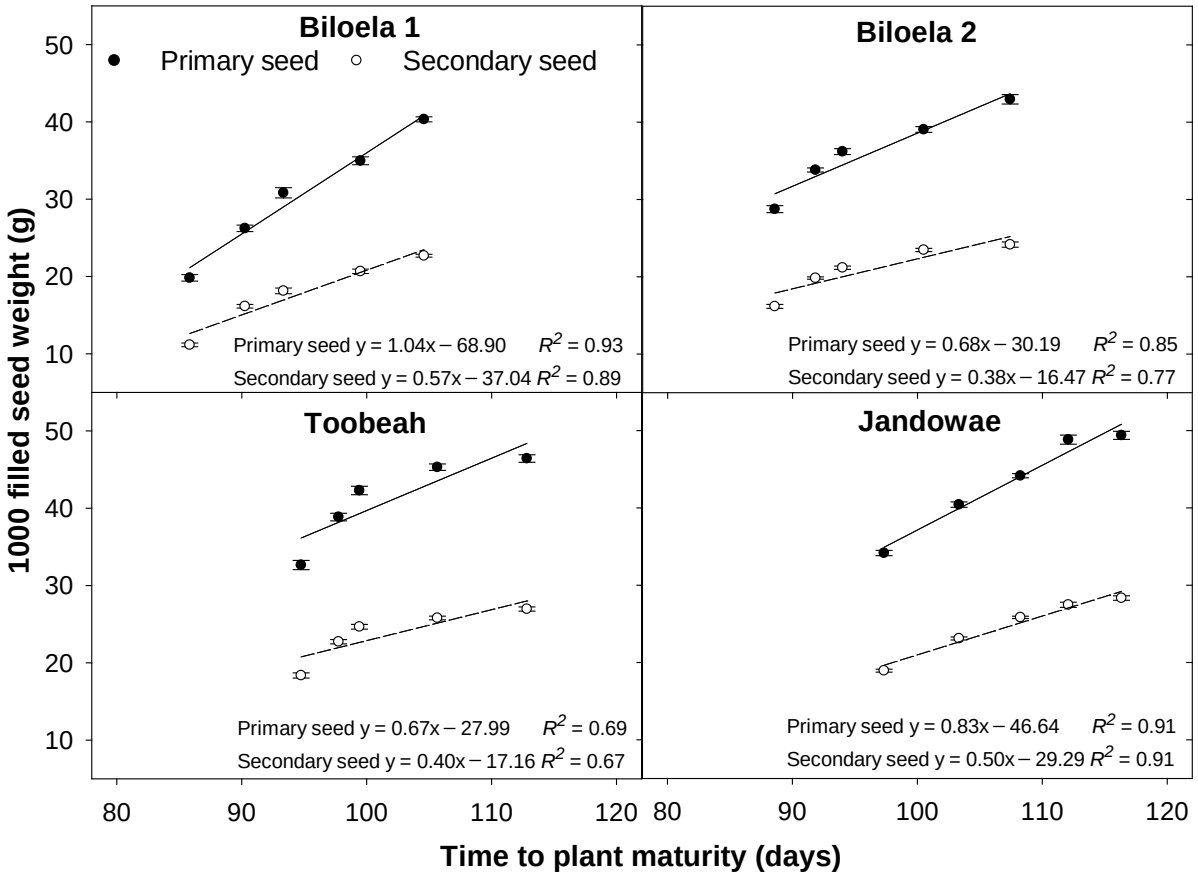

Figure 5. Relationship between the time to plant maturity and 1000 filled seed weight of both primary (solid symbol) and secondary (open symbol) seeds of four *Avena sterilis* ssp. *ludoviciana* biotypes. Error bars represent standard errors of the mean of 12 replicates and represent pooled data from two experimental runs. Lines represent fitted linear regressions.

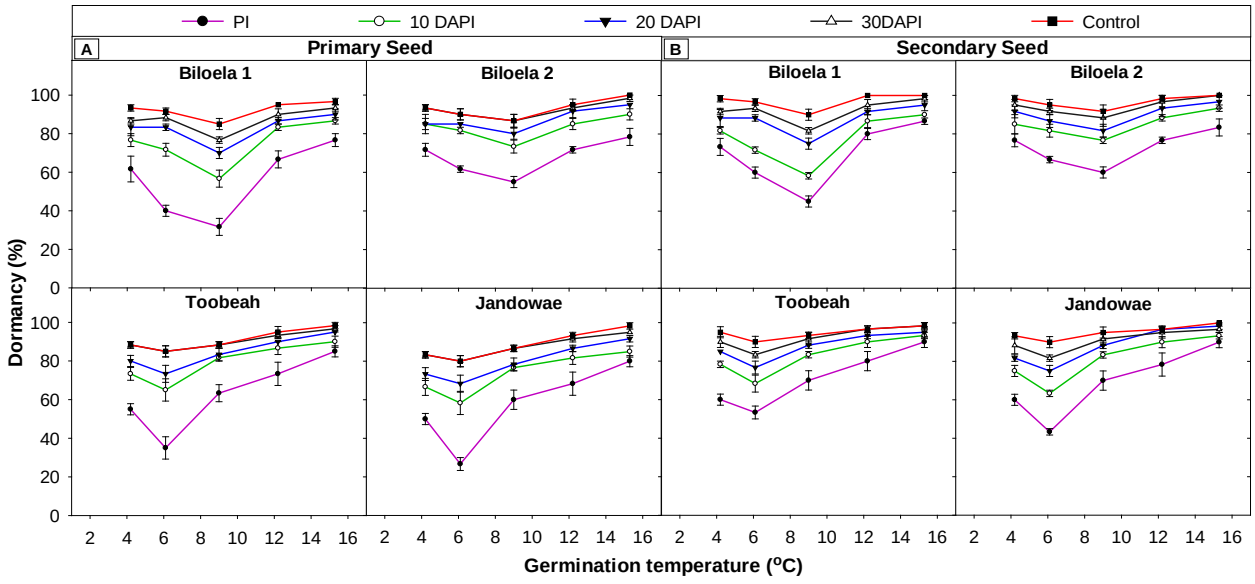

Figure 6. Effect of elevated temperature applied at panicle initiation (PI), 10 days after panicle initiation 10 DAPI, 20 DAPI or 30 DAPI, on the dormancy (%) of freshly harvested (**A**) primary seeds, and (**B**) secondary seeds of four *Avena sterilis* ssp. *ludoviciana* biotypes. Error bars represent standard errors of the mean of six replicates of 20 seeds and represent pooled data from two experimental runs.

3.5. Dormancy Test of Caryopses in the Germination Incubator

Significant main effects of the elevated temperature treatment applied at different times during seed development ($p \leq 0.001$) as well as biotypes ($p \leq 0.001$) were observed to impact on the dormancy status of both primary and secondary caryopses (Figure 7). Dehulling the seeds (i.e., removing palea and lemma) was found to significantly reduce seed dormancy. Primary caryopses were found to have less dormancy than secondary caryopses in all biotypes. More than 90% of primary caryopses were found to germinate under PI of all biotypes (70% germination in the case of Biloela 2). A 20 to 30% greater dormancy was observed in the secondary caryopses (compared to primary caryopses) under each growing environment (Figure 7).

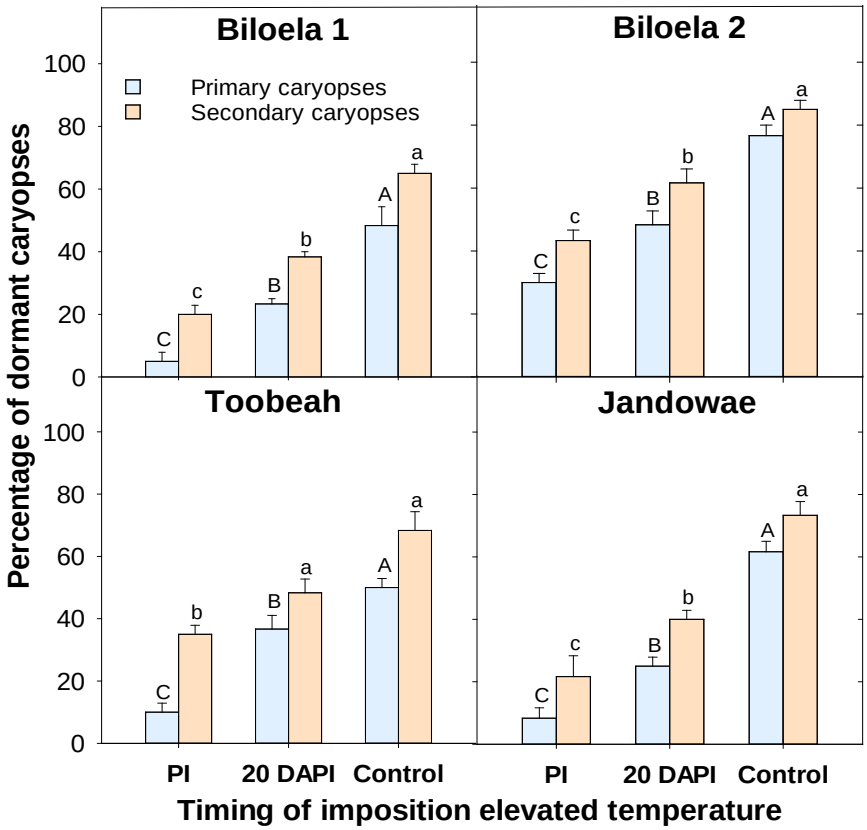

Figure 7. Effect of elevated temperature applied at panicle initiation (PI) or 20 days after panicle initiation (20 DAPI) along with a control (no imposition of elevated temperature) treatment on the dormancy (%) of the freshly harvested primary and secondary caryopses (palea and lemma removed) of four *Avena sterilis* ssp. *ludoviciana* biotypes. Error bars represent standard errors of the mean of six replicates of 20 caryopses and represent pooled data from two experimental runs. Letters within a biotype indicate significant differences among the treatments (Bonferroni test). Upper- and lower-case letters are used for primary and secondary caryopses, respectively.

3.6. Seed Longevity Determined by CAT

The caryopses coming from secondary seeds retained viability longer than primary caryopses in every treatment (Figure 8; Table 2), and for all biotypes. However, caryopses of primary and secondary seeds produced under PI lost their viability faster than 20 DAPI and control for all the biotypes ($p \leq 0.0001$; Figure 8). Among the biotypes, primary and secondary caryopses of Biloela 1 lost their viability faster under different treatments compared to other biotypes (Figure 8). Both the southern biotypes lost their viability at the same time (Figure 8). The other northern biotype Biloela 2 took the longest time to decrease its viability to 50% compared to other biotypes (Figure 8).

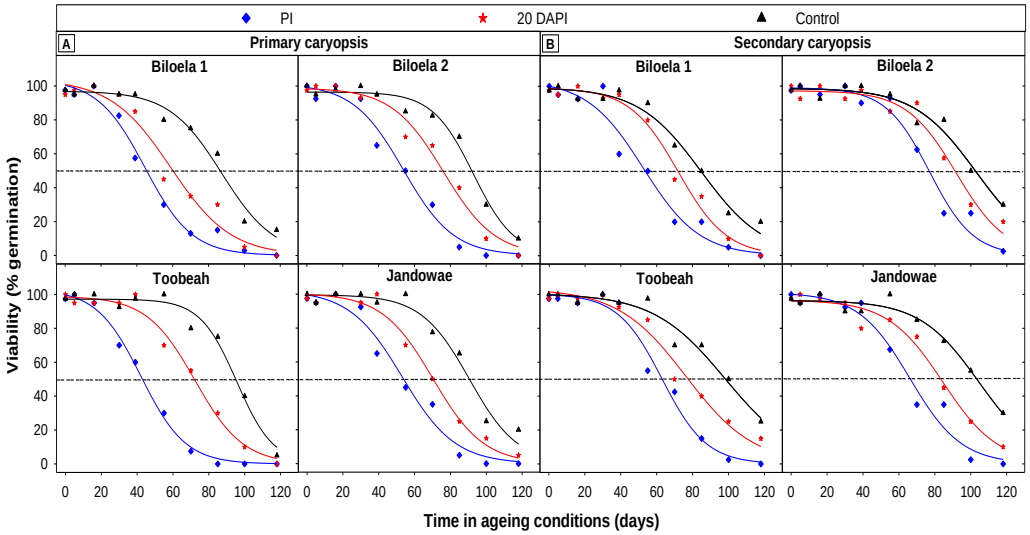

Figure 8. Response of (**A**) primary caryopses, and (**B**) secondary caryopses from four *Avena sterilis* ssp. *ludoviciana* biotypes to controlled aging at 48 °C and 60% relative humidity. Caryopses used in the test were either produced under elevated temperature applied at panicle initiation (PI) or 20 days after panicle initiation (20 DAPI) along with a control (no imposition of elevated temperature) treatment. Viability is expressed as the percentage of normal germination during 21 days of incubation at 15/5 °C day/night temperature with a matching 12/12 h light/dark photoperiod. The horizontal dashed line running across each panel identifies the time for a 50% reduction in viability of the seeds produced under different treatments.

Table 2. Fitted initial viability percentage (*a*), rate of viability loss in the rapidly declining section of the curve (*b*), days taken to 50% viability loss (P_{50}) and coefficient of determination (R^2) of primary and secondary caryopses of four biotypes of *Avena sterilis* ssp. *ludoviciana* found in the controlled aging test (CAT) at 48 °C and 60% RH. Caryopses used were produced under elevated temperature applied at panicle initiation (PI) and 20 days after panicle initiation (20 DAPI) along with a control (no imposition of elevated temperature).

Treatment	Biotype	Caryopsis Type	*a*	*b*	P_{50}	R^2
PI	Biloela 1	Primary	102	12	45	0.98
		Secondary	104	16	53	0.95
	Biloela 2	Primary	101	14	54	0.98
		Secondary	99	12	77	0.97
	Toobeah	Primary	103	12	42	0.99
		Secondary	100	12	63	0.98
	Jandowae	Primary	102	15	53	0.97
		Secondary	101	14	66	0.97
20 DAPI	Biloela 1	Primary	97	9	61	0.99
		Secondary	99	14	72	0.98
	Biloela 2	Primary	99	14	76	0.97
		Secondary	97	14	92	0.96
	Toobeah	Primary	99	13	72	0.98
		Secondary	103	19	76	0.97
	Jandowae	Primary	100	14	70	0.98
		Secondary	97	15	84	0.97
Control	Biloela 1	Primary	111	15	87	0.97
		Secondary	99	18	85	0.97
	Biloela 2	Primary	96	11	93	0.98
		Secondary	99	17	103	0.95
	Toobeah	Primary	97	10	96	0.97
		Secondary	100	20	98	0.95
	Jandowae	Primary	99	13	91	0.96
		Secondary	96	16	105	0.96

Primary seeds of all biotypes produced under PI had a predicted longevity of 1 to 2 years (short-lived) in the soil seedbank (Table 3). Interestingly, secondary seeds produced under the same stress environment (PI) had predicted longevity of about >2 to 4 years in most biotypes (Table 3), meaning they will have a greater seedbank life than the primary seeds. The predicted longevity of seeds (either primary or secondary) increased under 20 DAPI (>2 to 4 years or >4 years) and from the control treatment (>4 years) (Table 3).

Table 3. Response of primary and secondary caryopses of four biotypes of *Avena sterilis* ssp. *ludoviciana* to controlled aging test (CAT) at 48 °C and 60% RH and their predicted longevity in soil. Caryopses used were produced under elevated temperature applied at panicle initiation (PI) and 20 days after panicle initiation (20 DAPI) along with a control (no imposition of elevated temperature). Caryopses that lost 50% viability (P_{50}) in 40 days were categorized as transient (predicted longevity in the soil <1 year), caryopses reaching P_{50} in >40 to 60 days were categorized as short-lived (predicted longevity 1 to 2 years), reaching P_{50} in >60 to 80 days categorized as medium-lived (predicted longevity >2 to 4 years), and reaching P_{50} in >80 days categorized as long-lived (predicted longevity >4 years).

Biotype	PI		20 DAPI		Control	
	P_{50} Value (Days)	**Predicted Longevity in the Seedbank (Years)**	**P_{50} Value (Days)**	**Predicted Longevity in the Seedbank (Years)**	**P_{50} Value (Days)**	**Predicted Longevity in the Seedbank (Years)**
Primary caryopses/seed						
Biloela 1	41	1 to 2	62	>2 to 4	78	>2 to 4
Biloela 2	60	1 to 2	78	>2 to 4	91	>4
Toobeah	48	1 to 2	71	>2 to 4	82	>4
Jandowae	45	1 to 2	66	>2 to 4	84	>4
Secondary caryopses/seed						
Biloela 1	57	1 to 2	69	>2 to 4	83	>4
Biloela 2	74	>2 to 4	89	>4	102	>4
Toobeah	66	>2 to 4	82	>4	95	>4
Jandowae	63	>2 to 4	77	>2 to 4	97	>4

4. Discussion

4.1. Phenology

Periods of elevated temperature have an adverse effect on cereal crop growth, but the effect varies depending on the timing of the stress event, its duration, and its severity [31–34]. In the present study, it was observed that when plants were exposed to elevated temperatures early, this accelerated their maturation more (Figure 1). In addition, when plants were exposed to a long duration of elevated temperature, they matured more quickly (Figure 1). The PI treatment shortened *A. ludoviciana* maturity time by 18 days as compared to the control, and mature seeds were also produced more rapidly under PI than 30 DAPI (Figure 1). Earlier studies have shown that elevated temperature applied during the reproductive stage of *A. fatua* resulted in plants undergoing more rapid seed development [8,11,12]. These findings support the fact that thermal time is a determinant of plant maturation time [35], to which elevated temperature contributes (see Table 4). It can therefore be assumed that if a warmer condition occurs close to maturity, it will have less impact on the time of maturity and reproductive biology of this weed. In addition, in the field, it is unlikely for a weed to be exposed to elevated temperature throughout its entire seed development phase as was applied in this study. A shorter warmer period at PI might therefore result in a lower-level effect than those seen in this study. However, any kind of elevated temperature can adversely affect important plant physiological processes, such as photosynthesis, transpiration, and respiration [36–40]. Plant water loss is increased under an elevated temperature due to increased transpiration and this causes a fall in net

photosynthesis [36]. Elevated temperature has also been reported to reduce the size of the root system, an action that presumably would limit the supply of water [36,41,42].

Table 4. Thermal time (degree-days) of four *Avena sterilis* ssp. *ludoviciana* biotypes. Plants were grown in an ambient greenhouse until panicle initiation. Plants were exposed to the elevated temperature (29/23 ± 2 °C) at either panicle initiation (PI), 10 days after PI (DAPI), 20 DAPI or 30 DAPI.

Treatment	Days to Panicle Initiation	Thermal Time until Plants Exposed to Elevated Temperature (Degree-Days)			Days to Maturity	Thermal Time until Maturity (Degree-Days)		
		2018–2019	2019–2020	2-Years Average		2018–2019	2019–2020	2-Years Average
Biloela 1								
PI	58	852	884	868	86	1580	1612	1596
10 DAPI		1032	1063	1048	90	1604	1635	1620
20 DAPI		1224	1236	1230	93	1614	1626	1620
30 DAPI		1421	1437	1429	100	1733	1749	1741
Control		852	884	868	105	1795	1795	1795
Biloela 2								
PI	58	852	884	868	89	1658	1690	1674
10 DAPI		1032	1063	1048	92	1656	1687	1672
20 DAPI		1224	1236	1230	94	1640	1652	1646
30 DAPI		1421	1437	1429	101	1759	1775	1767
Control		852	884	868	107	1837	1837	1837
Toobeah								
PI	63	946	965	956	95	1778	1797	1788
10 DAPI		1124	1147	1136	98	1774	1797	1786
20 DAPI		1315	1332	1324	99	1731	1748	1740
30 DAPI		1515	1546	1531	106	1853	1884	1869
Control		946	965	956	113	1980	1980	1980
Jandowae								
PI	65	978	1002	990	97	1810	1834	1822
10 DAPI		1166	1180	1173	103	1894	1908	1901
20 DAPI		1356	1375	1366	108	1954	1973	1964
30 DAPI		1561	1583	1572	112	2003	2025	2014
Control		978	1002	990	116	2059	2039	2049

The northern biotypes were found to mature almost 7 days earlier than the southern biotypes (Figure 1). This could be because northern biotypes have become adapted to higher average seasonal temperatures in their place of origin (see Table 5), and in addition to avoid drought conditions that have been reported to occur later in the season [43]. By examining the 3-year (2015 to 2017) average maximum and minimum August/September temperatures experienced at the collection sites, there is about 3 °C of temperature difference between northern (27/9 °C day/night) and southern (24/7 °C day/night) sites (Table 5). A previous study reported that a 3 °C temperature change from 20/16 °C to 23/19 °C forced some northern NGR *A. fatua* biotypes to mature about 7 days earlier than their southern counterparts [12]. Clearly, seed maturity time for *A. ludoviciana* has both a genetic and environmental component.

Table 5. Monthly average temperature (°C) of the seed collection sites of *Avena sterilis* ssp. *ludoviciana* biotypes during their seed development time from August to October. The temperature data were collected from the nearest weather station of the seed collection sites (source: Bureau of Meteorology, Australian Government; www.bom.gov.au; accessed on 15 July 2021). The data were taken from 2015, 2016 and 2017 to understand temperature effect on the parent seeds and to interpret the experimental results.

Location		Year	Monthly Average Temperature (°C)						3-Month Average Temperature (°C)	
			August		September		October			
			Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.
Northern NGR	Biloela	2015	25.4	6.3	27.3	8.2	30.9	12.9	27.8	9.1
		2016	24.0	7.5	27.0	13.0	30.3	11.6	27.1	10.7
		2017	26.1	6.6	30.3	9.1	29.2	17.6	28.5	11.1
Northern NGR's 3-year average			25.2	6.8	28.2	10.1	30.1	14.0	27.8	10.3
Southern NGR	Toobeah	2015	21.9	5.8	26	7.9	33.7	16.9	27.2	10.2
		2016	21.3	5.5	23.0	10.2	27.5	11.7	23.9	9.1
		2017	23.9	3.6	28.9	8.4	29.6	15.0	27.5	9.0
		3-year average	22.4	5.0	26.0	8.8	30.3	14.5	26.2	9.4
	Jandowae	2015	21.7	3.9	24.5	6.8	29.7	12.3	25.3	7.7
		2016	20.7	5.8	21.9	9.9	27.5	9.6	23.4	8.4
		2017	23.8	5.3	29.7	8.1	27.2	15.6	26.9	9.7
		3-year average	22.1	5.0	25.4	8.3	28.1	12.5	25.2	8.6
Southern NGR's 3-year average			22.2	5.0	25.8	8.7	29.2	13.5	25.7	9.0

4.2. Reproductive Biology

An elevated temperature treatment applied at PI resulted in fewer filled seeds being produced (30% less) and more empty seeds (70% more) (Figure 3). Elevated temperature has been shown to increase floret sterility in rice (*Oryza sativa* L.) by diminishing pollen release and germinability, by reducing stigma receptivity to pollen, and causing damage to the ovary, all resulting in reducing fertilization [34,44,45]. In addition, present studies have shown that the filled seeds produced under the elevated temperature treatment were smaller in mass (Figure 4), and the mass reduction rate was dependent on the maturity time, which changed in response to the timing and duration of elevated temperature (Figure 5). An elevated temperature treatment applied at PI reduced the seed mass by about 37% as compared to the control. The reproductive biology of *A. ludoviciana* therefore largely depends on the timing and duration of the elevated temperature event. Although seed production and seed mass were greatly reduced under the PI treatment, the early maturity time of those plants would allow for most of the filled seed to shed to the soil surface sooner than without the elevated temperature treatment (Figure 5). Left on the soil surface, the germination results (Figures 6 and 7) suggest that most of these seeds under a NTCA system would be ready to germinate when the next available opportunity is present and produce healthy seedlings, and this could coincide with the time of planting next season's crop [25].

4.3. Dormancy Status

The dormancy present in seeds produced under all of the elevated temperature treatments was less intense than in the control, as indicated by their seed germination response, especially when imbibed at a cool temperature below 10 °C (Figure 6). Application of elevated temperature at PI resulted in seeds being produced with 35 to 40% lower dormancy than seeds produced from the control (Figure 6). However, the rate of dormant seed production was increased when elevated temperature was imposed late and for a shorter duration, though this rate was less than seen in the control (Figure 6). For example, 20 DAPI produced 27% more dormant seeds than was produced for PI, but 10% less dormant seeds

than the control. These findings are similar to those observed for *A. fatua* [20,46–48]. It was reported that elevated temperature during the reproductive stage reduced seed dormancy of *A. fatua* by increasing the α-amylase content in seeds (a requirement for seed germination) [7,8]. Gallagher et al. [49] also reported that certain stress conditions can reduce the phenolic acid (phytochemicals responsible for seed dormancy) concentration in the palea and lemma of *A. fatua* seeds—being a second reason for less dormancy in seeds.

The present study observed that secondary seeds possess a stronger dormancy mechanism than primary seeds (Figure 6), which confirms the work by Quail and Carter [20]. This presents a challenge in terms of management, as the less dormant primary seeds would be responsible for early infestation, whereas the more dormant secondary seeds would germinate at a later stage of crop growth, where they would avoid herbicide applications and produce enough seeds to replenish the seedbank [25,50]. Interestingly, the germination response of the northern and southern biotypes to the incubation temperature (northern biotypes had maximum germination at 9 °C, southern biotypes at 6 °C; Figure 6) indicates that the northern biotypes can germinate under marginally warmer conditions than the southern biotypes. O'Donnell [51] also observed a similar trend in northern and southern biotypes of *A. fatua*.

When the seeds were dehulled, a higher proportion of the caryopses were able to germinate under favorable incubation conditions and this occurred across all the stress treatments and biotypes (Figure 7). Numerous researchers have reported that germination of dormant *A. fatua* seeds is enhanced by removing the hull [11,49,52,53], as this is the location of one of several dormancy mechanisms present. Under current conditions, where elevated temperature events occur more frequently, it would be expected that the rapid development of seeds on the parent plant would result in poorly formed paleas and less developed physiological dormancy mechanisms in the caryopsis. The rate of hull decay might be an important factor to reduce the seed dormancy and longevity of this weed in the soil seedbank [53].

4.4. Longevity Status

Field seed persistence of both species of wild oat remains a major barrier to eradication of this weed from the cropping field [29]. Interestingly, in the present study, the rate of viability loss of *A. ludoviciana* seed differed between the four biotypes, the types of seeds studied, and importantly, based on their growing conditions (Figure 8). A prolonged elevated temperature was shown to reduce life expectancy in the soil seedbank. Seeds produced under PI treatment had a lower life expectancy (50% less) than the seeds produced under optimal conditions (Figure 8). In addition, this reduction in life expectancy seen in the primary caryopses was higher than for secondary caryopses. The slower viability loss seen in the secondary caryopses may be due to their inherent genetic characteristics [54]. This may also be illustrated by the variation in caryopses viability loss and seedbank longevity among the biotypes (Figure 8; Tables 2 and 3). In Australia, many researchers have identified *A. fatua* seeds to be short- to medium-lived types [31,55–58]. The life of *Avena* spp. seeds in the soil therefore differs depending on the environment in which their mother plants grow as well as due to their genetic variability.

5. Conclusions

In the present experiment, it was observed that the maturity time of biotypes, their seed number, seed mass, seed dormancy and seed longevity all decreased under elevated temperature and increased in a cool and wet environment. It is therefore understandable that more frequent elevated temperature events of the NGR results in the production of less dormant *A. ludoviciana* seeds, but a year of cool and wet environment results in the production of more filled seeds with greater dormancy. In addition to this environmental variability, the genetic variability between seed types contributes to a seedbank of *A. ludoviciana* that represents a combination of both less dormant and more dormant seeds. The less dormant seeds can germinate immediately in the following seasons, but the more

dormant seeds contribute to the longevity of the seedbank. This is likely to be a major contributor to the survival of this weed in the NGR cropping environment.

Author Contributions: M.A. and S.A. contributed to the conception and design of the experiment. M.A. and A.W. contributed to acquisition, analysis and interpretation of data. M.A., A.W., M.W. and S.A. contributed to drafting and revision of the manuscript. All authors have read and agreed to the published version of the manuscript.

Funding: This research was funded by the Grains Research and Development Corporation (GRDC; project ID 9175899).

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: Not applicable.

Data Availability Statement: The data presented in this study are openly available in 10.6084/m9.figshare.21729014.

Acknowledgments: The authors would like to thank the grain growers of Australia, and GRDC for their significant contributions to undertaking the PhD research.

Conflicts of Interest: The authors declare no conflict of interest.

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