

REVIEW PAPER

Identifying target traits and molecular mechanisms for wheat breeding under a changing climate

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Abstract

Global warming is causing changes in temperature at a rate unmatched by any temperature change over the last 50 million years. Crop cultivars have been selected for optimal performance under the current climatic conditions. With global warming, characterized by shifts in weather patterns and increases in frequency and magnitude of extreme weather events, new ideotypes will be required with a different set of physiological traits. Severe pressure has been placed on breeders to produce new crop cultivars for a future, rapidly-changing environment that can only be predicted with a great degree of uncertainty and is not available in the present day for direct experiments or field trials. Mathematical modelling, therefore, in conjunction with crop genetics, represents a powerful tool to assist in the breeding process. In this review, drought and high temperature are considered as key stress factors with a high potential impact on crop yield that are associated with global warming, focusing on their effects on wheat. Modelling techniques are described which can help to quantify future threats to wheat growth under climate change and simple component traits that are amenable to genetic analysis are identified. This approach could be used to support breeding programmes for new wheat cultivars suitable for future environments brought about by the changing climate.

Key words: Crop modelling, deconvoluting complex traits, drought and heat stress, G×E interactions, wheat genetics.

Introduction

The largest temperature changes of the past million years happened as a result of the glacial cycles, during which global mean temperature changed by 4–7 °C between the ice ages and the warm interglacial periods (Solomon *et al.*, 2007). The changes in temperature during the last 450 000 years at Vostok station in east Antarctica, as derived from deuterium isotopic measurements on ice cores, are shown in Fig. 1 (Jouzel *et al.*, 1987; Jouzel *et al.*, 1993; Jouzel *et al.*, 1996; Petit *et al.*, 1999). Although changes in temperature were large in the past, global warming at the end of each ice age was a relatively gradual process taking approximately 5000 years (Solomon *et al.*, 2007). The current rate of global climate change is much more rapid. If, as predicted, an increase of 5 °C in global mean temperature is achieved by the end of the century (this is the upper end of the range

predicted by Global Climate Models in the IPCC 4th Assessment Report), then the Earth will have experienced a rate of change which could not be matched by any global mean temperature increase of the last 50 million years (Solomon *et al.*, 2007).

Breeders select new cultivars of agricultural crops that are better suited to a specific environment utilizing available resources in the most optimal way. However, cultivars that are recommended for use at present might not be suitable if the climate changes. Breeding for a new cultivar usually takes 10–12 years, if the target traits are known and the environment in which to test new lines is available. Faced with the prospect of a rapidly changing climate, breeders do not have access to the climatic conditions of even the near future in which to carry out field trials, and they do not

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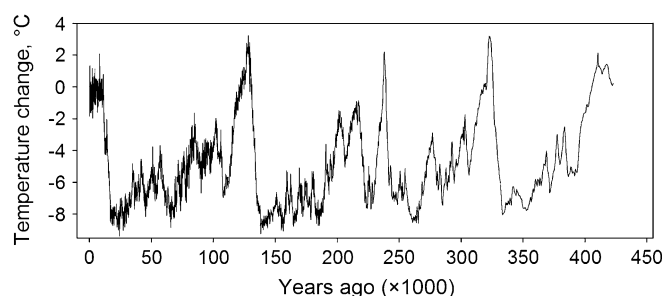


Fig. 1. Temperature changes during the last several glacial cycles from the Vostok ice core in Antarctica as derived from deuterium isotopic measurements on ice cores (figure created from a dataset published in Petit *et al.*, 1999).

know which wheat traits might be important in 15–25 years time. For example, breeding for drought tolerance in wheat could be justified for the current climate in the UK. However, in the future, heat stress at flowering, resulting in substantial yield losses, could be a greater threat to wheat production.

Most Global Climate Models predict increases in summer dryness and winter wetness in most parts of the northern middle and high latitudes during this century (Fig. 2). They also predict a substantial increase in temperature and in the frequency and magnitude of extreme weather events (Solomon *et al.*, 2007). Using climate projections for the UK, based on the UKCIP02 climate modelling experiments completed by the Hadley Centre (Hulme *et al.*, 2002), it has been shown that heat waves will increase substantially in frequency (by an order of magnitude), length, severity, and peak temperature by the end of the century (Semenov, 2007). Even isolated incidents of extreme high temperature during sensitive stages of crop development, flowering for example, could reduce grain yield significantly, while a continuous period of extreme high temperature could ruin a harvest altogether.

With global warming, changes in climate and extreme weather events are likely to impact agricultural crops, but it is not yet clear what the extent of yield losses will be and whether breeding for new, stress-tolerant cultivars will be required. In this review, drought and high temperature are considered; two key stress factors associated with global warming that have a high potential impact on crop yield, focusing on their effects on wheat. Modelling techniques are described that can help to quantify future threats to wheat growth under climate change and to identify the component wheat traits and genes that can be used for wheat genetic improvement. These techniques will support breeding programmes in a rapidly changing climate.

Predicting the impacts of drought and heat stress under climate change

Crop simulation models are used increasingly in basic and applied research in plant sciences (Passioura, 1996; Sinclair and Muchow, 2001; Debaeke and Aboudrare, 2004; Porter and Semenov, 2005). Simulation models provide the best-

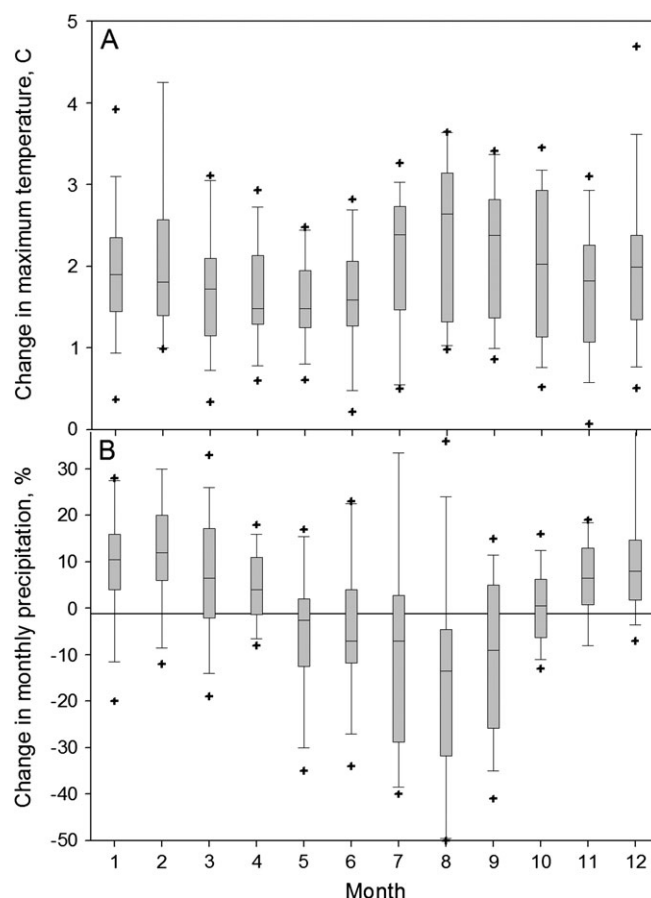


Fig. 2. Absolute changes in monthly mean maximum temperature (A) and relative changes in monthly mean precipitation (B) as predicted by global climate models used in the latest IPCC 4th Assessment Report for the SRES-A1B emission scenario for 2050s compared with the baseline scenario (1960–1990) at Rothamsted, UK. The boundaries of the box indicate the 25th and 75th percentiles, the line within the box marks the median, whiskers below and above the box indicate the 10th and 90th percentiles and outliers show minimum and maximum values.

known approach for integrating our understanding of complex plant processes that are influenced by weather and other environmental factors. They are useful in guiding the direction of fundamental research by providing quantitative predictions and highlighting gaps in our knowledge (Tardieu, 2003; Hansen, 2005; Semenov *et al.*, 2007). Combined with high-resolution climate scenarios based on Global Climate Models, crop simulation models are extensively used to assess the impact of climate change and to identify potential future threats (Semenov *et al.*, 1993, 1996; Jamieson *et al.*, 2000; Ewert *et al.*, 2002; Carbone *et al.*, 2003; Richter and Semenov, 2005; Olesen *et al.*, 2007).

In the following example, the relative importance of drought and high temperature stress on wheat yields under climate change has been quantified using a crop simulation model combined with high resolution climate change scenarios (Semenov, 2009). According to the UKCIP02 projections, the reduction of precipitation during summer and the substantial increase in maximum temperature

during spring and summer could be major stress factors for wheat production in the UK in the future (Hulme *et al.*, 2002).

In an experiment on the effects of CO₂ and temperature on grain yield, Mitchell and co-workers (1993) observed that a temperature of 27 °C or higher half-way through anthesis, when 50% of the ears in a population had flowered, resulted in a high number of sterile grains. Although the effect of reduced grain numbers on final yield could be compensated for during grain-filling by the production of larger grains, the yield losses could still be high. In another study, Wheeler *et al.* (1996) used temperature-gradient tunnel systems to demonstrate that a temperature of 31 °C or higher prior to anthesis could reduce the number of grains per ear considerably, with a concomitant effect on grain yield. A similar result was obtained by Ferris *et al.* (1998). These studies provide convincing evidence that a short episode of high temperature around the time of flowering can reduce wheat grain yield substantially (Wheeler *et al.*, 2000). In our example study (Semenov, 2009), heat stress around flowering was quantified by the probability P_{ant}^{T27} of the maximum temperature exceeding 27 °C at least once during the 10 d after the beginning of anthesis.

Considerable yield losses can also be the outcome of prolonged drought over the growing season. The reduction in grain yield due to water stress can be quantified by the drought stress index (*DSI*), which is calculated as $DSI = 1 - Y_{WL}/Y_{Pot}$, where Y_{WL} and Y_{Pot} are simulated water-limited grain yields and potential grain yields, respectively. The potential yield is calculated for a crop for which daily water demands are satisfied. The 95-percentile for *DSI*, Q_{DSI}^{95} , represents the level of yield losses due to water stress that can be expected, on average, once every 20 years.

Daily site-specific climate scenarios were constructed by using the LARS-WG stochastic weather generator (Semenov, 2007), which downscaled UKCIP02 predictions (Hulme *et al.*, 2002) to the resolution required by crop simulation models. Weather generators have been adopted in climate change studies as a computationally inexpensive tool to generate climate scenarios with high temporal and spatial resolutions, based on the output from Global Climate Models (Wilks, 1992; Barrow and Semenov, 1995). Two winter wheat cultivars, cv. Avalon and cv. Mercia, were analysed; both are obligate winter wheat cultivars with moderate to weak day-length responses that have been calibrated previously using field experiments in the UK (Wolf *et al.*, 1996; Ewert *et al.*, 2002; Lawless *et al.*, 2005). Mercia is a late-flowering cultivar that matures, on average, 2 weeks later than cv. Avalon.

The baseline scenario, representing 1960–1990, was compared with the climate predictions for the 2050s based on the high emission scenario (2050HI) (in other words the climate predicted if greenhouse gas emissions remain ‘business as usual’; Nakicenovic and Swart, 2000). The predicted increases in maximum temperature for the 2050HI scenario were between 2 °C and 4 °C and the probability of the maximum temperature exceeding 27 °C around flowering would be affected significantly by such large increases in

temperature mean. However, this would be offset somewhat because wheat development is driven by thermal time, so in a warmer climate wheat flowering would occur earlier in the season, before the summer temperature peak. Table 1 shows the average day (day of the year) of flowering and average maximum temperature \bar{T}_{max} for this day for cvs Avalon and Mercia for the baseline and 2050HI scenarios. The increase of \bar{T}_{max} at flowering in the 2050HI scenario compared with the baseline was only 0.35 for cv. Avalon and 1.06 °C for cv. Mercia, because the wheat was predicted to flower almost 2 weeks earlier. The relative changes between the baseline and 2050HI scenarios in probability P_{ant}^{T27} for early-flowering cv. Avalon were significantly smaller in magnitude (Fig. 3c) than changes for late-flowering cv. Mercia, which increased more than 2-fold for most of England and Wales (Fig. 3d).

To calculate changes in 95-percentiles of the *DSI* distribution, Q_{DSI}^{95} , 150 years of daily weather for the baseline and 2050HI climate scenarios were used (Fig. 3a, b). For both cultivars, Q_{DSI}^{95} was predicted to decrease with a significantly larger decrease for early-flowering cv. Avalon compared with late-flowering cv. Mercia. For future scenarios, despite the fact that monthly precipitation was predicted to be lower for the summer months, Q_{DSI}^{95} was predicted to decrease in England and Wales. Two factors contributed to this decrease. The first was wheat phenology: both cultivars were predicted to mature almost 3 weeks earlier for the 2050HI scenarios compared with the baseline scenario (Table 1). Because soil water deficit increases towards the end of crop growth, a crop can avoid the most severe drought stress by maturing earlier. The second factor was related to changes in the precipitation pattern. Although summer was predicted to be drier for the UKCIP02 projections, winter was predicted to be wetter. Additional precipitation during winter and early spring would be stored in the soil (the exact amount of stored water would depend on soil available water capacity) and made available to the crop during late spring and early summer.

This study demonstrates that the impacts of changing climate on wheat can be counter-intuitive and that the severity of the impact depends strongly on cultivar characteristics and spatial and temporal patterns of climate changes. Drought is the most significant environmental stress in agriculture worldwide and improving yield in water-limited environments is a major goal of plant breeding (Tambussi *et al.*, 2007; Cattivelli *et al.*, 2008). Some researchers suggest that the impact of drought will increase with climate change (Foulkes *et al.*, 2007; Witcombe *et al.*, 2008) and emphasize the importance of breeding for drought-tolerant crops. The analyses presented here, however, predict that the impact of drought stress on two existing wheat cultivars in the UK will decrease with climate change. Therefore, drier and warmer summers, which are expected in the UK, will not necessarily mean additional yield losses due to water stress. An increase in the frequency of heat stress around flowering as a result of global warming represents a greater risk for sustainable wheat production in the UK (Barnabás *et al.*, 2008).

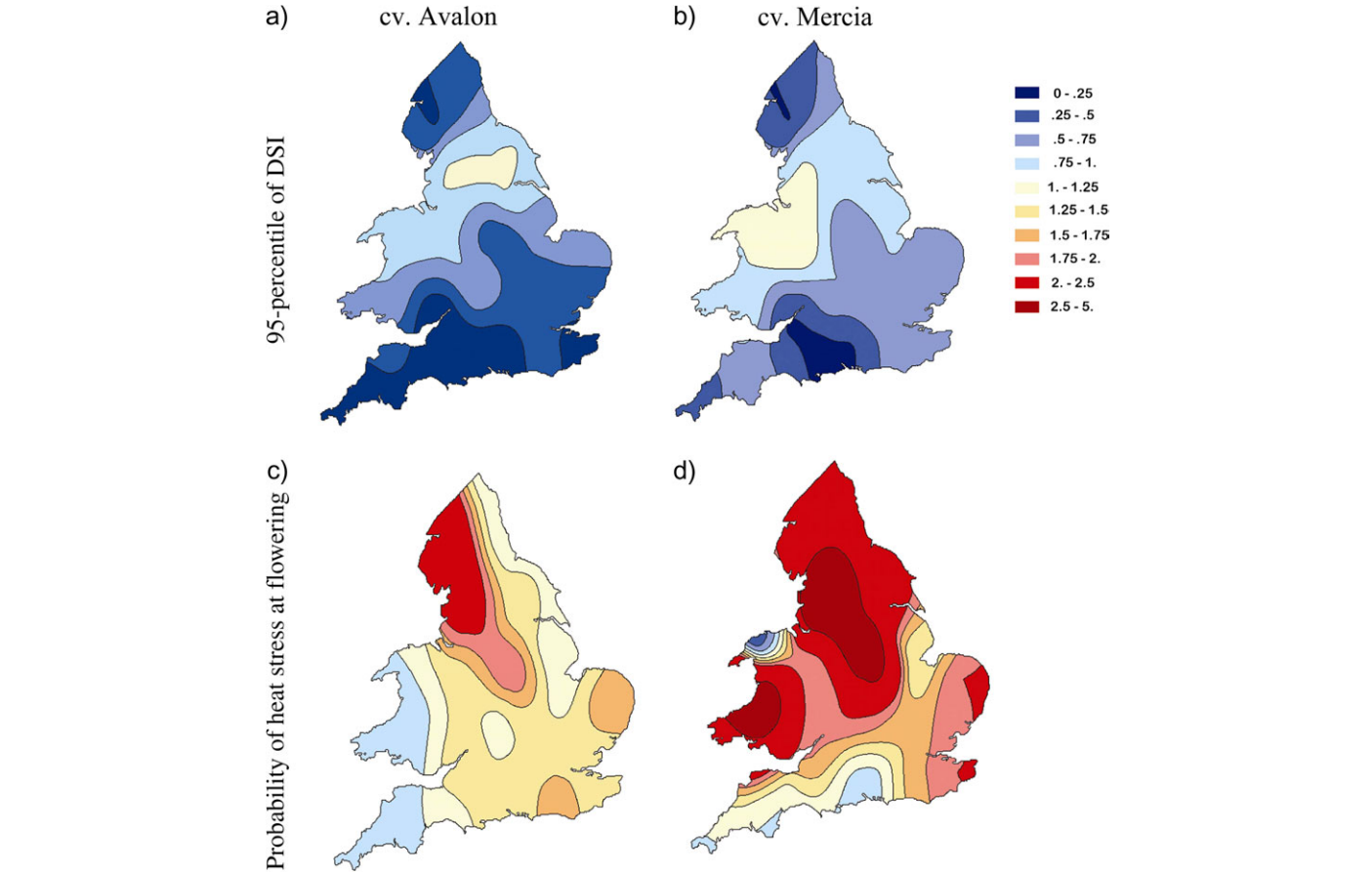


Fig. 3. Relative changes in 95-percentile for drought stress index and the probability of maximum temperature exceeding 27 °C around flowering for early developing cv. Avalon and late developing cv. Mercia for the 2050s high emission scenario compared with the 1960-1990s for England and Wales, UK.

Table 1. The average date of flowering and maturity and the average maximum temperature \bar{T}_{max} at flowering calculated for cv. Avalon and cv. Mercia and for baseline and 2050HI climate scenarios at Rothamsted

Cultivar		Baseline	2050HI
Avalon	Flowering	9 June	24 May
	Maturity	8 Aug	18 July
	\bar{T}_{max} at flowering (°C)	18.50	18.85
Mercia	Flowering	19 June	5 June
	Maturity	23 Aug	2 Aug
	\bar{T}_{max} at flowering (°C)	19.36	20.42

Deconvoluting complex wheat traits

Even when abiotic threats are known, it may be difficult to progress with crop breeding if the target for improvement is a complex trait, such as water-use efficiency or thermo-tolerance. It may be difficult to establish relationships between such traits and simple component traits, which can be assigned to quantitative trait loci (QTL), markers or single genes and targeted by breeders and geneticists. Crop simulation models may be useful here to deconvolute a complex trait into a ranked list of simpler traits suitable

for further genetic analysis and breeding. As an example, there follows a demonstration of how modelling works for water-use efficiency in wheat (Semenov *et al.*, 2009).

A considerable amount of work has been done to develop ways of improving crop yield under limited water supply (Collins *et al.*, 2008), in particular for wheat (Richards *et al.*, 2002; Condon *et al.*, 2004). The term ‘water use efficiency’ (WUE) has many definitions, depending on the range of biological processes studied and the temporal scale. At the leaf level, WUE can be defined as the ratio of instantaneous carbon dioxide assimilation over transpiration (Jones, 1992), whereas at the crop level, WUE is usually defined as the ratio of final crop yield over total seasonal evapotranspiration. It has been shown experimentally that crop WUE is sensitive to environmental conditions, with humidity being particularly important because it directly affects stomatal conductance (Day *et al.*, 1978; Lawlor *et al.*, 1981). However, improving WUE in itself is of limited interest if the crop produces a very low grain yield and it may be more sensible to explore the potential of modifying other, less complex physiological traits to improve wheat yield in water-limited environments (Sinclair and Muchow, 2001).

Plants exhibit different strategies for survival and growth under conditions of limited water supply or high

evaporative demands (Jones, 2004; Tambussi *et al.*, 2007). Plants may avoid the effects of severe drought by developing early and shortening the growing season, by conserving available water through reducing leaf size and regulating stomatal closure, or by extracting water more efficiently with an improved root system. By conserving water or extracting it more efficiently they avoid becoming water-stressed despite the drought conditions. Plants may also develop improved *tolerance* to water deficit; in other words they become water-stressed but are able to maintain productivity anyway. The Sirius wheat simulation model was used to quantify the effects of variations in both groups of traits on wheat performance under water-limited conditions at two contrasting European sites representative of major wheat-growing regions (Semenov *et al.*, 2009).

Water stress avoidance traits: phenology

Modifying the duration of crop photosynthesis and its timing in relation to seasonal variations of solar radiation may have significant effects on yield (Akkaya *et al.*, 2006; Richards, 2006). The phyllochron (P) is the thermal time required for the appearance of successive leaves, and is a major driver of phenological development (Jamieson *et al.*, 1995, 1998a, 2007). By modifying P , the rate of crop development is altered and, therefore, the date of flowering and maturity. The rate at which the leaves appear, determined by P , will influence the rate at which the canopy develops and water is depleted; increasing this rate shortens the duration of the vegetative development phase. Genetic variations of P of up to 20% have been reported for wheat (Mossad *et al.*, 1995; Ishag *et al.*, 1998).

Increasing the duration of the grain-filling period (GFD) has also been suggested as a possible trait for increasing grain yield in wheat (Evans and Fischer, 1999). The rate of grain growth depends on intercepted radiation during grain-filling, and the recycling of water-soluble carbohydrates that are stored in the stem or produced by the breakdown of leaf tissue during senescence. In the Sirius model, the labile carbohydrate pool is calculated as a fixed 25% of biomass at anthesis, and is translocated to the grain in thermal time at a rate proportional to GFD^{-1} . Increasing GFD has the potential to increase the amount of radiation intercepted by the crop during grain-filling and, therefore, grain yield. However, if the end of grain-filling were to occur earlier as a result of leaves senescing, grain yield would decrease, both through the loss of intercepted radiation and the fact that there would be insufficient time for all of the labile carbohydrate pool to be translocated to the grain. Genetic variations of GFD for wheat of up to 40% have been observed (Robert *et al.*, 2001; Charmet *et al.*, 2005; Akkaya *et al.*, 2006).

Water stress avoidance traits: root growth and distribution

In the Sirius model, it is assumed that only a proportion of available soil water can be extracted from the soil layer by

the plant on any day. A model parameter λ describes the efficiency of the root system to extract water through the vertical soil profile. This simple approach to soil water extraction by wheat crops has been proven to be robust for contrasting environments and soil conditions (Meinke *et al.*, 1997; Jamieson *et al.*, 1998b), as well as for several other crop species (Robertson *et al.*, 1993; Dardanelli *et al.*, 2004). A faster water uptake would reduce the stress experienced by the plant in anticipation of additional water coming in the form of precipitation or irrigation later in the season. In environments with a low probability of additional water, however, an alternative strategy that reduced water uptake would be less risky and might achieve a higher yield (Manschadi *et al.*, 2006).

Root vertical extension rate ($RVER$) is constant in Sirius (Jamieson *et al.*, 1998b). In the model, roots can potentially grow up to a maximum depth and stop growing at anthesis. Allowing roots to extend at a higher rate would enable plants to capture water more efficiently and prevent water leaching to deeper, unavailable soil layers.

Water stress avoidance traits: canopy expansion

The Sirius model describes the canopy as a series of layers associated with individual, main-stem leaves, and simulates the effect of tillering only through the potential size of any layer (Lawless *et al.*, 2005). Individual leaf layers are described according to their lifetime, growth and senescence periods, and their potential maximum surface areas. Sirius uses one cultivar parameter, α_{\max} , the maximum potential surface area of the largest culm leaf layer, to describe potential growth of all culm leaf layers. By varying α_{\max} , the rate of canopy expansion and maximum achievable canopy size is changed. This, in turn, changes the pattern of light interception and transpiration and therefore affects grain yield. The reported range of genetic variations for flag leaf area under unlimited water and nitrogen supplies is up to 40% (Fischer *et al.*, 1998; Shearman *et al.*, 2005).

Water stress tolerance traits

In Sirius, water stress is predicted to affect the growth of the crop in two ways: by limiting production of new biomass and by accelerating leaf senescence. Both of these limitations depend on a stress factor SF , that is calculated daily as a ratio of actual over potential evapotranspiration. Daily production of new biomass decreases proportionally to the drought biomass reduction factor DBF defined as $DBF = SF^{\beta}$, where β is currently a cultivar-independent constant.

In the current version of Sirius, the ontogenic rate of leaf senescence is constant in thermal time. This rate could be accelerated by low nitrogen availability (inadequate to sustain either leaf expansion or grain-filling) or water stress. Maintaining green leaf area longer after anthesis results in increases in yield and crop nitrogen (N), if N uptake is also maintained (Austin, 1999; Triboi and Triboi-Blondel, 2002). In the presence of water stress, however, the rate of leaf senescence increases because the daily increment of thermal

time is modified by the drought leaf senescence factor, which is a function of *DSF*, a maximum possible acceleration of senescence. Reducing *DSF* should make leaves stay green longer under water deficit.

Effects of trait variations on grain yield

Sirius was run with the perturbed values of parameters described above. Changes in mean yield are presented in Table 2. The two parameters that had the largest impact on grain yield under limited water availability were the response of the plant with respect to leaf senescence (*DSF*) and biomass accumulation (β) (Fig. 4). Both of these parameters are linked with drought tolerance and are calculated using *SF*, the water stress factor. The model predicted that, under severe water limitation (*DSI*>0.6) at a site in Seville, Spain, grain yield of modified cv. Cartaya in which *DSF* is decreased by 20% could be up to 70% higher than that of the unmodified control, while a 20% reduction of *DBF*, the drought biomass reduction factor, could increase yield by up to 12% in dry years. There is some experimental data to support this: it has been shown for wheat and sorghum that cultivars with a stay-green trait that allow the plant to retain more green leaves when drought stress is applied post-anthesis have a higher grain yield and biomass than normal cultivars (Richards, 2006; Foulkes *et al.*, 2007).

Changes in the maximum potential surface area of culm leaves (α_{\max}) were predicted to have a relatively small, but consistent effect on grain yield (Table 2). A 20% increase in α_{\max} resulted in mean yield increases of nearly 4% at Rothamsted in the UK and 3.5% at Seville.

An increase of the root vertical extension rate (*RVER*) was predicted to have a very small positive effect on grain yield at both sites for wheat grown on shallow, sandy soil. Increasing the rate of relative crop water uptake (*k*) was beneficial at both sites, but changes in mean yield were small (0.6% at Rothamsted and 1.1% at Seville) and would be difficult to measure in practice. With the higher value of *k*, the plant would take up soil water more quickly and therefore require precipitation later in the growing season. This would seem to be a better strategy at both sites. The vertical distribution of *k* can be associated with root architecture (Dardanelli *et al.*, 2004), which has been shown to have significant implications for water uptake and crop productivity in water-scarce environments (Manschadi *et al.*, 2006). In experimental and simulation studies, Manschadi and co-workers have shown that differences in root architecture between drought-tolerant wheat (SeriM82) and barley (Mackay) and the standard wheat cv. Hartog arise from two contrasting adaptation strategies. The compact, uniform, and deep root architecture of SeriM82 reduces water use early in the season, but increases access to water during grain-filling. On the other hand, barley cv. Mackay develops a large and shallow root system with greater potential for water extraction early in the season, thereby optimizing the timing of soil water extraction. A simulation analysis using APSIM has shown that modifica-

Table 2. Relative changes (%) in mean yields simulated by Sirius for cv. Avalon at Rothamsted, UK and cv. Cartaya at Seville, Spain for 100 years of the baseline scenario in response to changes in model and cultivar parameters

The * symbol indicates that the differences in means are significant at the 0.05 level calculated using paired *t* test.

Symbol	Description	Perturbed values	Relative changes in mean yield, %	
			Rothamsted	Seville
<i>P</i>	Phyllochron	1.2× <i>P</i>	2.1	−0.1
		0.8× <i>P</i>	−14.3*	−1.9
<i>GFD</i>	Grain-filling duration	1.2× <i>GFD</i>	0.6	−3.6*
		0.8× <i>GFD</i>	−6.6*	0.2
<i>RVER</i>	Root vertical extension rate	2× <i>RVER</i>	0.0	0.2*
		0.5× <i>RVER</i>	−0.6*	−4.3*
λ	Efficiency of root to extract water	1.4	−2.6*	−5.6*
		0.7	0.6*	1.1*
α_{\max}	Maximum potential surface area of the largest culm leaf layer	1.2× α_{\max}	3.9*	3.4*
		0.8× α_{\max}	−5.8*	−5.1*
<i>DSF</i>	Maximum acceleration of leaf senescence in response to water deficit	1.2× <i>DSF</i>	−5.6*	−17.6*
		0.8× <i>DSF</i>	5.8*	19.7*
β	Parameters modifying the sensitivity of crops response to water deficit	1.5× β	−1.8*	−5.1*
		0.5× β	1.9*	5.7*

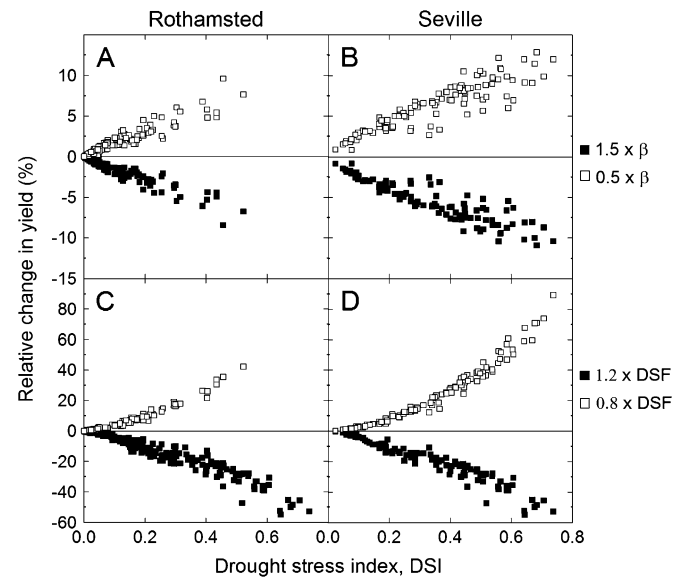


Fig. 4. Relative changes in grain yield versus drought stress index, *DSI*, calculated for 100 years in response to an increase (closed symbols) or a decrease (open symbols) of scaling exponent of the drought stress factor β (A, B), and of maximum acceleration of leaf senescence *DSF* (C, D) for cv. Avalon at Rothamsted, UK, and cv. Cartaya at Seville, Spain, simulated by Sirius for sandy soil with 90 mm AWC at each site (Semenov *et al.*, 2009).

tion of the rooting pattern could lead to a long-term average gain of 14.5% of yield in dry seasons for a wide range of environments in southern Queensland, Australia (Manschadi *et al.*, 2006).

Another simulation study performed in low-rainfall areas of Southern Australia predicted that yields could be enhanced by an increased depth of rooting (Dreccer *et al.*, 2002). Moreover, this analysis showed that limiting water uptake from deeper soil layers early in the season through greater root-length distribution in the surface soil layers would result in increased availability of water for post-anthesis growth, and therefore would improve grain yields. Richards and Passioura (1989) investigated experimentally the effect of root xylem vessel diameter on the ability of roots to extract subsoil water during drought in field trials in eastern Australia. They found that a wheat cultivar with approximately 20% narrower vessels yielded 8% more than the control cultivar in dry environments, whereas yield differences in wetter environments were not significant (Richards and Passioura, 1981; Richards and Passioura, 1989).

Surprisingly, changes in the parameters controlling crop development (P and GFD) were not predicted to improve grain yields consistently either at Rothamsted or Seville (Fig. 5). Indeed, changes in P produced an almost random scatter of yield responses for all levels of DSI . A possible explanation for this is that the cultivars used in the study, cvs Avalon and Cartaya, have an optimal rate of development for climates in the UK and Spain, respectively. According to the results presented here, 20% changes in P would not improve crop performance under water-limited conditions. In an experimental study of the effect of early flowering on drought resistance in two mapping populations, Beaver \times Soissons and Rialto \times Spark, phenotypic

correlations amongst the lines between flowering date and yield or yield loss under drought were all non-significant (Foulkes *et al.*, 2007).

Changes in GFD were predicted to produce positive or negative changes in yield, depending on the value of DSI , if the soil were shallow with 90 mm available water capacity (AWC). For wet years with low DSI , an increase in GFD would improve yield.

This analysis illustrates how crop simulation models can be used to explore the relationships between simple and complex traits. By modelling crop growth in variable environments, the stability of these relationships can be tested and a better understanding of the behaviour of a complex trait in response to changes in simple, underlying component traits can be achieved. Attempts to identify QTL for better yields under limited water supplies that are based solely on a limited number of experiments may lead to incorrect conclusions for those traits that demonstrate highly variable responses in different environments. For example, as shown in Fig. 5, for many 'trait-individual year' combinations, trait effects on yield associated with an individual year can change sign (negative to positive) and magnitude.

Linking model parameters with QTL and genes

Crop simulation models integrate the current understanding of crops derived from physiological studies, but very few, if any, incorporate knowledge derived from genetic studies (White and Hoogenboom, 2003). Crop models include cultivar parameters that have been derived by inference from phenotypic characteristics measured in different environments, using calibration procedures with subsequent validation. The criteria for success in using crop models as an integral aspect of crop genetics research and breeding is the ability to associate model cultivar parameters with measurable traits and resolvable QTL. If this link is established, then genetics research will benefit from crop modelling by focusing the search for genes and QTL for those component traits that are identified by modelling analysis as having the best potential (Tardieu, 2003; Quilot *et al.*, 2005; Tardieu *et al.*, 2005).

The next step in utilizing crop models for genetic research would be the development of a theoretical framework that allows reliable predictions of the phenotypic consequences when making alterations to the genetic make-up of a plant (Hammer *et al.*, 2005, 2006). Progress in the design of molecular breeding strategies for complex traits would be greatly accelerated as a result (Cooper *et al.*, 2005). One of the possible approaches is to link phenotypic consequence to changes in genetics via stable associations with crop model parameters. This approach was used to study sorghum breeding scenarios for a broad range of water-limited environments in Australia using APSIM (Hammer *et al.*, 2005). Fifteen QTL for four component traits of grain yield were defined and the phenotypic variation associated

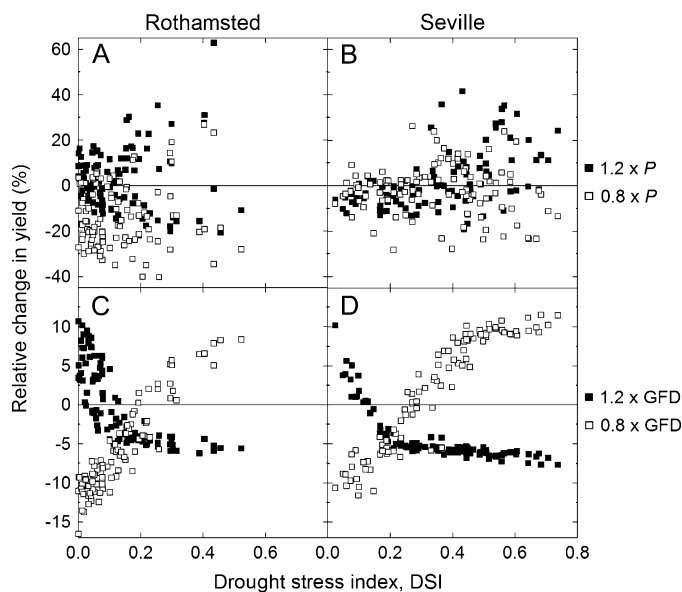


Fig. 5. Relative changes in grain yield versus drought stress index, DSI , calculated for 100 years in response to a 20% increase (closed symbols) or 20% decrease (open symbols) in phyllochron P (A, B) and grain-filling duration GFD (C, D) for cv. Avalon at Rothamsted, UK, and cv. Cartaya at Seville, Spain, simulated by Sirius for sandy soil with 90 mm AWC at each site (Semenov *et al.*, 2009).

with these QTL was modelled in terms of the influence of each QTL on control processes in the APSIM model. There were significant differences in rate of increase in average yield in the target population of environments (TPE) with cycles of selection among three marker-assisted selection scenarios. The first two scenarios require physiological understanding and integrative modelling; in the third scenario markers have been assigned to physiological traits and marker weights have been derived from the simulated value of that trait in the TPE. When physiologically weighted marker selection was used, the rate of yield improvement was enhanced and the average yield reached a higher level.

In a different approach, a gene-to-phenotype ($G \rightarrow P$) modelling framework for quantitative genetics was proposed that explicitly deals with the context-dependent gene effects that are attributed to genes functioning within networks, i.e. epistasis, $G \times E$ interactions and pleiotropy (Podlich and Cooper, 1999; Cooper and Podlich, 2002). Using ($G \rightarrow P$) models that are based on the $E(NK)$ gene-network model and the QU-GENE simulation platform for quantitative analysis of genetic models (Podlich and Cooper, 1998), it has been demonstrated that it is possible to design molecular breeding strategies for complex traits that, on average, will outperform phenotypic selection (Cooper *et al.*, 2005).

Elucidating drought and heat stress response mechanisms at the molecular level and their manipulation in plant biotechnology

Crop simulation models may also guide the use of genetic manipulation to produce crop varieties that can tolerate the effects of climate change. Drought tolerance is already a target for wheat in the UK, but as we have described above, crop simulation models indicate that heat tolerance may be of equal if not greater importance. As we have discussed above, both are complex traits in which the effects of single genes may be difficult to discern. Nevertheless, genes that play an important role in imparting these traits will have to be identified if biotechnology is going to play a useful part in producing crops for future climates.

The classic molecular biology approach to stress tolerance is to impose the stress and look for genes that are expressed in response. A group of candidate genes are then selected based on likely function. Proteins involved in signalling (such as protein kinases) or the control of gene expression (such as transcription factors) are often favoured on the basis that they have the potential for wide-ranging effects on plant physiology. In the case of drought and heat tolerance, proteins that act as protectants under stress conditions have also attracted much attention. The candidate genes are then tested by modifying their expression in transgenic plants, or by analysing mutants that lack their

activity. Typically, the stress that is applied is extreme and this attracts scepticism from some plant physiologists. Nevertheless, there have been notable successes in elucidating the systems that control responses to both drought and heat stress and some of the genes that are involved do increase tolerance when over-expressed in transgenic plants, at least under experimental conditions.

Water stress brings about a wide range of effects on plants that differ from species to species and between different varieties, developmental stages, organs, and tissue types (see Barnabás *et al.*, 2008, for a comprehensive review). The hormone abscisic acid (ABA) plays a key role, initiating a network of signalling pathways involving multiple protein kinases. These include ATH1, a transmembrane histidine kinase receptor (Wohlbach *et al.*, 2008), mitogen-activated protein kinases (MAPKs) (Colcombet and Hirt, 2008), calcium-dependent protein kinases (CDPKs) (Hrabak *et al.*, 2003) and sucrose non-fermenting-1-related protein kinases (SnRKs). SnRKs are divided into three subfamilies: SnRK1, 2, and 3 (Halford *et al.*, 2003; Halford and Hey, 2009). Of these, SnRK2 and SnRK3 have been known to be involved in stress responses for several years. For example, some *Arabidopsis* SnRK2s have been shown to be activated by hyperosmotic and saline stresses (Boudsocq *et al.*, 2004; Kobayashi *et al.*, 2004) and over-expression of one has been shown to improve drought tolerance (Umezawa *et al.*, 2004). The *Arabidopsis* SnRK3 family includes SOS2, which is involved in conferring salt tolerance (Liu *et al.*, 2000). Transcription factors of the ABA response element binding protein class (AREBPs) are substrates for members of all three SnRK families (Kobayashi *et al.*, 2005; Furihata *et al.*, 2006; Zhang *et al.*, 2008).

SnRK1 is better known as a central regulator of metabolism (Halford, 2006), and while the nature of its relationship with ABA requires further study it is a possible conduit for cross-talk between metabolic and stress signalling. Plants manipulate carbohydrate metabolism, for example, by interconverting insoluble starch with soluble sugars, to mitigate the effects of osmotic stress brought about by drought (Wingler *et al.*, 1999; Reddy, 2000; Hoekstra *et al.*, 2001; Villadsen *et al.*, 2005). Regulation of gene expression is not the only mechanism by which such changes can be brought about. For example, ADP-glucose pyrophosphorylase, a key enzyme in the starch biosynthetic pathway, is redox-activated in a process that requires SnRK1 (Tiessen *et al.*, 2003), while trehalose phosphate synthase is a substrate for SnRK1 (Harthill *et al.*, 2006). Trehalose 6-phosphate is a key signalling metabolite in plants while trehalose itself is present at relatively high levels in resurrection plants. Furthermore, transgenic rice plants containing high levels of trehalose have been shown to have increased drought tolerance (Garg *et al.*, 2002).

Another substrate for SnRK1 is fructose-6-phosphate, 2-kinase/fructose-2,6-bisphosphatase (F2KP) (Kulma *et al.*, 2004) and this enzyme has been implicated in bringing about drought-induced changes in carbohydrate metabolism in barley; these changes include the accumulation of hexoses at the expense of sucrose and starch (Villadsen

et al., 2005). Regulation of F2KP by SnRK1 also involves a 14-3-3 protein (Kulma *et al.*, 2004).

Calcium-dependent protein kinases (CDPKs) are also involved in transducing stress signals, including signals for water and heat stress. There are too many studies on this subject to describe here, but they have been reviewed extensively by others (Hrabak *et al.*, 2003; Ludwig *et al.*, 2004; Wan *et al.*, 2007). A theme that emerges from these reviews is the interrelationship of different stress responses, particularly those of cold, salt, water, and osmotic stress. Indeed, cold, salt, and water stress will all induce osmotic stress. It is also notable that over-expression of a CDPK has been shown to increase drought tolerance in rice, at least under experimental conditions (Saijo *et al.*, 2000).

CDPKs are closely linked with ABA signalling. For example, Arabidopsis CDPKs AtCPK10 and AtCPK30 have been shown to be required for the activation of an ABA-inducible promoter (Sheen, 1996). Many CDPK genes themselves contain an ABA response element in their promoter and some have been shown to be induced at the transcriptional level by ABA (Wan *et al.*, 2007).

Transcription factors that are known to be involved in water stress responses include dehydration-responsive element binding protein (DREB)-1 and -2 (Sakuma *et al.*, 2006; Seki *et al.*, 2001), ABA response element binding proteins (AREBPs) (Choi *et al.*, 2000), transcription factors of the zinc finger homeodomain (ZFHD)-1 type (Tran *et al.*, 2007), members of the myeloblastosis (MYB) and myelocytomatosis (MYC) families (Abe *et al.*, 1997), and of the no apical meristem (NAM), ATAF1 and 2, and cup-shaped cotyledon (CUC) family (NAC) (Olsen *et al.*, 2005). A comprehensive review of their roles was provided by Shinozaki and Yamaguchi-Shinozaki (2007). The action of AREBPs, DREB1, MYC, and MYB requires ABA, while that of DREB2, ZFHD1, and NAC is ABA-independent. Over-expression of another transcription factor, plant nuclear factor-Y (NF-Y) has been shown to confer increased drought tolerance in maize in the field (Nelson *et al.*, 2007).

Many of the factors that are expressed during water stress are also expressed when heat stress is applied. In some cases this may be misleading because elevated temperatures will cause water stress unless ambient humidity is adjusted to prevent it. The effects of different abiotic stresses, including drought and heat, do overlap, as we have discussed above, but each different stress also presents the plant with some specific problems and heat stress is no exception. As we have described above, high temperatures cause wheat and other cereals to develop and mature more quickly; they also bring about an increase in respiration and an inhibition of photosynthesis. The latter is caused by a reduction in the activity of ribulose 1,5-bisphosphate carboxylase/oxygenase (Rubisco) and the efficiency of photosystem II (Al-Khatib and Paulsen, 1999). The reduction in Rubisco activity occurs because the enzyme responsible for maintaining its activity, Rubisco activase, is labile at even moderately high temperatures. Genetic manipulation of Rubisco activase to improve its stability at high temperatures is a potentially important target (Kurek *et al.*, 2007).

Another effect of high temperature is oxidative damage and high activities of superoxide dismutase and catalase have been shown to be associated with good thermotolerance in wheat (Sairam *et al.*, 2000). Temperatures greater than 35 °C during wheat grain development have also been shown to cause changes in the expression of different groups of seed storage proteins, with consequent effects on dough quality (Blumenthal *et al.*, 1993; Irmak *et al.*, 2008). Heat stress is also likely to increase the levels of free asparagine (Lea *et al.*, 2007), one of the precursors of acrylamide, a toxic contaminant that is formed during high-temperature processing of wheat and other crops. On the other hand, moderate increases in summer temperature in the UK may actually have a beneficial effect in reducing the levels of free asparagine (Curtis *et al.*, 2009).

Transcription factors that are specifically associated with heat stress include heat shock factors (HSFs). The HSFs are quite a large family with at least 21 members, and their interaction appears to be complex (Baniwal *et al.*, 2004; Kotak *et al.*, 2007). Nevertheless, simple over-expression experiments with HSFs have resulted in increased thermotolerance in transgenic plants (Ogawa *et al.*, 2007; Yokotani *et al.*, 2008). Heat stress can cause proteins, RNA and other molecules to fold incorrectly, affecting their assembly, translocation, turnover, and activity. Heat-shock proteins (HSPs) and other chaperones that keep proteins and RNA in their correct conformation are expressed to mitigate this problem and these have therefore also attracted much attention (Wang *et al.*, 2004). The expression of HSPs is under the control of HSFs (Schoffl *et al.*, 1998).

The key question for plant biotechnology is: will the manipulation of any of these genes provide a consistent improvement in drought and/or heat tolerance under field as opposed to laboratory conditions? At present there are no transgenic crop varieties being marketed on the basis of improved drought or heat tolerance that we are aware of, but all of the major plant biotechnology companies claim to have such varieties in development. Monsanto appears to be leading the way with plans to market drought-tolerant corn possibly as early as 2012. The exact nature of the traits involved is not yet in the public domain and there may be more than one; Monsanto has experimented with over-expression of transcription factors (Nelson *et al.*, 2007) and RNA chaperones (Castiglioni *et al.*, 2008). The yield increases that are claimed are relatively modest, from 6.7% to 13.4% under drought conditions (http://www.monsanto.com/pdf/droughttolerantcorn/drought_slides.pdf), so these varieties are not going to green the desert. Nevertheless, Monsanto claims that the yield increases are significant and, of course, these varieties would hopefully represent the start of a process of long-term improvement.

Conclusions

A step-by-step procedure is described here for a rational design of wheat ideotypes for future environments under a changing climate using mathematical modelling and in-

depth knowledge of molecular regulatory mechanisms and wheat genetics. This approach can be used to underpin the breeding process for new wheat cultivars that are suitable for the rapidly changing environments brought about by global warming. The aim is to enable breeders to focus their efforts on those traits that promise an enhanced performance of the wheat crop under climate change.

By running crop simulation models for future scenarios brought about by climate change, the abiotic stresses that will have major impacts on wheat in the future can be identified. Those wheat physiological traits that need improvement to adapt to changing environments can then be shortlisted. The outcome depends on predicted changes in weather patterns, which have a high degree of uncertainty. However, important conclusions can be drawn. For example, wheat is particularly sensitive to heat stress during flowering, with potentially severe consequences for grain yield. Severe heat stress is therefore likely to have an increasing impact on wheat yield as the climate warms. On the other hand, global warming will accelerate wheat development, reducing the impact of summer drought, at least in the UK.

Some caution is required when using process-based crop simulation models to analyse complex traits, since the ability of the model to predict complicated trait \times environment interactions depends on the assumptions made in the model. Nevertheless, such an approach allows us to investigate these complex interactions in a way that is not possible in field experiments. Crop simulation modelling can be used to deconvolute the complex traits that are selected for improvement, breaking down the responses of complex traits to variation in simpler component traits. By modelling crop growth in variable environments, a better understanding of the relationships between the complex and component traits can be achieved and the simple traits can be ranked in order of their influence on the complex traits. The simple traits may then be amenable to mapping to genetic loci and used to prioritize research on QTL or single marker genes and in the assessment of the available genetic variability in wheat populations.

If traits can be assigned to single genes or small numbers of genes they may also be amenable to genetic modification. However, much of the work at the molecular level on elucidating the systems that enable plants to respond to drought and heat stress has been done in *Arabidopsis* and transferring the technology to wheat with its relatively complex genetics will be difficult. Furthermore, while the market for biotech corn, soybean, and cotton is well established in the Americas and Asia, the market for biotech wheat is not and wheat is attracting much less investment from plant biotech companies as a result. Wheat is the major crop in Europe, of course, but with the development of plant biotechnology stalled in Europe under the weight of legislation and lack of public confidence, there is no prospect of investment in biotech varieties for the European market.

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