



## Quantifying effects of simple wheat traits on yield in water-limited environments using a modelling approach

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### ABSTRACT

Availability of water for plant growth is a key factor determining plant distribution in natural ecosystems and is the most important limiting factor in agricultural systems. The high environmental and economical cost of irrigation, required to maintain grain yields in water scarce environments, gives an incentive for improvements in water use efficiency of the crop. The objective of our study is to quantify the effects of changes in simple component plant traits on wheat yield under limited water supplies using a modelling approach. The Sirius wheat simulation model was used to perform analyses at two contrasting European sites, Rothamsted, UK and Seville, Spain, which represent major wheat growing areas in these countries. Several physiological traits were analysed to explore their effects on yield, including drought avoidance traits such as those controlling wheat development (phyllochron and grain filling duration), canopy expansion (maximum surface area of culm leaves) and water uptake (root vertical expansion rate and efficiency of water extraction) and drought tolerance traits such as responses of biomass accumulation and leaf senescence to water stress. Changes in parameters that control the effect of water stress on leaf senescence and biomass accumulation had the largest impact on grain yield under drought. The modified cultivar produced up to 70% more yield compared with the control for very dry years. Changes in phenology parameters, phyllochron and grain filling duration, did not improve yields at either site, suggesting that these parameters have been already optimised for climates in the UK and Spain through the breeding process. Our analysis illustrates the power of modelling in exploring and understanding complex traits in wheat. This may facilitate genetic research by focusing on experimental studies of component traits with the highest potential to influence crop performance.

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### 1. Introduction

Availability of water for plant growth is a key factor determining plant distribution in natural ecosystems and is the most important limiting factor in agricultural systems (Bacon, 2004). Biomass production is intrinsically linked to transpiration, because stomatal aperture and leaf area determine the rate of both photosynthesis and transpiration. 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 risk of severe drought by (a) developing early and shortening the growing season, (b) conserving available water through reducing leaf size and regulating stomatal closure, and (c) extracting water more efficiently with an

improved root system. Plants may also develop improved tolerance to water deficit by maintaining productivity under water stress.

Considerable amount of work have been done to analyse possible ways to improve crop yield under limited water supply (Collins et al., 2008), in particular for wheat (Condon et al., 2004; Richards et al., 2002). The term “water use efficiency” (WUE) has many definitions depending on the scale of biological processes and temporal scale studied. On a leaf scale 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 the final crop yield over the total seasonal evapotranspiration. By integrating instantaneous carbon dioxide assimilation and transpiration over the season, it is theoretically possible to explicitly derive crop WUE from leaf WUE. However, large diurnal variations in the saturated vapour pressure at leaf temperature and in the vapour pressure in the atmosphere make this approach impractical (Sinclair et al., 1984). Moreover, the proportion of CO<sub>2</sub> assimilated by photosynthesis lost as

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respiration needs to be considered. In practice, leaf and crop WUE can be only very loosely connected and it was demonstrated that improvements of leaf WUE often do not translate into higher crop WUE or yield (Condon et al., 2004).

It was shown in experimental studies that crop WUE is sensitive to environmental and weather conditions, especially to the variation in humidity, since it directly affect the stomatal conductance (Day et al., 1978; Lawlor et al., 1981). Improving WUE in itself would have limited interest, if the crop produces a very low grain yield. In our study we explore theoretically the potential to improve wheat yield in water-limited environments by varying simple physiological traits.

Wheat growth and development is a complex process with many components interacting with the environment in a non-linear fashion (Brooks et al., 2001; Mearns et al., 1997; Porter and Semenov, 2005). The effect of changes in a single trait (e.g., leaf size) on grain yield can theoretically be determined in a field experiment. However, because crop responses will also depend on weather and water supplies, experimental analysis of how changes in several plant characteristics, either individually or in combination, will affect grain yield under varying growing conditions, becomes an intractable practical task. But this could be achieved by using a virtual crop represented by a crop simulation model. By perturbing model parameters, that are associated with simple physiological traits, crop simulation allow investigating *in silico* yield responses in multiple environments and various weathers and identify those traits that lead to a consistent and stable yield increase under water-limited conditions for a targeted population of environments. Model results, however, should be interpreted with care, since the ability of a model to predict these complex interactions depends on the simplifications and assumptions made in the model (Boote et al., 2001).

Crop simulation models are used increasingly in basic and applied research in plant sciences (Debaeke and Aboudrare, 2004; Passioura, 1996; Sinclair and Muchow, 2001; Sinclair and Seligman, 1996). Models provide the best-known approach for integrating our understanding of complex plant processes as influenced by weather and environment. They are useful in guiding the direction of fundamental research by providing quantitative predictions and highlighting gaps in our knowledge (Semenov et al., 2007; Tardieu, 2003). Several simulation analysis on the effects of variations in plant traits on crop WUE and grain yields under limited water supplies were carried out previously, including studies on maize in the USA (Sinclair and Muchow, 2001), and on sorghum (Chapman et al., 2002; Hammer et al., 2005), wheat (Condon et al., 2002) and barley (Manschadi et al., 2006) in Australia. However, such simulation analysis has not been performed for European conditions. The objective of this paper is to use a wheat simulation model, Sirius, to analyse the effect of variations in simple physiological wheat traits on crop performance under water-limited conditions at two contrasting sites. These sites are representative of major wheat growing regions in Europe. Drought avoidance and drought-tolerant traits in wheat were examined for two wheat cultivars grown in these regions. Although crop simulation models have been previously used to explore ways of improving crop performance under drought, comparing results from a range of crop models in diverse environments may lead to a better understanding of WUE and highlight gaps in our knowledge. This is because each crop model has a distinct sensitivity to variations in environmental conditions and cultivar parameters resulting from differences in the description of biological processes and model structure. Comparisons of crop simulation models in the past facilitated new advances in crop modelling (Ewert et al., 2002; Jamieson et al., 2000; Semenov et al., 1996).

Sirius is a crop simulation model that was used in this study (Jamieson and Semenov, 2000; Jamieson et al., 1998c). It requires daily weather data, a soil physical description and management information (N fertilisation and irrigation amounts) to calculate biomass accumulation from intercepted photosynthetically active radiation (PAR) day by day. Grain growth is calculated from the biomass using simple partitioning rules. Leaf area index (LAI) is calculated using a simple canopy model (Lawless et al., 2005). Phenological development is linked to the mainstem leaf appearance rate (determined by temperature) and the final leaf number, determined by responses to daylength and vernalisation (Jamieson et al., 1998a). Soil is used as a reservoir for water and N, and as these are used up the effects of deficits are calculated through their influences on LAI expansion and senescence, and light use efficiency (Jamieson and Semenov, 2000). The model was calibrated for several modern wheat cultivars and was able to simulate accurately the behaviour of crops exposed to a wide range of conditions, including Europe, NZ, USA and Australia and under conditions of climate change (Brooks et al., 2001; Ewert et al., 2002; Jamieson et al., 2000; Jamieson and Ewert, 1999; Jamieson and Semenov, 2000; Martre et al., 2006; Semenov et al., 1996).

## 2. Methods

### 2.1. Simulation setup

We used Sirius version 2005, which is available from [www.rothamsted.bbsrc.ac.uk/mas-models/sirius.php](http://www.rothamsted.bbsrc.ac.uk/mas-models/sirius.php). We selected two contrasting sites in Europe for our analysis, Rothamsted, UK (51°47'N, 0°21'W, 128 m elevation), and Seville, Spain (37°25'N, 5°52'W, 12 m elevation), which represent major wheat growing regions in these countries and encompass a large part of the climate in the European wheat growing zones. Long term averages of cumulative thermal time and total rain rainfall over the wheat growing seasons are 2550 °C days (ranging from 2135 to 2941 °C days) and 580 mm (ranging from 415 to 778 mm) at Rothamsted and 2330 °C days (ranging from 2090 to 2579 °C days) and 272 mm (ranging from 122 to 451 mm) at Seville (Fig. 1).

We used cultivar parameters calibrated previously for two local wheat cultivars (Table 1). These are *cv. Avalon*, an obligate winter wheat with moderate to weak daylength response, at Rothamsted and *cv. Cartaya*, a spring wheat with weak daylength response, at Seville (Lawless et al., 2005; Wolf et al., 1996). We used 100 years of synthetic daily weather for each site, generated by the LARS-WG stochastic weather generator which was calibrated for both sites using observed daily weather (17 years at Seville and 31 years at Rothamsted) (Semenov, 2007; Semenov and Brooks, 1999). The previous validation of LARS-WG at Rothamsted and Seville demonstrated that weather statistics important for crop simulation models were reproduced well at these sites including weather extreme events (Semenov, 2008; Semenov et al., 1998) and approximately 20 years of daily weather are required to produce a robust set of parameters for LARS-WG. To ensure water-limited conditions for most simulation experiments, we used a shallow sandy soil with a 0.75 m rooting depth and 90 mm plant available water content (AWC) at both sites. The 50th and 95th percentiles of the expected losses in simulated grain yield due to water stress were 10% and 40% at Rothamsted, and 35% and 65% at Seville compared with the potential yield for 100 years of synthetic weather. A deeper soil with a 1.5 m rooting depth and 144 mm AWC was also used in some simulations. The sowing date at Rothamsted was set at 10 October and at Seville at 1 January, which are typical sowing dates at both sites. All simulations were run without nitrogen limitations (i.e., plant nitrogen demand was always satisfied), and assuming no water deficit at sowing.

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