Breeding Focus 2018 - Reducing Heat Stress

Edited by

Susanne Hermesch

Animal Genetics and Breeding Unit, University of New England, Armidale, Australia

Sonja Dominik

CSIRO Agriculture and Food, Armidale, Australia

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Contents

Preface

“Breeding Focus 2018 – Reducing Heat Stress” is the third workshop in the series. The Breeding Focus series was developed to provide an opportunity for exchange between industry and research across a number of agricultural industry sectors. With this goal in mind, workshops have included presentations across the livestock and aquaculture industries to take participants outside their area of expertise and encouraged them to think outside the box. This year we increased the scope even further by also inviting presentations from the cropping and horticulture industries. Since the topic of heat stress has recently gained increased attention, we will discuss a wide range of aspects associated with heat stress, such as the physiology of heat stress and phenotypic indicators, genetic approaches and industry impacts.

Heat stress in animals describes a situation where an animal is exposed to high temperatures and unable to dissipate body heat, which causes an increase in body temperature. In the short term, an animal will react to heat stress with behavioural strategies (e.g. seeking shade, panting) to reduce the heat load. With prolonged excessive heat load, feed intake is reduced and production losses occur. Under extreme circumstances, excessive heat load can lead to death. In plants, heat stress can be defined as irreversible damage to plant function and development as a consequence of hot temperatures. Environmental causes of heat stress in plants and animals include high temperatures and high humidity over a long period of time, which is exacerbated by low cloud cover and high solar radiation.

With raising average temperatures, agricultural industries are faced with the challenge to manage potential impacts of heat stress on their crops, their pasture base and welfare and production of their livestock or aquaculture species. Management strategies such as shade and irrigation are effective but costly and, depending on the severity of climatic conditions, may have limited success. Susceptibility of organisms to heat stress can vary due to factors such as age and general health, but also genetic factors, such as breed or variety. Further, as we will hear during the workshop, genetic variation exists within breeds that enables genetic approaches to address heat stress in plants and animals. Selective breeding provides a long term approach that facilitates improvement of the physiology of plants and animals to cope with excessive heat load. The challenge here is to obtain cost-effective phenotypes to describe heat stress.

The chapters of this book discuss where the current climate is trending, and outlines opportunities for the crop, orchard, livestock and aquaculture industries to describe and measure heat stress, all with the focus on genetic improvement.

We would like to thank everyone who has contributed to this event for their time and effort: the authors for their contributions to the book and presentations, the reviewers who all readily agreed to critique the manuscripts. We would like to express a special thanks to Kathy Dobos for her contributions into the organisation of this workshop and the publication. Thank you!

Susanne Hermesch and Sonja Dominik
Armidale, September 2018

Turning the heat up on independent culling in crop breeding

Wallace A. Cowling[1] and Li Li[2]

[1]The UWA Institute of Agriculture, The University of Western Australia, 35 Stirling Highway, Perth, WA 6009, Australia

[2]Animal Genetics and Breeding Unit, University of New England, Armidale NSW 2351, Australia

Abstract

Most grain crops are sensitive to heat stress during anthesis which causes substantial reductions in grain yield, and heat stress tolerance (HST) is therefore an important trait for selection in crop breeding programmes during the 21st century. We stochastically modelled breeding for flowering time, disease resistance, stem strength, and grain yield in a self-pollinating grain crop over the next 60 years, assuming 3-year selection cycles and 1,000 progeny per cycle, with or without priority selection for HST, and with moderate or high selection intensity (10% or 4% selection proportion). HST is measured at 30 °C during anthesis (HST_{30}), and is assumed to be moderately heritable ($h^2 = 0.3$). Genetic progress in a traditional crop breeding programme with independent culling on phenotypic values of individual traits was compared to progress under index selection and optimal contributions selection (OCS) on a BLUP-based economic index. In all three breeding strategies, near-homozygous lines were formed by rapid single-seed descent and selection occurred on S_5-derived lines. Priority was given to selection on HST_{30} to match rising ambient temperatures of +4 °C during the experiment. At 60 years, all breeding strategies achieved the HST_{30} target of +4 units, but economic index was lowest in the traditional breeding programme (2.27-fold), intermediate in index selection (2.57-fold) and highest in OCS (2.81-fold) under moderate selection intensity. Grain yield rose from 1.50 to 3.38 t ha^{-1} in OCS compared to 2.88 t ha^{-1} in the traditional strategy. Without selection for HST_{30}, grain yields under all scenarios reached a maximum of 2.30 t ha^{-1} and began falling around 2060, despite continued investment in breeding for yield. Independent culling on phenotype was the least effective strategy to breed for HST and grain yield during 60 years of global warming.

Introduction

Wheat, rice and maize produce more than 60% of the calories for global human consumption (Nelson *et al.* 2010), and they are sensitive to heat stress during reproduction which reduces grain yield (Farooq *et al.* 2011; Kaushal *et al.* 2016; Atlin *et al.* 2017). Heat sensitivity in grain crops is the basis of predictions that yield will decrease by 10% to 25% in the late 21st century due to higher global temperatures (Intergovernmental Panel on Climate Change 2014). Global average surface temperatures are predicted to increase from +1 to +4 °C in a range of climate change models by the end of the 21st century (Intergovernmental Panel on Climate Change 2014). Within a relatively short time period, breeders must improve breeding populations with adequate levels of heat stress tolerance (HST) to protect grain yield and other economic traits from rising global temperatures.

Independent culling, where "a certain level of merit is established for each trait, and all individuals below that level are discarded, regardless of the superiority or inferiority of their other traits" (Hazel and Lush 1942), is the most common form of selection in autogamous crops, and normally occurs on phenotypic values during the selfing process (Bos and Caligari 2008). BLUP breeding based on an economic index has not been adopted widely in self-pollinating grain crops (Bauer and Léon 2008), despite the fact that independent culling was shown to be less efficient than index selection for economic traits in the context of animal breeding (Hazel and Lush 1942) and self-pollinating crops (Pesek and Baker 1969). A major goal of this paper is to compare pedigree-BLUP breeding, based on an economic index, with traditional independent culling for multiple traits, in a self-pollinating crop, and to assess the impact of adding HST_{30} as a priority trait in the breeding programme.

One consequence of independent culling in crop breeding is that relatively few lines survive the selection process in each cycle and mating tends to be among relatively few closely-related inbred lines. While inbreeding depression in self-pollinating crops is not normally a problem, genetic drift is potentially serious because effective population size is often low (<12) (Cowling 2013). Historically, selection cycles are long (6 to 10 years per cycle), and the rate of genetic improvement is low, for example, traditional rates of genetic improvement in yield of wheat are less than one percent per year (Brancourt-Hulmel *et al.* 2003). This rate of genetic improvement is too low to meet the demands of the 2009 Declaration of the World Summit on Food Security, which requires a sustainable increase in global food production of 70% by 2050.

It was shown recently by stochastic modelling of breeding in a self-pollinating crop that optimal contributions selection (OCS) out-performed selection based on random mating among selection candidates (Cowling *et al.* 2017). OCS with moderate selection intensity (50 matings per cycle, equivalent to 10% selection proportion in a population size of 1,000) achieved higher long-term genetic gain compared with selection based on the economic index followed by random mating among selection candidates (Cowling *et al.* 2017). Long-term genetic progress with OCS on S_0-derived progeny was competitive with OCS on S_3- or S_5-derived progeny (Cowling *et al.* 2017).

Five or more selfing generations of cereal or legume grain crops can be achieved in one year (Croser *et al.* 2017; Watson *et al.* 2018; Zheng *et al.* 2013), which opens up the possibility of three-year cycles if all goes to plan, with selection based on S_5-derived S_6 plots (Fig. 1). Here, we compare by stochastic modelling over the next 60 years of global warming with or without selection for HST, three crop breeding strategies: (i) traditional breeding with independent culling among S_5-derived selection candidates, followed by random mating among selections (ii) pedigree-BLUP with selection on economic index on S_5-derived candidates followed by random mating among selections, and (iii) OCS on the economic index with a mating design to maximise genetic gain for a desired increase in population coancestry. In each breeding strategy, cycle duration was three years with five generations of selfing (single seed descent) (Fig. 1), with or without priority selection for HST in each cycle. The aim was to find the most sustainable method for improving HST to prevent negative impacts of global warming of +4 °C in the 21st century, while achieving sustainable improvements in grain yield and other economic traits.

Materials and Methods

In this paper, we model selection in a wheat breeding program over the next 60 years of global warming, including selection for HST. Selection for HST in grain crops requires an understanding of the concept of effective temperature – this is the temperature half-way between the mean and the highest temperature each day for four days during anthesis (Deryng *et al.* 2014). Yield of current spring wheat varieties decreases by 10% per 1 °C increase above a critical effective temperature of 25 °C during anthesis, reaching zero yield at the limiting effective temperature of 35 °C (Deryng *et al.* 2014). It follows that an effective temperature of 30 °C causes 50% yield loss in the current wheat varieties, and we allocate the base population an average HST_{30} score of 30. Since genetic diversity for heat stress tolerance exists in wheat landraces and contemporary lines (Atlin *et al.* 2017; Farooq *et al.* 2011), we assume HST_{30} to be heritable (we estimate $h^2 = 0.3$). In our modelling, we genetically improve population mean HST_{30} from 30 to 34 over 60 years, so that 50% yield loss in the selected population in 60 years will occur at an effective temperature of 34 °C. That is, genotypes with HST_{30} score of 34 in 60 years will suffer no greater yield loss than today, if global warming occurs at +4 °C over the next 60 years. The value of HST for grain yield depends on the prevailing climate, with little benefit from excess tolerance, but a reduction in yield resulting from insufficient tolerance. We thus use strict constraints to ensure that HST_{30} matches the prevailing requirements predicted by global warming models, while targeting maximum long-term response in other traits including grain yield.

Simulation and selection of HST_{30}

In our model, effective temperature of 30 °C is simulated in a growth room with 21 °C minimum, 27 °C mean and 33 °C maximum for four days during anthesis, which represents a heat wave during flowering. This effective temperature will cause 50% yield loss in the base population, in the absence of moisture stress, and the base population is allocated an average HST_{30} score of 30. In our simulated environment, a HST_{30} score of 30 is recorded when 50% of the tested plants set viable seed at an effective temperature of 30 °C, and the score ranges from 25 when no plants set seed to 35 when all plants set viable seed.

Breeding and selection strategies

Three crop breeding strategies were compared by stochastic simulation, with or without selection for HST_{30}, and in each strategy there were three-year cycles with five rapid selfing generations and selection on 1,000 S_5-derived progeny (Fig. 1). Selection for HST_{30} to match an increase in global temperatures of +4 °C over the next 60 years requires an increase in HST_{30} of 0.2 in each cycle (with three-year cycles). This represents an increase in 20% of initial standard deviation units of HST_{30} per cycle (Table 1), or 6.7% per year.

- Breeding strategy 1 represents a traditional crop breeding programme with independent culling on phenotypic values for four traits (Table 1), with or without priority selection for HST_{30} (phenotypic values) to match an increase in global temperatures of + 4 °C over the next 60 years, followed by random mating among selection candidates;
- Breeding strategy 2 is pedigree-BLUP with selection on an economic index with economic weightings for each trait (Table 1), with or without priority selection for HST_{30} to match an increase in global temperatures of + 4 °C over the next 60 years, followed by random mating among selection candidates;
- Breeding strategy 3 is optimal contributions selection (OCS) for economic index, with mating design provided by OCS. In the HST_{30} option, an overriding constraint is placed on achieving HST_{30} to match an increase in global temperatures of + 4 °C over the next 60 years.

The emphasis placed on each trait in the economic index was calculated using the desired gains approach (Brascamp 1984) and implemented using the program Desire (Kinghorn 2018b), with an emphasis on high rates of genetic improvement for disease resistance (Cowling *et al.* 2017).

Table 1. Starting values for mean, standard deviation, narrow-sense heritability and economic weights in the base population for several traits including heat stress tolerance (HST_{30}) (based on Cowling et al. *2015; 2017).*

		Starting values			
Trait	Unit	Starting value	Standard deviation	Narrow-sense heritability	Economic weight
Disease resistance	%	100	20	0.3	0.141
Stem strength	mm	1.2	0.3	0.3	4.124
Flowering time	days	80	20	0.5	-0.025
Grain yield	t ha^{-1}	1.5	0.25	0.3	4.265
HST_{30}	units	30	1	0.3	0

In breeding strategy 1 (Traditional), independent culling occurred on 1,000 S_5-derived S_6 progeny per cycle as follows (Fig. 1): (i) if selection for HST_{30} was required, this occurred first on HST_{30} by eliminating the most susceptible phenotypes sequentially so that the mean HST_{30} phenotype of the survivors equalled the required level to match the average global warming over the previous three-year cycle; then (ii) the remaining progeny were selected for flowering time so that the survivors flowered in the range 75 to 85 days; then (iii) the top 20% of the remaining progeny were selected for disease resistance phenotype; then (iv) the top 70% of the remaining progeny were selected for stem strength phenotype; and finally (v) the survivors were selected on the basis of grain yield phenotype, and the top 100 (moderate selection intensity) or 40 (high selection intensity) individuals were randomly mated to begin the next cycle of selection. The underlying true breeding values in PopSim were used to generate phenotypic values of progeny in the next cycle.

In breeding strategy 2 (Index), selection for HST_{30} BLUP values occurred first to match the average global warming over the previous three-year cycle as above, and the survivors were selected for an economic index calculated from estimated breeding values of four traits with economic weights shown in Table 1. Pedigree-BLUP analysis was based on phenotypes and pedigree information generated in the simulations. The top 100 (moderate selection intensity) or 40 (high selection intensity) individuals based on economic index were randomly crossed in pairwise matings to begin the next cycle of selection. The underlying true breeding values in PopSim were used to generate phenotypic values of progeny in the next cycle.

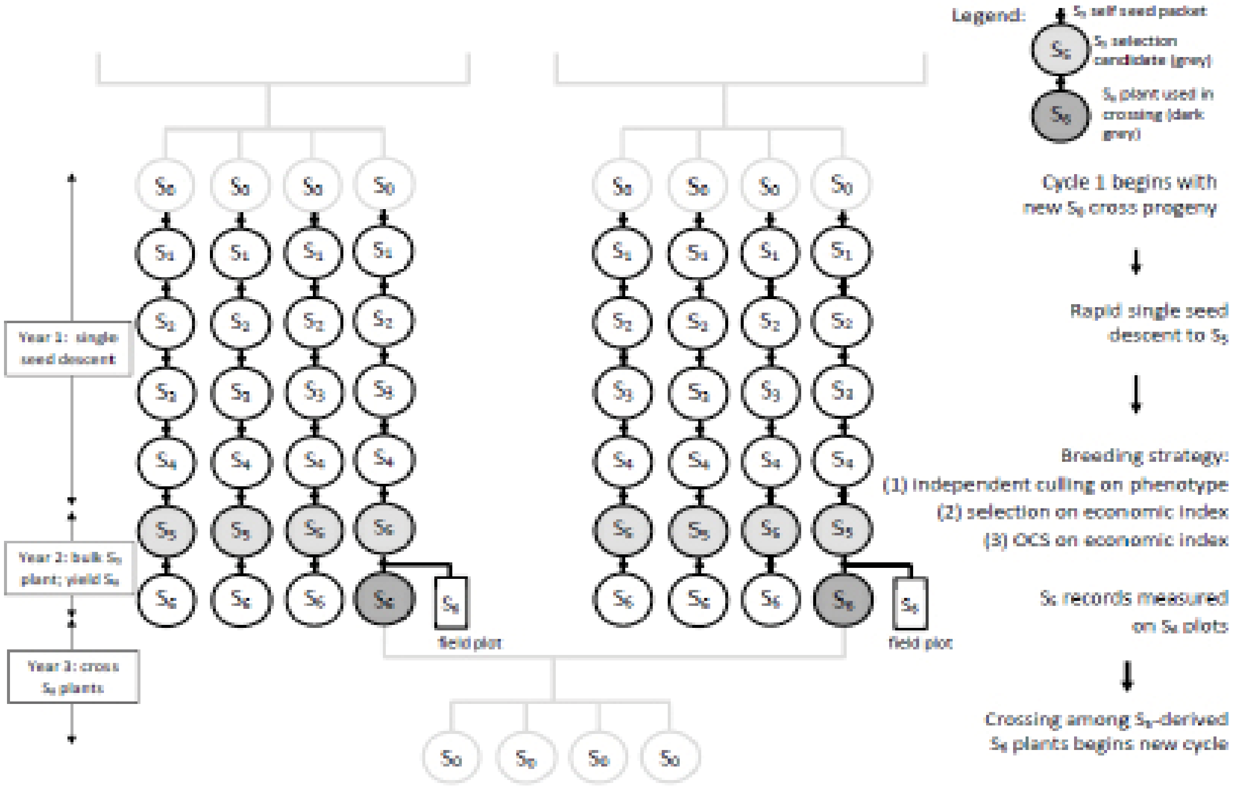

Figure 1. Diagram of single seed descent in three-year selection cycles, showing three breeding strategies on S_5 selection candidates, with phenotypes measured on S_5-derived S_6 plots (following Cowling et al. 2017).

In breeding strategy 3 (OCS), if selection for HST_{30} was required, this was achieved by placing an overriding constraint on BLUP-values for HST_{30} to match average global warming over the previous three-year cycle while economic index selection was optimized in the face of that constraint. OCS was based on the breeding program implementation platform “Matesel” (Kinghorn and Kinghorn 2018). The practical implementation of this method is based on an evolutionary algorithm (Kinghorn and Kinghorn 2018), with constraints easily invoked to ensure practical relevance and precise control of response in HST_{30}. Matesel dictates which individuals to select and the actual mating allocations and/or selfings to be made. Economic index of progeny and their relationships were used to optimise a design for 50 matings (moderate selection intensity) or 20 matings (high selection intensity) based on a balanced strategy of target 45 degrees, where 0 degrees gives full emphasis to short-term genetic gain in index and 90 degrees gives full emphasis to minimizing parental coancestry (Cowling *et al.* 2017). The underlying true breeding values in PopSim were used to generate phenotypic values of progeny in the next cycle.

In summary, six different scenarios were modelled, with and without selection for HST_{30}:

- “Traditional-moderate” (independent culling on phenotype with moderate selection intensity);
- “Traditional-high” (independent culling on phenotype with high selection intensity);
- “Index-moderate” (index selection with moderate selection intensity);
- “Index-high” (index selection with high selection intensity);
- “OCS-moderate” (OCS selection with moderate selection intensity);
- “OCS-high” (OCS selection with high selection intensity).

Parameters for simulation

The starting parameters for mean, phenotypic standard deviation, narrow-sense heritability, and economic weights for grain yield, resistance to a hypothetical disease, stem strength, and flowering time are based on previous empirical evidence (Cowling *et al.* 2015; 2017), and we add a new trait defined as heat stress tolerance at an effective temperature of 30 °C during anthesis (HST_{30}) (Table 1). Genetic and phenotypic correlations among traits are based on previous empirical evidence (Cowling *et al.* 2015; 2017), except for HST_{30}, for which no previous empirical evidence exists. We assume zero genetic correlation of HST_{30} with other traits when temperatures are below the critical effective temperature during anthesis (Table 2), and because HST_{30} was selected in the traditional crop breeding model with independent culling based on phenotypic values. Traditional crop breeding by independent culling ignores genetic correlations between traits.

Table 2. Genetic and phenotypic correlations between traits (based on Cowling et al. *2015; 2017).*

Trait	Genotypic (below diagonal) and phenotypic (above diagonal) correlations				
	Disease resistance	Stem strength	Flowering time	Grain yield	HST_{30}
Disease resistance	-	-0.05	0.25	0.15	0
Stem strength	-0.1	-	0	0.1	0
Flowering time	0.3	0	-	-0.1	0
Grain yield	0.2	0.15	-0.15	-	0
HST_{30}	0	0	0	0	-

Simulation process

Simulations were carried out using the PopSim module of Genup (Kinghorn 2018a), which was developed and used in the context of the infinitesimal model, and has been applied to animal selection (Webb *et al.* 2012). PopSim was modified to include bisexuality and selfing as required for self-pollinating crops, as described previously (Cowling *et al.* 2017). Phenotypes were simulated and breeding values were estimated based on multi-variate BLUP analysis using pedigree information within PopSim. OCS was included as an option for mate selection and mate allocation decisions at each breeding cycle (Kremer *et al.* 2010). OCS was based on the breeding program implementation platform “Matesel” (Kinghorn and Kinghorn 2018).

The model was run 10 times for each scenario, and the average genetic progress for economic index, component traits, and parental coancestry in each cycle was reported.

To begin the modelling experiment, diverse founder groups of 100 inbred lines (moderate selection intensity) or 40 inbred lines (high selection intensity) were subjected to 50 random pairwise matings, and the F_1 progeny intercrossed in 25 random F_1 matings, to generate 1,000 S_0 progeny for selection by one of three breeding strategies as described below.

Heat-adjusted grain yield

Selection increases the mean population grain yield, but this must be “protected” by an appropriate increase in HST_{30} in each cycle to match the rate of global warming. The base population has a HST_{30} score of 30 (Table 1), which “protects” grain yield at an average of 1.5 t ha^{-1} at temperatures experienced in 2017. HST_{30} must increase in each generation by 0.2 units to avoid a heat stress penalty. Heat-adjusted grain yield in each cycle is the population mean predicted grain yield in that cycle reduced by 10% for every degree Celsius by which the achieved HST_{30} falls below the target HST_{30} in parents of the previous cycle (Deryng *et al.* 2014).

Results

Priority selection for HST_{30} (Fig. 2) was successful in reaching the target increase of +4 units HST_{30} over 60 years in all breeding scenarios (results not shown), but long-term genetic progress during global warming in other traits was affected by breeding strategy and selection intensity. The highest economic index was achieved by OCS-moderate (2.81-fold increase in economic index over 60 years) which out-performed Traditional-moderate (2.27-fold) and Index-moderate (2.57-fold) (Table 3, Fig. 2A). OCS-moderate was superior to Traditional-high and Traditional-moderate for all traits under selection (Fig. 2A,C,D,E), and heat-adjusted grain yield of OCS-moderate at 60 years (3.38 t ha^{-1}) exceeded Traditional-high by 0.50 t ha^{-1} and Traditional-moderate by 1.23 t ha^{-1} (Table 3, Fig. 2F), assuming global warming of +4 °C over 60 years. OCS-moderate achieved this result with 10% lower population coancestry than Traditional-high at 60 years (Fig. 2B).

When HST_{30} was not selected (Fig. 3), OCS-moderate achieved a final grain yield of 3.56 t ha^{-1} (Fig. 3E), compared with 3.50 t ha^{-1} when selection occurred for +4 units in HST_{30} (Fig. 2E). Therefore, in the absence of global warming, priority selection for HST_{30} did not impose a large "yield penalty" in OCS-moderate. In contrast, there was a major yield penalty of -0.51 t ha^{-1} in Traditional-high and -0.64 t ha^{-1} in Traditional-moderate when HST_{30} was included as a priority trait (Figs. 2E, 3E). Without priority selection for HST_{30}, heat-adjusted grain yield in OCS-moderate fell to 2.16 t ha^{-1} (Fig. 3F) over the course of the experiment, or 1.22 t ha^{-1} less than when HST_{30} was selected, assuming global warming of +4 °C over 60 years. Without selection for HST_{30}, heat-adjusted grain yield began falling by 2060 in all breeding strategies and never exceeded a maximum of 2.3 t ha^{-1} (Fig. 3F), despite continued investment in breeding for all traits except HST_{30}.

Moderate selection intensity normally outperformed high selection intensity for economic index and all traits at 60 years (Fig. 2). The notable exception was Traditional-moderate, which achieved lower index, stem strength and grain yield at 60 years than Traditional-high, although with much lower population coancestry (Fig. 2). The order of independent culling of traits influenced the outcome in Traditional-moderate: disease resistance was second in order after flowering time and showed competitive genetic progress (Fig. 2C), but there was much weaker genetic progress for stem strength (Fig. 2D) and grain yield (Fig. 2E).

Economic weighting of traits in the OCS and Index breeding strategies favoured disease resistance (Cowling *et al.* 2017), and therefore disease resistance was under high selection intensity in the Traditional breeding strategy. Despite this, genetic progress for disease resistance after 20 cycles in OCS-moderate (3.08-fold increase over base levels) out-performed Traditional-high (2.50-fold increase over base levels) (Fig. 2C). Also, OCS-moderate achieved 2.44-fold increase in stem strength over the base population after 20 cycles, compared with 2.00-fold increase in Traditional-high (Fig. 2D). In the OCS and Index strategies, flowering time required a small economic weighting in favour of earliness (Table 1), in order to keep flowering time approximately constant over cycles, due to the positive correlation between flowering time and disease resistance (Table 2). Flowering time was the first trait after HST_{30} to be selected in Traditional breeding, and it remained relatively stable over 20 cycles.

Index-high resulted in the highest coancestry at 60 years (Fig. 2B), and was consistently behind OCS for most traits (Fig. 2), and behind Traditional-high for adjusted grain yield at 60 years (Fig. 2F).

Table 3. Mean and fold increase over starting values after 20 cycles of selection for economic index and heat-adjusted grain yield for all breeding strategies and selection intensities under global warming + 4 °C, and priority selection for HST_{30} = + 4 units over 20 cycles.

	Economic index		Heat-adjusted grain yield (t ha^{-1})	
Strategy	Mean value	Fold increase over starting values	Mean value	Fold increase over starting values
OCS_moderate	66.19	2.81	3.38	2.27
OCS_high	62.57	2.69	3.17	2.11
Index_moderate	60.34	2.57	3.04	2.03
Index_high	54.63	2.35	2.72	1.82
Traditional_moderate	53.36	2.27	2.15	1.44
Traditional_high	53.92	2.32	2.88	1.92

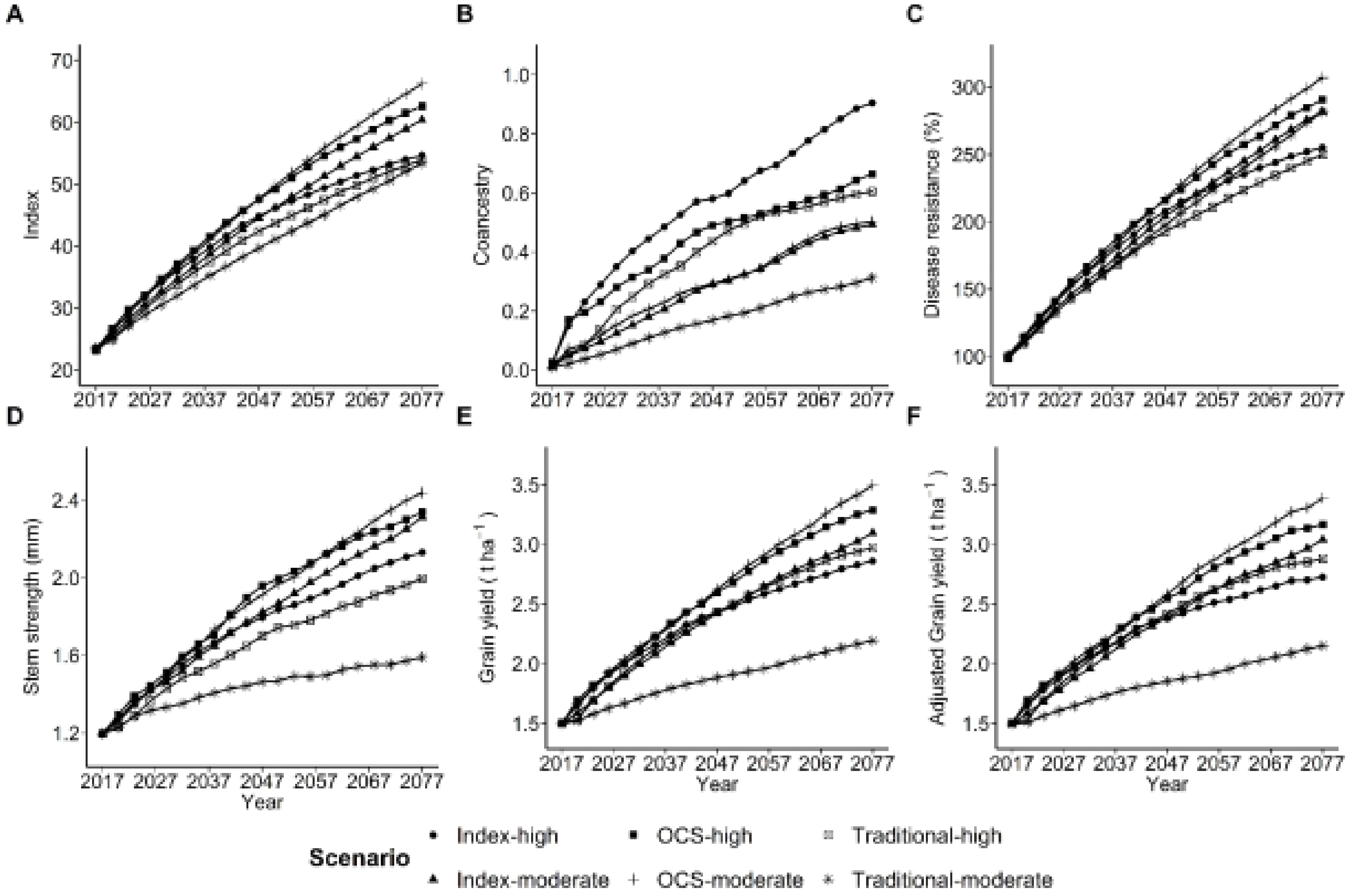

Figure 2. Response to selection in a self-pollinating crop with priority selection for heat stress tolerance (HST_{30}) of +4 units for three breeding strategies: Traditional (independent culling for traits in the order of flowering time, disease resistance, stem strength and grain yield); Index (selection for economic index followed by random mating); and OCS (optimal contributions selection for economic index with mating design from OCS). "High" and "moderate" represent selection intensities. Results are presented for (A) economic index, (B) population coancestry, (C) disease resistance, (D) stem strength, (E) grain yield in the absence of global warming, and (F) heat-adjusted grain yield during global warming of +4 °C over 60 years.

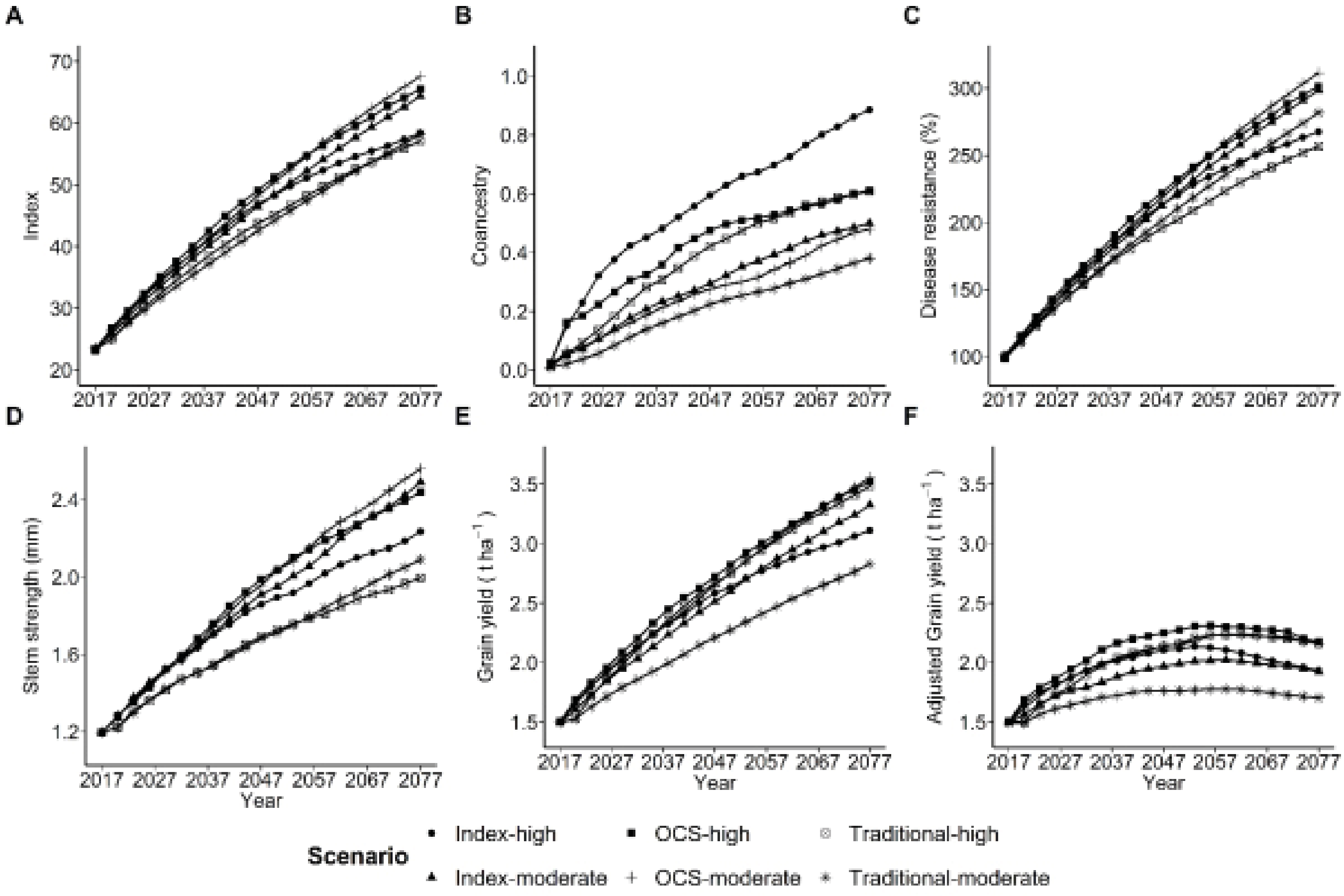

Figure 3. Response to selection in a self-pollinating crop without priority selection for heat stress tolerance (HST_{30}) of +4 units for three breeding strategies: Traditional (independent culling for traits in the order of flowering time, disease resistance, stem strength and grain yield); Index (selection for economic index followed by random mating); and OCS (optimal contributions selection for economic index with mating design from OCS). "High" and "moderate" represent selection intensities. Results are presented for (A) economic index, (B) population coancestry, (C) disease resistance, (D) stem strength, (E) grain yield in the absence of global warming, and (F) heat-adjusted grain yield during global warming of +4 °C over 60 years.

Discussion

This modelling experiment demonstrates several contrasts between traditional independent culling on phenotypes in pure-line crop breeding, and selection based on an economic index. It was expected from the early literature (Hazel and Lush 1942; Pesek and Baker 1969) that selection based on an economic index would out-perform independent culling. Index-high reached higher population coancestry than Traditional-high (Fig. 2B). While Index-high was similar to Traditional-high for economic index at the end of the experiment (Fig. 2A), it was lower performing than Traditional-high for grain yield (Fig. 2F). The rapid increase in population coancestry in Index-high was the result of mating of close relatives which were ranked highly by economic index. In animal breeding, higher rates of population inbreeding were experienced following the introduction of pedigree-BLUP, and as a result OCS was developed to help balance the rate of loss of genetic diversity with long-term genetic gain (Woolliams *et al.* 2015).

This study demonstrates the advantage of OCS over Index and Traditional breeding strategies for multiple traits in crops, especially when HST_{30} is added to help counter the yield-limiting effects of global warming. Traditional-high achieved lower gain in economic index and all component traits at 60 years compared with OCS-moderate at similar levels of population coancestry. Grain yield in Traditional-high was the last trait in order of independent culling. Consequently, the number of candidates for selection on grain yield was relatively few, and there was a significant "yield penalty" for including HST_{30} as a priority trait in the Traditional breeding strategy.

Grain yield in OCS-moderate plus HST_{30} increased during 60 years of global warming at an average rate of 2.1% per year from the base level of 1.5 t ha^{-1}. OCS-high and OCS-moderate were the only scenarios in which heat-adjusted grain yield exceeded 2.55 t ha^{-1} in 2050, and therefore met the requirements of the 2009 Declaration of the World Summit on Food Security to sustainably increase global food production by 70% in 2050.

The OCS and Index breeding strategies can readily incorporate genomic relationship information in "single-step" genomic prediction (Ashraf *et al.* 2016) and this should improve the outcomes of OCS-moderate even further. Crop genomic selection models to date mostly focus on selection for single traits such as grain yield (Gaynor *et al.* 2017), and have not yet tackled the larger issue of index selection or OCS for multiple traits. OCS will be very important for management of population coancestry in both genomic and pedigree-based selection models.

No breeding strategy was successful in preventing a loss in grain yield with global warming in the absence of selection for HST_{30}, despite continued investment in crop breeding (Fig. 3F). If crop yields fall due to global warming during the 21st century as predicted (Lesk *et al.* 2016; Teixeira *et al.* 2013), and no attempt is made to select for HST in grain crops, there will be large negative repercussions for global food security.

Our model for breeding self-pollinating crops in three-year cycles depends on achieving 5 generations of selfing in 12 months through accelerated single seed descent (Croser *et al.* 2017; Watson *et al.* 2018; Zheng *et al.* 2013). It also depends on sufficient S_5-derived seed to sow replicated plots of each line at more than one site in the second year of each cycle (Fig. 1), so that reliable estimates of grain yield, disease resistance, stem strength and flowering time may be obtained in each cycle. Any hold-up in single seed descent or bulking for field trials will extend cycles beyond three years. Two-year selection cycles with S_0-derived index selection were competitive with single seed descent (three or four-year cycles) for population improvement (Cowling *et al.* 2017). The substantial costs and time associated with single seed descent may not be necessary in the population improvement phase of crop breeding when selection is based on OCS. Single seed descent may be carried on high index selections if this is important for commercial purposes (Cowling *et al.* 2017).

Another potential disadvantage of single seed descent is unintentional selection under controlled environment conditions. For example, late maturing types may be discarded during single seed descent in order to complete 5 generations in 12 months. This may unintentionally bias the breeding programme towards early maturity, and inhibit future genetic progress for later maturity. We deliberately kept the population diverse for this trait and with an average suitable for the average target environment.

Our BLUP analysis includes historical records for individuals back to the base population. This is not the case in traditional crop breeding – historical records are not used in selection decisions on current selection candidates. In the animal model, information from relatives back to the base population is used to estimate breeding values of each related individual in the pedigree (Lynch and Walsh 1998). Accuracy of the selection index is increased by adding records from ancestors, progeny, full sibs and collateral relatives (Simm 1998). Accuracy of breeding values was also improved by adding records from self progeny, in addition to cross progeny, in the pedigree of a self-pollinating crop (Cowling *et al.* 2015).

In summary, HST_{30} was genetically improved as a priority trait to protect crops from global warming over 60 years in all breeding strategies. However, the traditional crop breeding programme with independent culling on S_5-derived lines suffered a substantial yield penalty when HST_{30} was added as a priority trait. OCS had the highest index and grain yield after 60 years of global warming and did not suffer a yield penalty when HST_{30} was added as a priority trait.

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