

A study of the vernalisation requirements of mountain rye (*Secale strictum* syn. *S. montanum*) may help explain low grain yields of perennial cereals compared to wheat

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Abstract

Mountain rye (MR: *Secale strictum* syn. *S. montanum*) is a forage grass that is considered a candidate for perennial grain development in Australia. A greater understanding of the triggers for flowering would aid the integration of this dual-purpose perennial into Australian grazing and cropping systems. The objective of this experiment was to determine the effects of cold incubation (vernalisation) periods of varying duration on the grain yield, biomass production, and phenology of MR, compared to a dual purpose annual winter wheat cultivar (AW: *Triticum aestivum* L), and the perennial intermediate wheatgrass (IWG: *Thinopyrum intermedium* (Host) Barkworth & D.R. Dewey). Plants were grown in pots to a three leaf stage, before being subjected to vernalisation treatments of varying length (0, 3, 5, 7, 9 and 11 weeks) using a growth chamber set to 5°C and 10h lighting. The plants were then transferred to a glasshouse set to 22°C and a minimum of 10h lighting. Glasshouse daylengths increased as the season progressed from winter into spring and summer. Exposure at ≤5°C for 5 weeks in MR optimised reproductive development, compared to approximately 3 weeks for winter wheat and 11 weeks for IWG. Both MR and IWG appear to have a dual induction requirement, needing a period of cold exposure and short days, followed by daylengths of 12-13 hours for MR, and at least 13 hours for IWG, to optimise their grain production potential. The observed higher vernalisation requirement of MR, compared to AW, helps delineate the grain production potential of the tested germplasm in current wheat growing areas of temperate Australia. Reproductive tiller percentages were much higher and developed earlier in AW compared to the perennial cereals. Improving the ratio and timing of reproductive tillers development in perennial cereals should be a target if grain yields are to be improved.

Keywords: Perennial grains, Perennial cereals, Intermediate wheatgrass, Vernalisation, Dual-induction, Wheat, Mountain rye.

Abbreviations: AW Annual Wheat, IWG Intermediate Wheatgrass, MR Mountain Rye, SD Standard Deviation.

1.1 Introduction

Introducing perennial cereals into Australian farming systems has many potential advantages including reduced tillage and improved soil organic matter accumulation (Kim *et al.*, 2022; Tang *et al.*, 2023), reduced nutrient leaching (Culman *et al.*, 2013), and potential production benefits from reduced farm inputs and extra grazing for livestock (Bell *et al.*, 2010; M. Newell *et al.*, 2025). A range of perennial cereals, potentially suitable for integration in Australian farming systems, have previously been evaluated (Hayes *et al.*, 2012; Hayes *et al.*, 2018; Larkin *et al.*, 2014). In those initial evaluations, mountain rye (MR: *Secale strictum* syn. *S. montanum*) was highlighted as a species with superior persistence compared to other perennial grain crops and is a candidate for *de novo* domestication, similar to the development of intermediate wheatgrass (IWG: *Thinopyrum intermedium* (Host) Barkworth & D.R. Dewey) to produce the grain crop Kernza™ (Bajgain *et al.*, 2022). As a forage species, MR is best adapted to cooler areas of south-eastern Australia (Bishop *et al.*, 1987; Oram, 1996), but has recently been found to have grain characteristics suitable for a range of food products (Baker *et al.*, 2021; Sinclair *et al.*, 2021).

In both annual and perennial temperate cereals, vernalisation requirements and photoperiod sensitivity are important considerations for optimal adaptation to different growing environments and grain production. Vernalisation is a requirement in some plants for exposure to cold temperatures to induce flowering (Chouard, 1960; Heide, 1994). The majority of temperate perennial grasses require dual induction to initiate the transition from vegetative to reproductive growth (Heide, 1994). Cool temperature and short daylength (primary induction) promote the development of inflorescence primordia in the meristem. The transition to warmer temperatures and longer daylength (secondary induction) promotes stem elongation and inflorescence development. There is variation in the induction requirements between species and within ecotypes of the same species (Fjellheim *et al.*, 2014). In wheat (*Triticum aestivum* L) this has been traced to the VRN1 gene system with orthologue genes across all three genomes (Eagles *et al.*, 2010; Sehgal *et al.*, 2024). Winter wheat can have substantial vernalisation requirements, while spring wheat is insensitive. Photoperiod genes (PPD complex in wheat) promote the transition to flowering, and in sensitive temperate species, are triggered by long-day thresholds (Sehgal *et al.*, 2024). In rye (*Secale* spp.), short-days may influence the expression of the VRN2 gene and delay the transition to reproduction (Cox *et al.*, 2002). An understanding of these requirements for candidate perennial cereal species will be important to allow integration of these findings into process-based crop models, to help identify potential zones of adaptation, and to inform plant breeding programs.

A commonly grown winter wheat (AW) in south-eastern Australia, and two candidate perennial cereals (MR and IWG) were included in the experiment. The winter wheat was known to have a vernalisation temperature requirement of 5-10°C, with a duration 8 days or more, and a subsequent photoperiod requirement of >10 hours (Bloomfield *et al.*, 2023; Matthews *et al.*, 2019). The other comparison species, IWG, has been grown as a perennial grain in the higher latitudes of the northern hemisphere. For optimal grain production in these environments, IWG has been found to have a vernalisation temperature requirement of 4-5°C, for a duration 5-7 weeks, and a daylength of <11h increasing to >13h for secondary induction (Ivancic *et al.*, 2021; Locatelli *et al.*, 2023; Locatelli *et al.*, 2022).

There are little data available regarding the vernalisation requirements of MR for flowering and grain yield optimisation. The annual cereal rye (*Secale cereale* L), a close relative of MR (Gruner

et al., 2021), is known to require a vernalisation temperature of 5-10°C, for a duration of 6-8 weeks, plus a subsequent photoperiod of greater than 14 hours for optimal grain production (Schlegel, 2013). The hypothesis was that MR would have higher vernalisation requirements than AW, but lower than IWG, and that all species would have reduced grain yields if not vernalised sufficiently. Further, it was proposed that insufficient vernalisation would reduce the ratios of reproductive to vegetative tillers and increase the aboveground vegetative biomass of each species.

1.2 Methods

1.2.1 Germplasm

The population of MR used has shown potential as a perennial forage species in Australasia (Oram, 1996). It exhibits a range of desirable grain attributes for a diversity of end uses (M. T. Newell *et al.*, 2021). The IWG plant material used (CPI-148055) was previously evaluated in Australia (Hayes *et al.*, 2012; Larkin *et al.*, 2014) and was from an early generation breeding population obtained from the Land Institute (Salina, KS) in 2009 (previously under the breeder code IWG 3182). Both MR and IWG populations displayed long maturity times and an ability to produce grain in Australian environments. The AW used was “EGA_Wedgetail”, a common industry benchmark winter wheat cultivar.

1.2.2 Glasshouse conditions

The experiment was conducted in the Glasshouse facilities of NSW Department of Primary Industries Cowra Agricultural Research and Advisory Station, NSW, Australia. Plants were grown in black plastic pots, dimensions 190mm high x 200mm diameter, each containing approximately 2.8L of a proprietary potting mix (Scotts Osmocoat® Premium). Treatments were replicated four times giving a total of 72 pots. Prior to sowing, seed of each entry was cleaned and graded to provide good quality seed for planting. In May 2023, five seeds from the same entry were sown in each pot and thinned to one plant once one leaf had fully emerged. The winter wheat was sown five days after the perennial cereal species to ensure that each species was exposed to the vernalisation treatments at a similar growth stage. Each pot received a complete nutrient solution (Thrive®: 25%N, 5%P, 8.8%K, 4.6%S, 0.5%Mg, 0.18%Fe, 0.01%Mn, 0.005%Cu, 0.001% Zn,

diluted to 2g L⁻¹ H₂O) once every two weeks, after the seedlings had fully established. Pots were placed on flood and drain benches and watered twice daily using an automated irrigation system. Temperatures in the glasshouse were controlled at an average 22.5°C (SD 2.6, min. 15, max. 28) throughout the experiment. The photoperiod was extended using auxiliary horticultural lighting (Hort. L2 Module, Samsung) to a minimum of 10 hours during the day period in the glasshouse. The photoperiod increased throughout the experiment as the natural daylength progressed with the season (Table 1).

Table 1. Glasshouse daylengths vs. elapsed days

Date	19 th Jun.	13 th Jul.	7 th Aug.	1 st Sep.	26 th Sep.	21 st Oct.	15 th Nov.	10 th Dec.	4 th Jan.
Elapsed days	0	25	50	75	100	125	150	175	200
Daylength (h)	10.0	10.1	10.7	11.4	12.3	13.1	13.8	14.3	14.3

1.2.3 Vernalisation treatment

Treatments included five periods of vernalisation (0, 3, 5, 7, 9, and 11 weeks). Plants assigned to the zero vernalisation treatment remained in the glasshouse for the entirety of the experiment. Plants undergoing vernalisation were all transferred to a growth chamber on the same day, by which stage all plants were at the three leaf stage. Average temperature within the growth chamber was 4.9°C (SD 0.4) with 10 hours of lighting (800µmol m⁻²s⁻¹ photosynthetic photon flux density) similar to the conditions used by Locatelli *et al.* (2022). Once each period was completed, pots within that treatment were returned to the glasshouse. Pots were re-randomised within each replicate group as they entered the growth chamber and when returned to the glasshouse.

1.2.4 Measurements

Tiller numbers and phenological development were assessed at three-to-four-week intervals, from 19th June 2023 to 6th Feb 2024 (1-233 days after the start of vernalisation treatments). As plants transitioned to reproductive development, a count of reproductive vegetative tillers was completed. Plants were assessed every three to four days once head emergence was initiated and anthesis dates

recorded. When plants reached full maturity total head numbers were counted and seed heads removed for drying, weighing and threshing. All other plant material was removed to 50mm above soil level and the combined stems and leaves, along with any senesced material, were dried and weighed.

1.2.5 Data analysis

The experimental design was a randomised complete factorial with two factors: species (AW, IWG, MR) and vernalisation treatment (0, 3, 5, 7, 9 & 11 weeks). The treatment factor included the effects of varying times in the growth chamber and glasshouse, including temperature, thermal time (Bonhomme, 2000), and photoperiod differences. The experimental unit was each pot containing one plant. The response variables (biomass, grain, tiller numbers) were analysed by ANOVA with the R programming language version 4.3.1 (R-Core-Team, 2021) using the *aov* command. ANOVA assumptions of normality were checked visually by plotting the residuals. When ANOVA identified an effect at $P \leq 0.05$, Fishers LSD (95% confidence level) was used to separate the means using the *LSD.test()* function supplied by the *agricolae* library for R (De Mendiburu *et al.*, 2020). Species were analysed together for main and interaction effects (Table 2). Analysis was also done at individual species level. The individual species analysis only produced significant results for AW yields and IWG reproductive tillers percentages (results not shown).

1.3 Results

The AW plants were harvested from November 2023 to January 2024 as the grain matured. The 3-9 weeks vernalisation treatments matured earliest. The MR matured between December 2023 and January 2024. The earlier MR harvests were in the 5-9 weeks vernalisation treatments. By March 2024, IWG had produced no grain at all, regardless of the vernalisation treatment. The main

and interaction effects of the species and vernalisation treatments on the grain yields, biomass and tiller numbers of each species are presented in Table 2. There was a 16-fold increase in MR grain production, from a low of 0.1g/plant at 0 weeks vernalisation treatment to a high of 1.6g/plant at 11 weeks treatment, with an 8-fold increase after just 3 weeks of treatment. IWG biomass weights decreased by 39% from a high of 51.3g/plant at 0 weeks treatment to a low of 31.5g/plant at 9 weeks of treatment. The effect of vernalisation treatment on MR reproductive tillers was not significant, but an increase in reproductive tillers can be observed after 5-7 weeks of treatment. There were no reproductive tillers evident for IWG until 7 weeks of vernalisation treatment but none of these proceeded to grain maturity. However, when analysed at individual species level, there was a significant increase in the IWG reproductive tiller percentage at 7 weeks (analysis not shown).

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Table 2. Species and treatment effects on yields and tiller numbers. Treatments are the number of weeks of vernalisation at 5°C. DM=Dry Matter, TKW=Thousand Kernel Weight. Grain and TKW were analysed without IWG as IWG produced no grain. Reproductive tiller numbers were recorded at the time of harvest. Total Tillers are the maximum recorded tiller count. Results are the means of the four replicates. Where results share a lower case letter the effects were not significantly different.

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<i>Species</i>	<i>Treatment</i>	<i>Total DM</i>	<i>Grain</i>	<i>TKW</i>	<i>Reproductive Tillers</i>	<i>Total Tillers</i>
	<i>weeks</i>	<i>g/plant</i>	<i>g/plant</i>	<i>g</i>	<i>%</i>	<i>count</i>
Annual Wheat	0	51.0 a	17.8 b	29.7	59.1 bc	36.8 ef
	3	27.1 de	15.4 bc	38.3	50.2 cd	20.5 f
	5	20.3 e	11.6 c	38.5	43.8 cd	17.3 f
	7	21.1 e	11.6 c	36.9	44.7 cd	17.8 f
	9	29.7 cde	15.4 bc	31.2	73.6 b	20.8 f
	11	50.2 a	23.0 a	35.8	97.9 a	19.0 f
Mountain Rye	0	40.6 abcd	0.1 d	14.2	6.8 f	120 a
	3	39.0 abcd	0.3 d	10.2	5.6 f	78.3 bc
	5	44.3 abc	0.8 d	13.6	15.5 ef	83.0 b
	7	44.2 abc	1.0 d	10.6	19.4 ef	78.0 bc
	9	47.4 ab	1.1 d	10.8	35.0 de	57.8 cde
	11	42.6 abcd	1.6 d	11.7	30.8 de	60.5 cd
Intermediate Wheatgrass	0	51.3 a	0.0		0 f	53.3 de
	3	41.8 abcd	0.0		0 f	73.3 bcd
	5	35.5 abcde	0.0		0 f	68.3 bcd
	7	26.5 de	0.0		0.3 f	61.0 bcd
	9	28.8 cde	0.0		0.4 f	55.5 de
	11	31.5 bcde	0.0		5.5 f	66.5 bcd
Species effect	<i>P Value</i>	0.02	<0.01	<0.01	<0.01	<0.01
Vern effect	<i>P Value</i>	0.01	0.01	0.02	<0.01	<0.01
Species:Vern	<i>P Value</i>	0.01	0.04	0.33	0.03	<0.01
	<i>LSD (P=0.05)</i>	16.61	5.03		21.0	22.5

1.3.1 Phenology: Zadoks growth scores during and after treatment periods

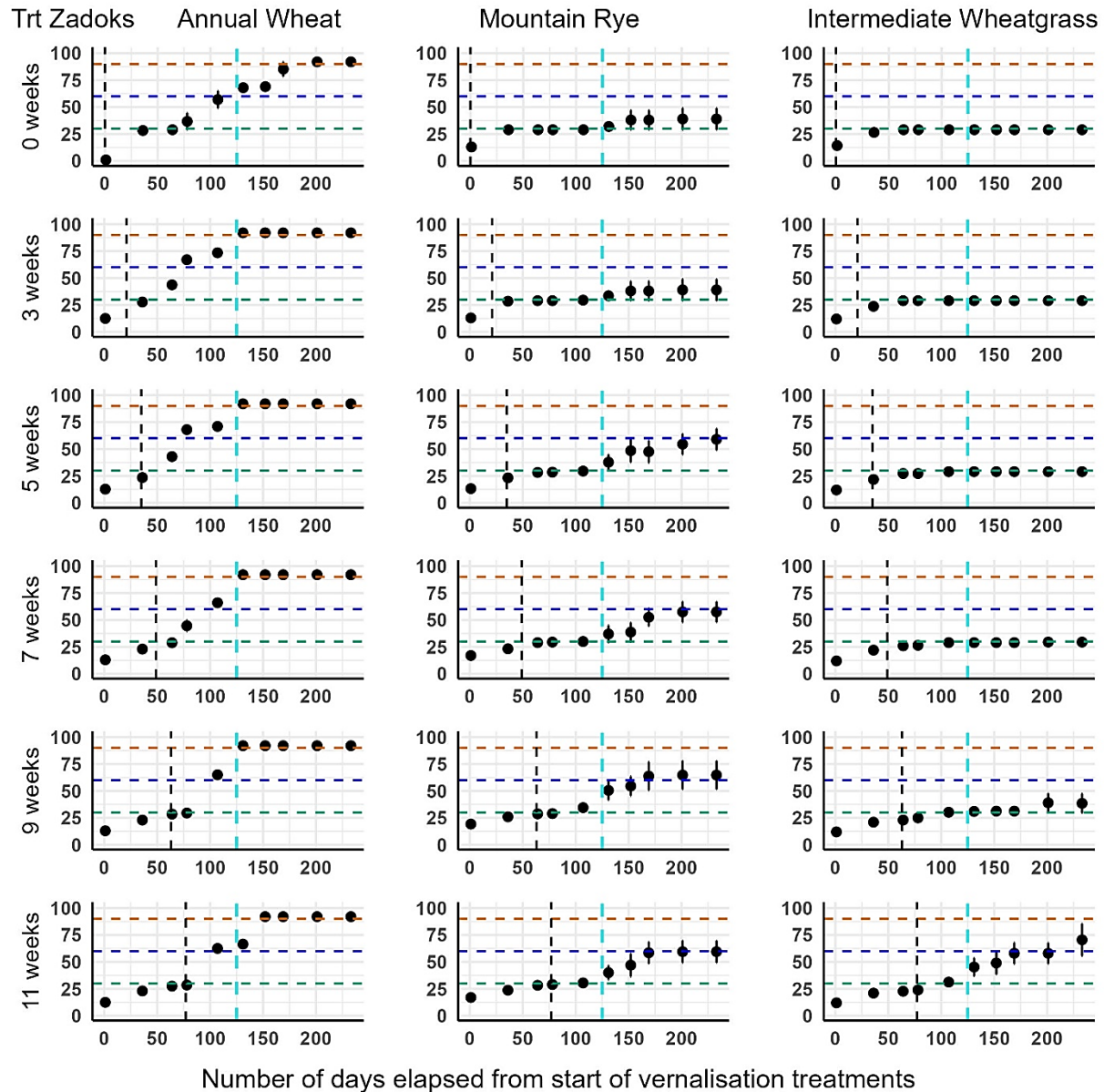


Figure 1. Zadoks growth scores vs. days from start of each vernalisation treatment. Points are the mean Zadoks score of the four replicates for each treatment. Error bars represent standard error of the mean. Points below the green horizontal dashed line are the vegetative stage, between the blue and green lines are early reproductive stages, and above the blue line are the grain development stages. The orange bar indicates grain maturity. The first vertical dashed line is the point where the plants were moved from the growth

chamber to the glasshouse. The second vertical dashed line at 125 days is the point where glasshouse daylengths increased to >13 hours (Table 1).

Alt-Txt for Figure 1. Three columns each showing one of the three species Zadoks scores plotted against days elapsed, for each vernalisation treatment. The annual wheat progresses to maturity faster than the mountain rye or intermediate wheat grass.

Annual Wheat reached grain ripe Zadoks stage (>90) for all treatments, but was slower for the control, compared to the vernalised treatments (Figure 1). MR progressed to the grain development stage (Zadoks > 60) after 5 weeks or more of vernalisation. The IWG only progressed beyond the vegetative stage (Zadoks > 29) when exposed to 9 or more weeks of vernalisation, but no plants progressed to the grain ripe stage.

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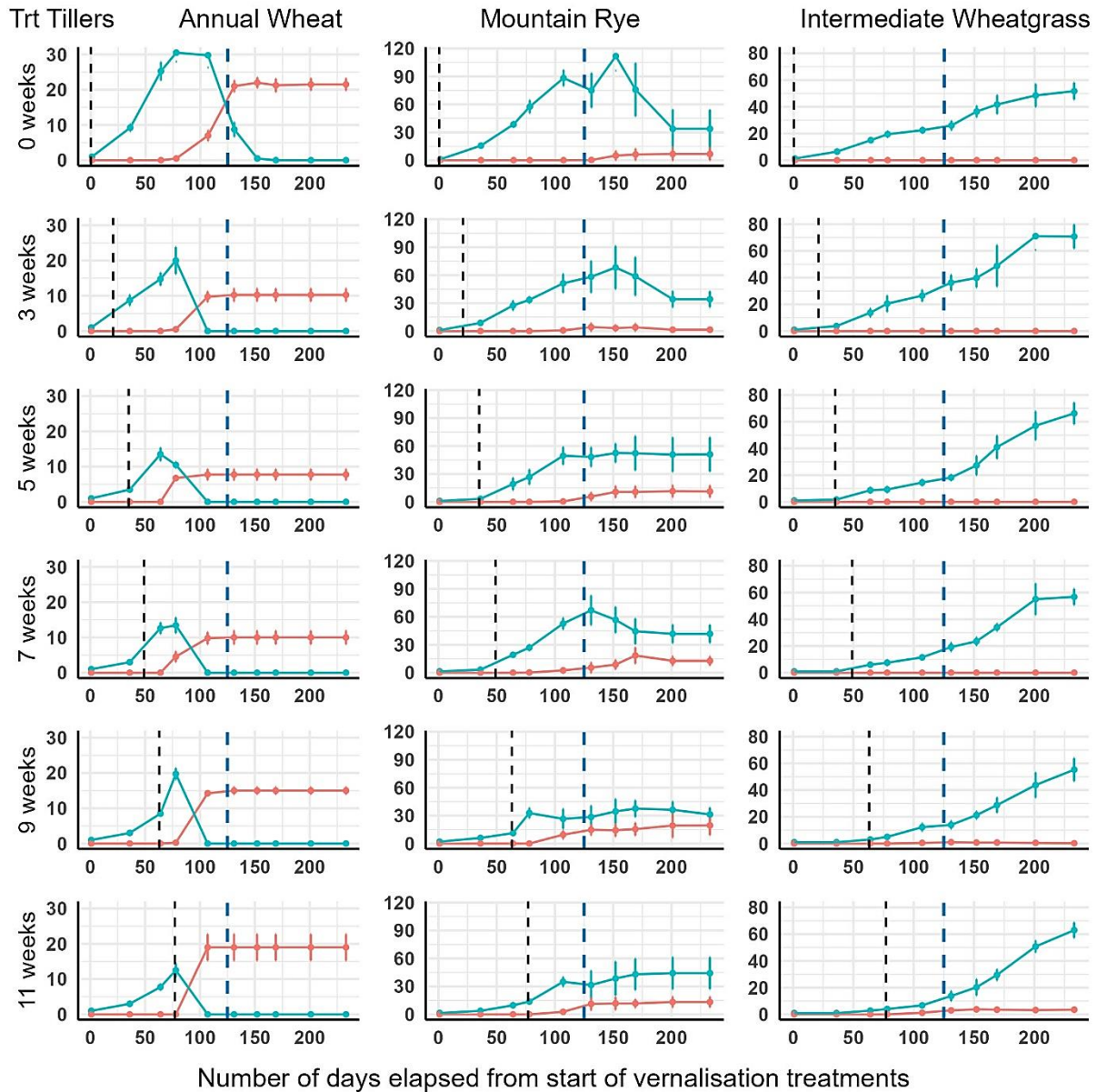


Figure 2. Number of vegetative and reproductive tillers of AW, MR, and IWG after different periods of vernalisation. Vegetative tillers are green dots and lines, reproductive tillers are orange dots and lines. ‘Trt’ is the treatment time in weeks at 5°C. Error bars are standard error of the mean. The first vertical dashed line is the point where the plants were moved from the growth chamber to the glasshouse. The second vertical dashed line at 125 days is the point where glasshouse daylengths increased to >13 hours.

Alt-Txt for Figure 2. Three columns each showing one of the three species vegetative tillers compared to reproductive tillers plotted against days elapsed, for each vernalisation treatment. After 100 days and through to maturity, the annual wheat has a much higher proportion of reproductive tillers compared to the mountain rye and intermediate wheatgrass.

Annual wheat (Figure 2) had the highest number of vegetative tillers in the 0 and 3 weeks treatment groups. Vegetative tiller numbers in MR were suppressed by 5 weeks or more of vernalisation, with a corresponding increase of reproductive tillers. Reproductive tiller development in IWG was only apparent within 9 and 11 weeks treatment groups and occurred after the end of the vernalisation treatment periods (i.e. after 77 days).

1.4 Discussion

It was hypothesised that MR would require a longer period of vernalisation than AW and less than IWG. The results of this experiment support the hypothesis, indicating MR may require 1-2 extra weeks of cold exposure than AW, plus a 12-13 hour day length for secondary induction (see Figure 1), compared to around 11 hours for AW. The IWG seemed to need an even longer cold exposure, of at least 9 weeks, and a 13 hour day length for secondary induction. The experiment was not specifically designed to test the effects of daylength on floral initiation as that would have required daylengths in both the growth chamber and glasshouse to be controlled (e.g. be equal) for up to 11 weeks. However, other researchers have noted that, in the case of perennial cereals, calendar days (and thus daylengths) can be a better predictor of secondary induction than thermal time (Barriball *et al.*, 2022; Duchene *et al.*, 2021). The 7-11 week treatment plants had shorter initial daylengths in this experiment, remaining at 10 hours photoperiod duration in the growth chamber, while those moved to the glasshouse (3-5 week treatments) experienced 11.5 hours daylengths by 11 weeks (Table 1). The AW would have been most affected by the longer glasshouse daylengths, having a relatively shorter daylength requirement to progress to reproduction, while MR and IWG appear to have at least a 12 hour requirement. Thus, the photoperiod differences between the growth chamber and glasshouse would be less important for MR and IWG, as the longer initial glasshouse daylengths should not have triggered secondary induction in these species. Additionally, it was

proposed in the current study that all species would have reduced grain yields if not vernalised sufficiently. For MR, this was confirmed as grain yields were optimised after five weeks of vernalisation treatment. The results for AW and IWG were inconclusive. The 0 weeks vernalisation treatment for AW produced a higher grain yield than the 3 to 9 week vernalisation treatments. The higher thermal time experienced by the 0 weeks treatment possibly increased the AW grain yield, although lack of vernalisation in AW is known to extend the thermal time to reproduction (Bloomfield *et al.*, 2023). It is also known that a sufficient number of short daylengths may override the need for low vernalisation temperatures in some plants (Heide, 1994), but it is not known this was the case for AW. The IWG did not progress to grain development for any of the treatments. It is possible that the daylengths in the growth chamber and glasshouse did not match the daylengths required for the phenology to proceed to flowering. Locatelli *et al.* (2022) in a similar experiment grew their plants to 3 leaf seedling stage with a mixture of 8 hours winter daylight plus 8 hours of low intensity incandescent light per day, resulting in a shorter period of darkness per day compared to our experiment that used 10 hours of light and 14 hours of darkness per day. There can be an interaction between daylength and temperature for some dual induction plants (Heide, 1994). Also, if the time between vernalisation and the requisite daylength for induction is too long (and subject to higher temperatures), plants may devernalise (Locatelli *et al.*, 2022). This may not be the case for IWG, but if it was, it could explain why the plants that remained longest in the growth chamber (at low temperature with less devernalisation risk) proceeded to flowering. It is also possible that a stress factor, such as a heat episode, affected canopy level reproductive organs. Recorded glasshouse temperatures ranged as high as 28°C during early October. It is known that reproductive development in IWG is susceptible to higher temperatures (Ivancic *et al.*, 2021), but the critical temperature levels and durations are unknown. Farooq *et al.*

(2011), in their review of heat stress in wheat, reported damaging temperatures occurring at $21.4 \pm 2.33^{\circ}\text{C}$ for the terminal spikelet stage and $32 \pm 1.74^{\circ}\text{C}$ for the flowering stage.

It was also expected that the ratio of reproductive to vegetative tillers would increase with sufficient vernalisation. The ratio of reproductive to vegetative tillers in MR increased after 3-7 weeks of treatment, possibly when optimal vernalisation was achieved. Reduction in vegetative tiller numbers after vernalisation has been noted in previous studies (Steinfort *et al.*, 2017). The IWG only produced reproductive tillers when subjected to a 7-11 week vernalisation treatment, making it difficult to draw any conclusion about the effects of vernalisation on the tiller dynamics of IWG in this experiment, although there was a significant increase in the percentage of reproductive tillers at 7 weeks. Locatelli *et al.* (2022) observed an increase in spikes in IWG from 3 to 7 weeks of vernalisation treatment and inferred a concurrent decrease in total tiller numbers, due to competition for assimilates during the stem elongation to flowering stages (Colvill *et al.*, 2008). The proportion of fertile tiller numbers are an important consideration for perennial cereals and have been found to be a good predictor of grain yield (Fernandez *et al.*, 2020). However, perennial cereals need to retain a proportion of vegetative meristems to ensure the plant continues growing into the next season (Fjellheim *et al.*, 2014). Thus, there is a trade-off between reproductive tiller development and vegetative tiller retention in perennial cereals.

It was proposed that vernalisation would decrease the vegetative biomass of each species. There was no apparent trend in biomass for either AW or MR. Therefore, the hypothesis of decreasing total biomass after sufficient vernalisation treatment was not confirmed for these species. However, there may have been an influence from the different thermal time accumulations during the vernalisation treatment periods. In such experiments, it is almost impossible to isolate the effects of vernalisation and thermal time accumulation as, by definition, vernalisation period reduces thermal time accumulation. The 11-week vernalisation treatment had less thermal time accumulated at the time of harvest than the other treatments. The difference in thermal time accumulation between vernalisation treatments was greater for the earlier harvested plants, such as AW harvested in December 2023, and MR harvested in January 2024.

1.5 Conclusion

In this study, a vernalisation period of 5 weeks at 5°C optimised the grain production potential of MR, compared to 3 weeks for AW. The AW became fully reproductive when a 10-11 hour daylight period was experienced, while for MR it was 12-13 hours, and for IWG it was approximately 13 hours. Both MR and

AW produced a higher number of vegetative tillers when there was less than 3 weeks of vernalisation. These results help in the selection of viable cropping regions and management strategies for MR as a dual purpose perennial grain. The results also highlight the high vernalisation requirements of MR and IWG in relation to AW. The reduction of these requirements should be a priority for plant breeders if MR and IWG are to be viable dual purpose cropping options at lower latitudes. Of note is the much higher ratio of reproductive tillers to vegetative tillers in AW, post vernalisation, compared to MR and IWG. This should also be considered by plant breeders if grain yield to biomass ratios are to be improved in MR and IWG. In future experiments, a closer monitoring of both temperature and light exposure (e.g., loggers in individual pots), and varied photoperiods during vernalisation, may help disentangle the three-way effects of vernalising temperature, photoperiod, and thermal time on reproductive development in MR and IWG. Field experiments in contrasting environments would also be useful, to further define the interaction of latitude and seasonal temperatures with the dual induction requirements of MR and other perennial cereals, such as IWG.

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1.7 Conflict of Interest Statement

The authors declare no conflicts of interest associated with this research.

1.8 Author Contributions

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Writing – original draft: P.J. Innes

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1.9 Data availability

The datasets used to for the analysis presented in this article are available at:

<https://research.usq.edu.au/item/zvv51/a-study-of-the-vernalisation-requirements-of-mountain-rye-secale-strictum-syn-s-montanum-may-help-explain-low-grain-yields-of-perennial-cereals-compared-to-wheat>

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