

Research Article

Genetic solutions through breeding counteract climate change and secure barley production in Australia



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ABSTRACT

Climate changes threaten global sustainable food supply by reducing crop yield. Estimates of future crop production under climate change have rarely considered the capacity of genetic improvement in breeding high-yielding and stress-tolerant crop varieties. We believe that technological advancements and developing climate-resilient crop varieties may offset the adverse effects of climate change. In this study, we examined the historical record of barley breeding and yield, and the trends of climate changes over the past 70 years in Australia. We related the selection of fast development varieties to yield improvement, and revealed the genetic connections of fast development and yield potential through genome-wide association studies. Historical records show that Australia's barley yield has experienced a steady growth despite that the seasonal production window has been shortened due to increased risk of frost damage at flowering stage and terminal heat during maturity since the 1970s. The increase in yield is largely the result of higher yield capacity of the more recently developed varieties that develop faster to counteract the impact of increased terminal heat. We also show that the changing temperature may soon reach a critical point that dramatically changes the barley flowering behaviour to impact yield by pushing its growth beyond the seasonal production window to face increasing frost damage. For the first time, we provide evidence that the effects of climate change on crop production might be less severe than what is currently believed because the advancement of technologies and development of climate-resilient crop varieties may mitigate the adverse effect of climate change to some extent. The greater use of genetic techniques in crop breeding will play a vital role in sustainable global food production in the era of climate change.

1. Introduction

Seventy to one hundred per cent more food has to be produced to meet the demand of a global human population that is projected to exceed nine billion by the year 2050 [1,2]. Efforts in achieving this substantial increase in food production are further hampered by the adverse impact of climate change on crop yield. The future climate is projected to be warmer and hotter than the current climate; more frequent extreme weather events in the 21st century [3–5] are predicted to reduce the yields of most crop species dramatically [6,7]. Modelling crop growth and climate change have generated robust estimates of the potential impact of the projected climates under different emission scenarios on global crop production [8–10]. However, current modelling on

the impact of future climate change on crop yield are based on crop varieties, and agronomic practices used today [11]. Agronomic inputs, such as fertiliser, irrigation, and machinery, could potentially be managed within farming systems during extreme climate events to mitigate the negative impact of climate change [12,13]. Our capacity to breed high-yielding and stress-tolerant varieties through genetic improvement is critically important yet missing from current modelling and predictions on crop production under future climate change scenarios. Meanwhile, quantifying the effect of climatic factors, such as temperature and rainfall on plants forms the basis of simulation models of crop production. However, the effect of, for example, temperature on crop development may be not linear as current modelling commonly assumed [14], because crop development has an optimum temperature.

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In the past, the development of high-yielding and resilient cereal crop varieties through genetic improvement have led to a significant increase in food production around the world since the Green Revolution. Therefore, genetic improvement through crop breeding can be equally applicable to adapt climate change both presently and into the future.

Barley was introduced to Australia with the arrival of European settlers in the late eighteenth centuries. From the first crop of 3.24 ha sowed in 1788 [15], it grows into the second most important cereal crop (after wheat) in Australia with a record harvest of 13.5 million tons in 2016 [16]. Australia normally supplies around 40% of the global malting barley, and 20% of the feed barley [16]. Early barley varieties grown in Australia were from Europe with a slower maturity and late to flowering, producing low yield due to the impacts of terminal drought and high temperature typical in many parts of Southern Australia. The first Australian barley cultivar “Prior”, adapted to the dry South Australian environment, was developed in 1903, and became the backbone of the Australian barley industry until the end of the 1960s [15,17]. The establishment of government-supported breeding programs since the 1960s has seen new introgression of barley genetic material from Europe, North America, Japan, and North Africa, into Australian varieties with improved yield over a range of environments, improved malting quality, and tolerant to biotic and abiotic stress. The use of molecular genetic markers and wide implementation of molecular technologies have enabled greater efficiency with shorter cycle times in barley breeding [17]. Since 1960, Australian barley breeders have bred and released almost 100 barley varieties for the domestic market. Most current Australian barley cultivars are two-row spring type, usually sown in late autumn or early midwinter, flower in spring, and are harvested in early summer.

Meanwhile, global annual barley yield has been predicted to decline up to 17% as frequent climate extremes causing yield losses, causing great concern on the sustainability of world barley production [9]. The decline of barley production would impact brewery industry, food processors, feed mills, and livestock operations. Australia has also experienced dramatic climate changes, particularly with increased extreme heat events and drought and a 1–2 °C increase in annual temperature across the continent since the 1950s, with such climate change becoming more evident since the late 1970s [4,18,19]. As a consequence, wheat production in Australia has stalled since 1990 [20]. Meanwhile, recently increased frost occurrence in Australian grain production areas [21] has been estimated to cause 100 million AUD/year of production losses due to direct frost damage in wheat and barley [22].

History provides the best opportunity to guide the future. The extraordinary history of barley production and breeding in Australia over a short period of time, and the evident and clear trends of climate change in Australia, offers a unique opportunity to examine how genetic solutions through trait improvement in breeding have counteracted the adverse impacts of climate change and contributed to the steady improvement of barley production. In this study, we examine the historical climate data recorded across Australia's major barley production regions since 1980 and explore the climate change patterns in the three developmental periods in the growth cycle of barley: the maximum temperature during the grain filling period, the average temperature during the vegetative growth leading to flowering, and the minimum temperature during the flowering season. We investigate the trend of trait (flowering time in particular) improvement and its contribution to barley yield over the past 70 years in Australia. We further explore the mechanism of how earliness of flowering has been effective in counteracting the adverse effect of climate change while contributing to yield improvement. Specifically, we seek to answer the following questions: 1) Is the increased barley yield in Australia related to greater yield potential of more recently released barley varieties despite climate change? 2) Are newer varieties more likely to flower earlier to avoid terminal heat/drought stress during the grain filling? We also aim to identify the current threats of climate change to barley production, so that to pave a way for continuing production improvement in the future.

2. Materials and methods

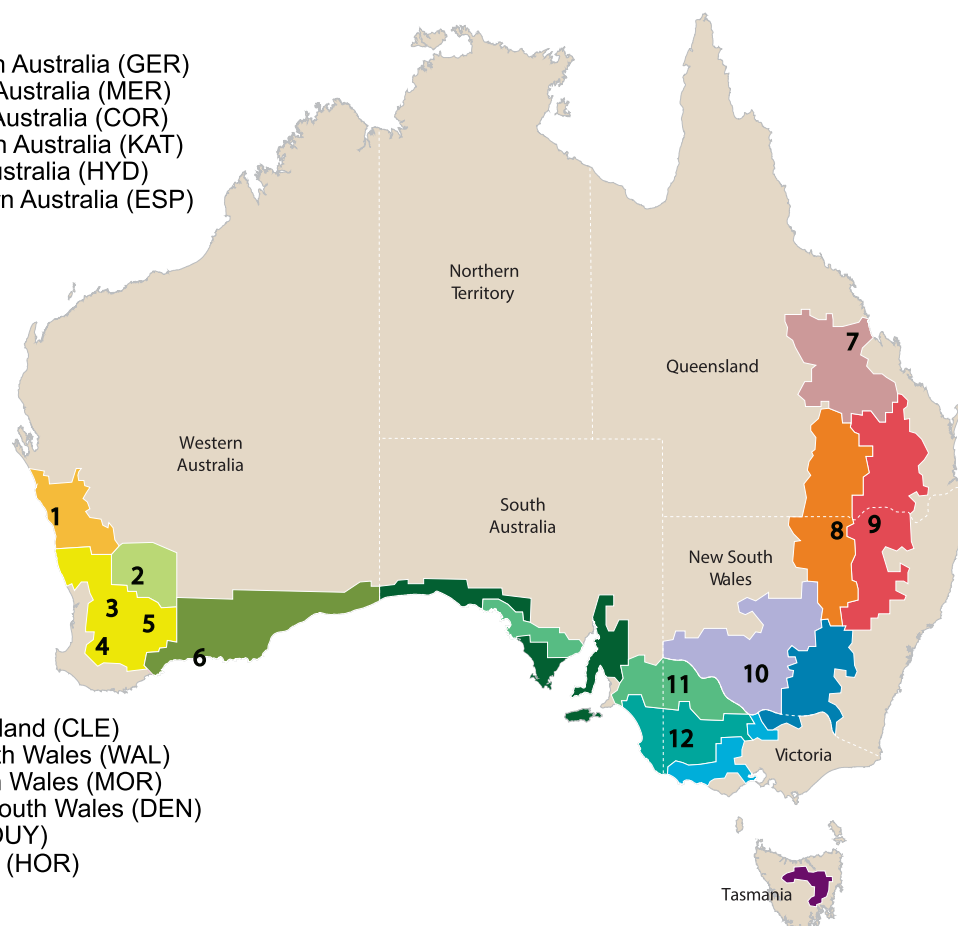
2.1. Climate change trends and historical production and yield of barley in Australia

Altered temperature and rainfall pattern has been proposed as clear evidence of climate change in Australia [4,18,19]. For the historical climate data, the daily maximum temperature (T_{\max}) and minimum temperature (T_{\min}) between January 1, 1980 and December 31, 2018, and the annual rainfall between 1980 and 2018 were extracted from the data archive at the Australian Bureau of Meteorology (www.bom.gov.au/). Climate data for 12 sites representing the Australian barley growing region were analysed (Fig. 1). The 12 sites were chosen to represent the range of temperature and climate conditions both present and historical as well as to appropriately sample to range of Australian soil types and crop adaptation regions. Arid and semi-arid barley growing zone was defined as regions with annual rainfall below 450 mm, while high-rainfall zone was defined as regions with 450–800 mm annual rainfall in Australia [23].

Trends in temperature change were examined for three periods within a year and related to the barley growth stages; vegetative growth phase, flowering phase and the grain filling phase. The first stage was associated with the vegetative growth leading to flowering, generally occurring between June 1 and September 30 in Australia. The rationale for examining this stage is that the average temperature of the vegetative growth period is closely correlated with the time to flowering. An increased average temperature was expected to shorten the time from planting to flowering in barley [24]. The accumulated average temperature to each day since June 1 was calculated, assuming a late May sowing of barley seed that is a common practice in Australia. Average temperature, instead of thermal time, was used, as daily temperatures were rarely below zero in Australian barley growing regions (Australian Bureau of Meteorology, www.bom.gov.au/). The second stage related to the flowering stage of barley. Barley and other cereal crops are vulnerable to frost damage during flowering [24]. To calculate the occurrence of frost events over the period since 1980, we considered thresholds of $T_{\min} < 1$ °C to correspond to the occurrence of ground frost [21]. A frost event was defined as a day when $T_{\min} < 1$ °C at 1.5-m above the ground. For each day between June 1 and September 30 at each of the 12 locations, the occurrence probability of frost event for each day was defined as the number of days (percentage) with $T_{\min} < 1$ °C within a ten-year period. For the purpose of comparison, we divided the 39 years (1980–2018) into two periods 1980–1999 and 2000–2018, with a roughly equal number of years in each period to minimise the effect of stochastic of climatic change when averaging climate elements. The day with an averaged frost probability greater than 20% is defined as a frost day. The third stage was related to grain filling time and maturity. The average T_{\max} from October 1 to December 31 was compared between 1980–1999 and 2000–2018. In addition, for each day between October 1 to December 15, the probability of occurrence of an extremely hot day was defined as the number of days (percentage) with $T_{\max} > 32$ °C within a ten-year period between 1980 and 2018, as 32 °C is believed as the threshold temperature above that causing heat damage in barley [25]. The day with the probability of maximum temperature above 32 °C greater than 20% was defined as a hot day to impact barley growth. Both frost probability and hot day probability were estimated following a generalised additive predictive model. Historical data on annual barley production and sowing area since 1950 were obtained from the Australian Bureau of Statistics. Yearly average yield was estimated as annual production divided by the growing area of that year.

Trends in climate change and barley yield and production were estimated by predictive modelling through generalised additive modelling (GAM). GAM was implemented in R package “mgcv” [26]. A breaking point analysis on the relationship between average temperature and flowering time was implemented in R package “segmented” [27]. The R package “ggplot2” [28] was used to plot the model (GAM and breaking

- 1: Geraldton, Western Australia (GER)
- 2: Merridin, Western Australia (MER)
- 3: Corrigin, Western Australia (COR)
- 4: Katanning, Western Australia (KAT)
- 5: Hyden, Western Australia (HYD)
- 6: Esperance, Western Australia (ESP)



- 7: Clermont, Queensland (CLE)
- 8: Walgett, New South Wales (WAL)
- 9: Moree, New South Wales (MOR)
- 10: Deniliquin, New South Wales (DEN)
- 11: Ouyen, Victoria (OUY)
- 12: Horsham, Victoria (HOR)

Fig. 1. Distribution of the Australian barley production regions (shaded areas) and the 12 sites that were selected based on detailed climate trends since 1980. The position of numbers indicates the approximate geographic location of the meteorological station from where the climate data were recorded. The map was obtained from the Australian Bureau of Agricultural and Resource Economics and Sciences [16].

point analysis), with 95% confidence bands. All statistical analyses were generated using R Language Version 3.0 [29]. A regression analysis, defined as $y = a + bx$ where y is the annual barley yield and x is the yield potential, was used to dissect the contribution of improved yield potential to annual barley yield by using SPSS Version 25 (SPSS Inc. IBM Corp. Chicago). The significance was tested for $P < 0.05$.

2.2. Flowering time and grain yield in worldwide barley germplasm

Flowering time and grain yield for each of the 1093 world-wide collected barley accessions, including 85 barley varieties bred in Australia, were collected through field experiments over three years in 2015, 2016 and 2017, at five locations (Esperance, Geraldton, Katanning, Merredin, and South Perth) in Western Australia that significantly differ in terms of rainfall and temperature during the growing seasons. All regional field trials were planted in a randomised, complete-block design with plots of 1.1 by 3.0 m² laid out in a row-column format with partial replications. Seven control varieties were used for a spatial adjustment of the experimental data. In each plot of each experiment in the study, measurements were taken to determine the flowering time and grain yield. Awn emergence, defined as the number of days from sowing to the first awn of ~2 cm emerging above the flag leaf (Z49) was recorded as an equivalent to flowering time, and Z91 as days from sowing to maturity [30] were also recorded when possible. Grain yield was estimated by harvesting all plant material from each plot to separate the grain from determining grain mass and from estimating the grain yield (kg ha⁻¹). Data on flowering time, grain yield and maturity are given in supplementary dataset S1 (available from Zenodo, <https://doi.org/10.5281/zenodo.4057266>).

5281/zenodo.4057266).

To evaluate the possible genetic correlation between flowering time and grain yield, we first obtained the average of flowering time of a variety across multiple environments. The original measurements of days to Z49 for each accession were transformed to standardised flowering time (FT_D) separately for each growing environment and year using the following formula [31]:

$$FT_D = \frac{\text{Days to Z49}_{\text{accession}} - \text{Min}(\text{Days to Z49})_{\text{site}}}{\text{Max}(\text{Days to Z49})_{\text{site}} - \text{Min}(\text{Days to Z49})_{\text{site}}}$$

Then, we averaged FT_D across locations and years for each barley variety to accommodate the environmental effect and other non-genetic influences. Genetic data on single nucleotide polymorphisms (SNPs) variations for 895 barley accessions from 41 countries in Europe, Asia, North and South America, Africa and Australia were extracted from our previous study [30,31]. A total of 2758 SNPs was enriched through targeted resequencing of 174 putative phenology genes that are related to phenology and the development of meristem and inflorescences. Full details on the targeted resequencing of the phenology genes and SNP discovery, filtering and archiving are provided in Refs. [32,33]. A bivariate GREML analysis was used to estimate the genetic correlation between flowering time and grain yield using GCTA [34]. Because both flowering time and grain yield were collected from the same set of samples, we opted for GCTA to model the residual covariance between the two traits. Statistical comparisons were implemented using SPSS Version 25 (SPSS Inc. IBM Corp. Chicago). Significance was taken at $P < 0.05$.

3. Results

3.1. History of barley production and trends of climate change in Australia

Australian barley production has increased dramatically since the first crop was sown on 3.24 ha after the arrival of the First Fleet in 1788 [15]. From these humble beginnings, extraordinary yield gains have transformed Australia into the world's largest premium malting barley exporter in 2017. The national census of Australian agricultural commodities (Australian Bureau of Statistics) showed a steady increase in barley production from 0.64 million (five-year average, 1950–1954) to 9.5 million tonnes (five-year average, 2013–2017), with the peak of 13.4 million tonnes in 2017, and an average yield increase from 1.1 tonnes to 2.4 tonnes per hectare (Fig. 2). The improved yielding capacity of barley varieties contributed 75.9% ($P < 0.001$) to the increase of annual average yield in our analysis.

Climate change in Australia has seen an increase in the frequency of extreme low temperatures and frost events in some parts of Australia in the winter. We examined the occurrence of frost events in the 12 locations since 1980. Daily frost probability remained below 20% in ten locations from May 1 to September 30 in 1980–1999, and the frost event probability remained below 20% in six locations in 2000–2018. In four sites, barley must have experienced frost events (with $>20\%$ probability) if seeds were sowed between May 15 to June 15 (which is current practice in Australian farms) and germinated within two weeks after sowing. In Deniliquin and Moree, both in Eastern Australia, frosty days lasted to early July in 1980–1999, while frost-free days occurred thirteen and six days later, respectively, in 2000–2018 (Fig. 3A). Barley varieties with earlier flowering would experience an increased chance to have frost damage in 2000–2018 compared to that in 1980–1999.

To evaluate the extent of increased terminal heat stress, we examined the change of temperature during grain filling to the maturity period of barley (October 1 to December 15). The average daily maximum temperature (T_{max}) increased significantly during the 2000–2018 period compared to the 1980–1999 period at all 12 barley growing regions examined across Australia, with an increase in T_{max} from 0.81 °C to 1.72 °C varying by location (Fig. 3B), though average annual rainfall showed no significant decline during the 2000–2018 period when compared to the 1980–1999 period at 11 out of the 12 sites except at Geraldton, WA (Fig. 4). The occurrence of hot days, defined as a daily $T_{max} > 32$ °C,

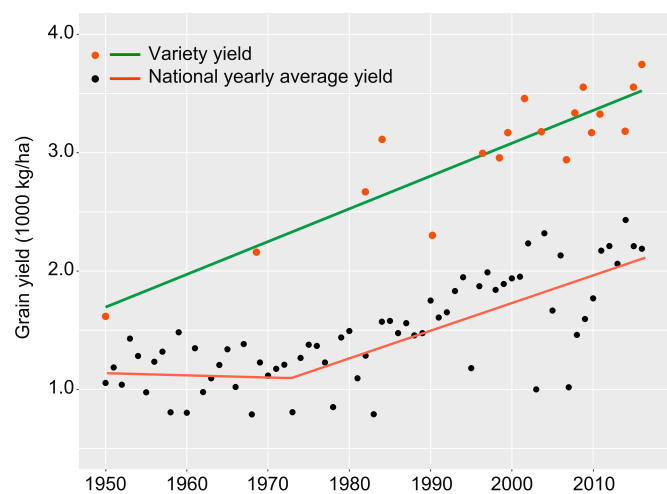


Fig. 2. Barley yields were observed in Australia from 1950 to 2017. Black dots represent the national average barley yield of the year. Red dots represent varieties that were developed and commercially released in years, and their observed grain yield obtained from the same field trials. The trend of variety yield was fitted with a linear regression, the trend of national average yield was fitted with breakpoint analysis.

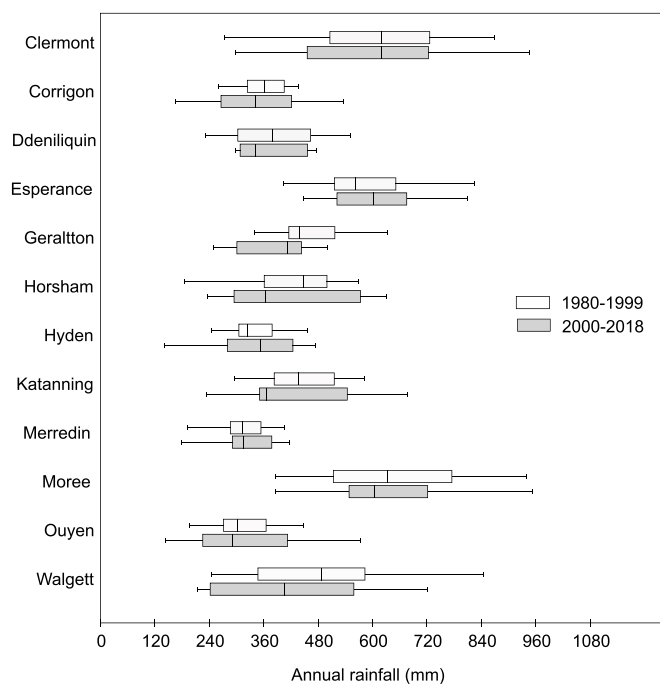


Fig. 3. Changing temperature and its impact on optimal growing window in Barley in Australia since 1980. A: Changing temperature shortening barley optimal growing window, defined as the period from the last day with less than 20% chance with frost event ($T_{min} < 1$ °C), and the first day with $<20\%$ chance with heat stress ($T_{max} > 32$ °C) in the 12 locations since 1980. B: Average daily maximum temperatures (T_{max}) during the barley grain filling period (October 1 to December 15) between 1980–1999 and 2000–2018 in 12 barley production regions across Australia (location abbreviations see Fig. 1). The increase in average maximum temperature in Celsius at each location is displayed using a red font under each location name. The box-whisker plots represent the third quartile, the median, and the first quartile, with whiskers of $1 \times$ standard deviation. Circles and stars represent outliers.

occurred 12 days earlier on average in the season in 2000–2018 when compared to that in 1980–1999 in nine locations (Fig. 3A). The increased maximum temperature and higher frequency of hot days (with $T_{max} > 32$ °C) resulted in earlier maturity of 3.1 days per 1 °C increase in T_{max} , as observed in the barley field trials conducted in the Australian western cropping belt. A shortened grain filling duration as a result of increased temperatures and heat stress events could potentially reduce barley yield and grain quality as a consequence of reduced plumpness and grain weight [25].

3.2. Potential impact of increasing temperature on barley yield

Changes in temperature can affect the plant in processes of photosynthesis, respiration and growth [35]. Earlier flowering in warming climates has been documented in crop plants [36,37] and natural plant populations [38]. We examined the effect on flowering time of the change of daily average temperature during the vegetative growth leading to flowering (June 1 to September 30). In field trials with 85 Australian-bred barley varieties growing over two years and at four locations (seven trials in total), we observed that increased average temperatures during the vegetative growth tended to promote early flowering. However, the relationship between temperature and flowering time was not linear. Barley varieties flowered dramatically earlier once the average temperatures exceeded 13.7 °C (Fig. 5), the tipping point from where the impact of increasing temperature become significant. Breakpoint analysis suggested that a 0.7 °C increase from 13.7 °C to 14.4 °C, flowering time become 32 days earlier (Fig. 5).

Across Australian barley production regions, the average temperature

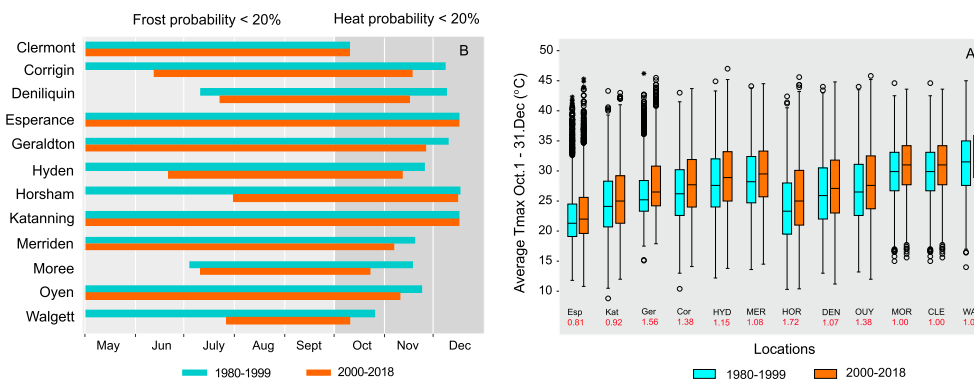


Fig. 4. Average annual rainfall in 1980–1999 and in 2000–2018 in the 12 sites. The locality of each site was shown in Fig. 2. Blank bar: The boxplot represents 20%–75% quantiles with whiskers representing a 1 × standard deviation.

from June 1 to September 30 (the vegetative growing period before flowering) had a small yet significant ($P < 0.05$ for a null hypothesis of no change) increase from an average of 11.9 °C in 1980–1999 to an average of 12.1 °C in 2000–2018. Though the overall increases of 0.05 °C per decade since 1980 is much lower than the warming trend of 0.17 °C per decade across Australia since 1970 [18], patterns of temperature change varied considerably among regions. Horsham, Walgett, and Clermont, all in Eastern Australia, have seen temperature declining during this period since 1980, while Moree (in Eastern Australia) and Esperance (in Western Australia) had temperature increased 0.65 °C and 0.62 °C, respectively. The temperature in none of the 12 locations has traversed the breakpoint threshold of 13.7 °C during the vegetative growth period in the 1980–2018. Likely, changing temperature during the vegetative growth leading to flowering (June 1 to September 30) has not been significant enough to influence flowering time in barley so far. However, with an average accumulated temperature of 13.4 °C with an increase of 0.15 °C per decade, as observed in Esperance in 2000–2018, the increasing temperature in this region would soon reach the tipping point (13.7 °C) to impact barley flowering in 20 years, which represent a real threat on the sustainable barley production in these regions.

3.3. Genetic correlation between fast developing and improved yield

Our field trials across multiple years and environments have shown that newer varieties have tended to have higher yield levels, particularly for those that were grown on more than 5% of the total barley growing area across Australia at least one year after it was released (termed production varieties, Fig. 6A). These production varieties tended to earlier flowering in our field trials (Fig. 6B), and the trends were even more evident for the varieties bred to grow in high-rainfall regions. For the traditional barley-growing areas with low to medium annual rainfall (<450 mm), the flowering time of the varieties released after 1980 was on average 5.3 days earlier than for those released before 1980. Barley varieties released since 2000 for high-rainfall regions flowered 9.1 days earlier than those released before 2000.

The timing of flowering in cereal crops is associated with yield and product quality [39]. Results from field trial involving 952 barley varieties grown at five locations across the Australian cropping belt over three years showed that flowering time was correlated with grain yield. The earlier flowering varieties tended to have a higher yield in our trials ($r = 0.506, P < 0.001$). The bivariate GREML analysis revealed that flowering time and grain yield were also genetically correlated ($r = 0.265 \pm 0.122, P = 0.034$), suggesting that the two traits have partial genetic overlap.

4. Discussion

Climate changes have been threatening global food security by reducing yields of most crop species. Australia's barley yield has experienced steady growth since 1950 despite that the optimal growing window has been shortened due to the increased risk of frost damage at the flowering stage and terminal heat during maturity. Our analysis demonstrated that genetic improvement through breeding early flowering varieties with high-yield potentials has been effective in adapting to climate change and improving Australia's barley production since 1980. The increased maximum temperature and higher occurrence of hot days during the barley grain filling stage since 1980 have led to an earlier crop maturity date. However, the barley varieties released and predominantly grown between 2000 and 2018 have started flowering seven days on average earlier than those released before 2000, which counteracts the adverse impact of increased maximum temperature by extending the grain filling period by four days on average. Genetic solutions have contributed significantly to maintaining a steady increase in barley production by breeding fast developing and high-yielding varieties since 1980. The higher yield of newly released cultivars is attributed to both the increased yield potential, and also reduced yield loss caused by the terminal heat and drought during maturity.

It is worth noting that novel and improved agronomic practices have also played an important role in mitigating the adverse impacts of climate

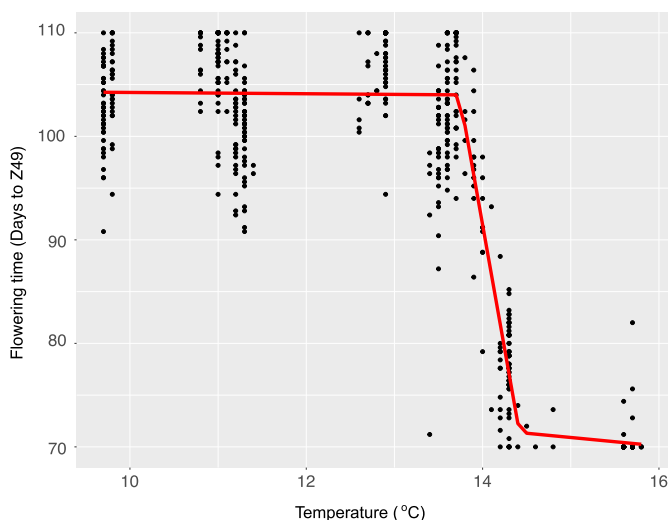


Fig. 5. Accumulated average temperature (from the day of sowing to the day of Z49) and flowering time (days to Z49) of the 85 Australia-bred barley varieties recorded over two years in four locations (seven trials in total) for Australia-bred varieties. The red line showing the breaking points of the correlation between temperature and flowering time, showing the two breakpoints, 13.7 °C and 14.4 °C, where the relationship between temperature and flowering changed.

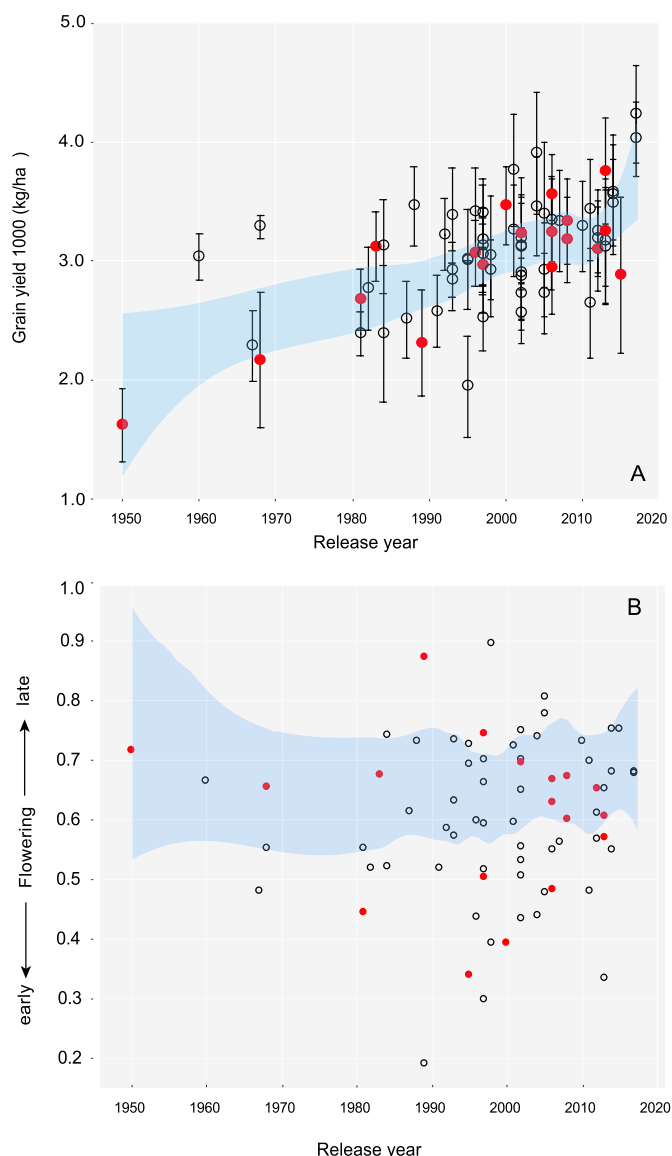


Fig. 6. The year of release, grain yield, and flowering time of 85 Australia-bred barley varieties. Grain yield and flowering time were averaged from measurement in seven trials (two years across four locations). A: Release year and grain yield. B: Release year and standardised flowering time. Production varieties (having a growing area >5% at least one year after their release) are indicated with red-filled circles.

and environmental changes, including dry seeding in regions with less reliable rainfall pattern, early sowing to avoid terminal heat [40], reduced land cultivation and controlled traffic to reduce soil compaction, integrated weed management, seasonally and locally targeted fertiliser use [40,41]. The rain-limited yield potential for barley in Australia was currently estimated to be (4200 ± 1100) kg ha⁻¹ [42], and current barley production in Australia only achieved 56% of that potential (with a current five-year average yield of 2347 kg ha⁻¹ in 2012–2017), providing ample space for further improvement in barley production. However, extreme climate events, such as extreme drought in the winter-spring of a particular year, could severely impact on barley production. For example, the three severe droughts in Australia in the 2000s saw a significant decrease in barley production.

The history of barley breeding in Australia has great implications beyond Australia and barley, especially for winter cereal crops because of the similar observed pattern of climate change across cereal-growing regions [8–10]. Our results demonstrated that genetic improvement for

early flowering in the new varieties has been the main reason of improving barley yield instead of climate change in Australia. Australia's barley breeding programme was initially designed to breed high-yield barley cultivars. While agronomically important traits such as lodging resistance, straw strength, height, phenology, head loss, and stem breakage were considered in various breeding programs, however, improved grain yield has been the primary objective of breeding activities. Thus, accelerating flowering of the new varieties has been a constant selection target as an indirect consequence of selection for grain yield in the breeding programmes, which has also been observed on maize breeding over the past 60 years in China and the United States [43]. The tight genetic correlation between flowering time and grain yield makes it possible to select high-yielding varieties with phenology adapted to changing climatic conditions. Since the 1960s, approximately 100 barley varieties have been bred and released in Australia, but less than 20% varieties have been cultivated in more than 5% of the total barley growing area. Apart from important agronomic traits, the genetic capacity to adapt to changing environments while maintaining high yields is crucial for variety's success. As a result, genetic improvement through initial artificial selection in breeding programmes and later selection in wider agricultural ecosystems (less-adapted varieties were selected against and become unpopular), have played a significant role in the enhancement of barley productivity in Australia. In the context of global food security under climate change, it is possible to breed new varieties of staple crops to counteract the adverse effects of climate change.

Despite the potential of technological advancements on mitigating the adverse effect of climate change, changing temperature could disrupt crop plant development [35], and fundamentally change the biology of crop plants to impact yield. Warming climates promote earlier flowering [36–38]. We show that the effect of climate change on crop biology may not be linear and that there may be a tipping point of effect. Natural selection could favour early reproduction (early flowering) to allow stress escape and completion of the life cycle in the non-stressful conditions [44], which, however, is a concern in terms of maintaining crop production. Cereal grain yield is determined by the biomass accumulated during the growing season and the proportion of dry matter allocated to the grains [45,46]. If a crop plant flowers too early, before it has had adequate time to accumulate sufficient biomass, it will have a limited capacity for seed production [47]. Moreover, a shift to a much early flowering would increase the risk of frost damage, therefore, significantly impact yield, which requires breeding frost tolerant barley varieties to maintain high yield. We observed a sudden shift to earlier flowering in our barley trials once temperatures reach a certain level (13.7 °C in our trials, Fig. 3). The effect of climate change on changing crop's biology to impact yield, therefore, is a growing concern that requires an urgent solution, as climate changes in some regions may reach the tipping point very soon.

5. Conclusions and implications

In this study, we examined the history of barley breeding in Australia since the 1950s and show that the increase in yield is largely the result of higher yield capacity of the more recently developed varieties that flower earlier to counteract the impact of increased terminal heat stress. We conclude that the effects of climate change on global crop production might be less severe so far than currently predicted because the advancement of technology may mitigate the adverse effect of climate change to some extent. However, great challenges remain in continuing improvement in crop production. Our results indicate that the changing temperature could soon reach a critical point to impact crop's biology dramatically in the near future, which along with extreme climate events, could be significant contributors of stalling crop production in some important grain-growing regions in the near future. Meanwhile, changes in temperature and rainfall may impact crop yield, for example through influencing the spread, growth and survival of crop pathogens [48].

Besides the contribution from constantly improving and optimising agronomic practices, new technologies such as, genomic-assisted breeding [49], speed breeding [50] and gene editing [51,52] could play a vital role in breeding crop varieties through rapidly introducing a desirable combination of beneficial genes into elite cultivars that are adapted to abiotic and biotic environments [53].

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Author contributions

CL: perceived the project concept; TH: performed data analysis, modelling and drafting the paper; TA, CH, XZ, PT and SW collected the genetic and phenotypic data. All authors have reviewed and approved the paper.

Data availability

Temperature data since 1950 are obtained from data archive at the Australian Bureau of Meteorology www.bom.gov.au. Annual barley production and growing area since 1950 are obtained from the Australian Bureau of Statistics www.abs.gov.au. *Flowering time and the maturity date in field trials are stored in Zenodo* (<https://doi.org/10.5281/zenodo.4057266>).

Declaration of competing interest

The authors declare no conflict interests.

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