Field Crops Research xxx (2016) xxx–xxx

Contents lists available at ScienceDirect

Field Crops Research

journal homepage: www.elsevier.com/locate/fcr

Simulating the impact of source-sink manipulations in wheat

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ARTICLE INFO

Article history:
Received 2 November 2015
Received in revised form 20 April 2016
Accepted 23 April 2016
Available online xxx

Keywords:
Nwheat
Grain yield
Model performance
Sink-source
Triticum aestivum L.

ABSTRACT

Grain yields in wheat can be limited by the assimilate supply (source) or by the carbohydrate demand of the grains (sink). Recently, there have been questions regarding the capability of crop models to simulate the physiology of source-sink interactions in crops; however, crop models have never been tested with source-sink manipulated data. We tested the Nwheat model with detailed measured field experimental data with treatments of manipulated source (i.e., assimilate supply), sink (i.e., kernel number), and their combinations. In general, the model could reproduce observed effects of shading before and after anthesis as well as the additional impact of halving the spikes. A 90% shading during grain filling reduced individual grain weights drastically, with the remaining yield mostly determined by carbohydrate remobilisation, which the model reproduced. The model also reproduced the decline of biomass accumulation due to shading, but was not sensitive enough to simulate the observed reduction of kernels per m^2 from a 90% reduction in solar radiation between booting and the beginning of grain filling, resulting in an overestimated grain yield. The model reproduced the positive impact of a 7% genetically increased radiation use efficiency (RUE) on growth and yield. A sensitivity analysis indicated that the yield response to increased RUE can vary among environments. The yield impact can be positive in many environments, but negative in terminal drought environments. In these environments, stimulated early growth from higher RUE can cause accelerated water deficit during grain filling and reduced yields.

The model adequately simulated source-sink interactions of most of the treatments, but there were obvious shortcomings in simulating kernel set and final grain size. Improving these will be critical for estimating crop-environmental interactions that affect assimilate supply, including breeding, industrialisation-induced or geo-engineered solar dimming, genetically and atmospheric CO_2-related increased RUE, and source manipulations, such as pest and disease impacts.

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1. Introduction

Increasing wheat productivity is needed to feed the growing world population, which is projected to reach over 9 billion by 2050 (Godfray, 2014). This aim is especially challenging because maintaining wheat production in some regions will be difficult because of rising temperatures (Asseng et al., 2015; Gourdji et al., 2013; Lobell et al., 2012) and decreasing solar radiation (Yang et al., 2013). Historical yield trends indicate that there was a substantial increase in wheat yields over the last decades, following the introduction of semi-dwarfing alleles into cultivars so that high inputs (e.g., N-fertilizer) could be used and lodging avoided – also called the Green Revolution in the 1970s, but initial signs show recent yield stagnation (Lin and Huybers, 2012; Ray et al., 2012). These new high-yielding cultivars had an increased number of grains per unit area, resulting in an increased harvest index and higher yields with higher fertilizer applications. Crop biomass, solar radiation interception, and radiation use efficiency (RUE) hardly changed as a consequence of wheat breeding (Calderini et al., 1997; Sun et al., 2009). Additionally, the current harvest index is close to its hypothetical limit of approximately 60% (Austin, 1980) in modern wheat cultivars (Foulkes et al., 2011). As a consequence, the next quantum leap in grain yield of wheat would be driven by higher biomass production combined with optimizing the source-sink ratio (Miralles and Slafer, 2007; Slafer and Savin, 1994; Sun et al., 2009; Bustos et al., 2013). In this context, source refers to photosynthesis capacity

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http://dx.doi.org/10.1016/j.fcr.2016.04.031
0378-4290/Published by Elsevier B.V.

Please cite this article in press as: Asseng, S., et al., Simulating the impact of source-sink manipulations in wheat. Field Crops Res. (2016), http://dx.doi.org/10.1016/j.fcr.2016.04.031

of green leaves, including formation, translocation/remobilization, and partitioning of photosynthetic products. Sinks refers to the growing capacity of organs (e.g., kernel number and grain size) to accumulate assimilates.

The rate and amount of dry matter accumulation and the growth of harvestable organs of a crop is determined by assimilate supply of green leaves (source strength) and the capacity of organs to store assimilates (sink strength). The photosynthetic capacity and storage strength of the various organs of a crop varies within the growth cycle. For cereals such as wheat, the growth cycle of organs is divided into three main phases (Kirby, 1988): (i) development of leaves, tillers and formation of terminal spikelet (ii) stem and ear elongation, differentiation and maturation of florets and (iii) fertilization and grain growth. Alterations in source-sink balance during these phases can affect growth, and yield and yield components.

The timing of source-sink limitations will have specific impacts and vary depending on the growth stage. For instance, a reduced source (e.g. shading) between booting and anthesis will not influence the number of spikelets initiated on a spike (determined by about jointing). The floret primordia have been initiated when the flag leaf has completed growth and subsequent development of floret structures has mostly occurred (Ferrante et al., 2013; Miralles et al., 1998). Leaf appearance and growth has been mostly completed at this stage and shoots that will abort have begun to do so by booting. Hence, a source limitation before anthesis will reduce the number of grains per unit area. Additionally, there is an established dynamic interaction between source and sink, in which the photo-assimilate demand from growing grains influences supply and vice versa. Therefore, optimizing source-sink interactions is critical to improve grain yield if more photosynthesis assimilates are transported to and fully used by the sink. Recently, Bustos et al. (2013) demonstrated that a more optimal source-sink balance can lead to step changes in yield potential of a doubled haploid (DH) population by crossing two elite cultivars in which the best DH lines out-yield both parents. Although the source-sink balance is important, little information is available about the sensitivity of the source-sink ratio under different scenarios of biomass growth, which is necessary to improve future grain yields.

Crop simulation models are widely applied in quantitative analysis of crop growth and cropping systems (Matthews et al., 2013; White et al., 2011). Most common wheat models such as Nwheat (Keating et al., 2001) and CERES (Ritchie et al., 1998) consider kernel number as the main determinant for yield formation. These models use empirical approaches and coefficients to determine the kernel number based on growth around anthesis. The models also consider intercepted radiation during the grain filling period and remobilisation as the main contributors to grain growth. Thus, grain yields in a crop model are simulated as a function of kernel numbers per unit area (sink) and the availability of assimilates (source); such models are source-sink co-limited.

Environmental changes affecting source-sink relations, including increasing temperature and elevated atmospheric CO_2 concentrations have different effects on main physiological processes, such as demand of grains for assimilates (sink strength) and the availability of assimilates from photosynthesis and translocation (source supply) (Uddling et al., 2008). In addition, industrialisation-induced and geo-engineered solar dimming (change in solar radiation) as well as crop pest and disease effects can alter source-sink balances under future environmental change. For instance, climate change may severely affect the dynamics of pests and diseases and alter their geographical distribution, possibly leading to increased crop losses from reduced light interception (Gregory et al., 2009); most crop models do not take these scenarios into account yet.

Evaluating the capability of crop models to simulate the physiology of source-sink interactions is therefore an important step to apply crop simulation models to future challenges. These challenges include breeding (i.e. specific direct and indirect changes in source and/or sink) and environmental changes such as dimming of global solar radiation (i.e., decreased source), temperature (i.e. increased or decreased source), elevated atmospheric CO_2 (i.e., increased source), and biotic stresses (i.e., reduced source and/or reduced sinks), all affecting source-sink interactions and finally crop productivity.

The aim of this study was to test the Nwheat model with detailed measured field experimental data of manipulated source (i.e., assimilate supply) and sinks (i.e., kernel number). These experiments included manipulations of source-sink interactions by reducing incoming solar radiation, using different levels of shading (reduced source), increased assimilate supply by growing cultivars with genetically increased radiation use efficiency (increased source) and reduced kernels per unit area (reduced sink).

2. Materials and methods

2.1. Wheat crop module

Nwheat, a crop simulation model for wheat (version 1.55) was originally developed within the Agricultural Production Systems SIMulator (APSIM), but is now used as a stand-alone model. It consists of modules that incorporate aspects of soil, water, nitrogen, crop residues, crop growth and development, and their interactions within a crop/soil system driven by daily weather data (Keating et al., 2003). Nwheat has been tested extensively against a range of field measurements from many different environments (Asseng et al., 2001; Asseng et al., 2004; Asseng et al., 1998; Asseng et al., 2000; Asseng and van Herwaarden, 2003). However, like many other crop models, Nwheat has never been tested with source-sink manipulated data sets.

The model simulates wheat phenology, leaf area development, light interception, biomass production and distribution within the plant organs, yield development, including translocation of pre-anthesis assimilates to grain and root system development, and soil-water and nitrogen dynamics (Keating et al., 2001). Nwheat uses seven main cultivar coefficients to simulate wheat growth dynamics during a growing season. These include vernalization requirement, photoperiod sensitivity, thermal time requirement, kernel number per biomass, kernel growth rate, maximum stem dry weight, and phyllochron interval (Table 2). Vernalization and photoperiod affect phenology between emergence and floral initiation. Grain yield potential is affected by a cultivar specific parameter of kernel number per stem weight (Grno) and maximum daily kernel growth rate (Fillrate). Tillering depends on the potential final dry weight of a single stem (cultivar specific parameter (stmwt)) and total above-ground biomass. Leaf appearance is associated with thermal time and the phyllochron (phyll – a cultivar specific parameter). Potential leaf area growth is calculated in the model as: $\mathrm{Plag} = 1400 \times \mathrm{cumph(istage)}^{0.6} \times \mathrm{ti} \times \mathrm{optfr} \times (0.3 + 0.7 \times \mathrm{TPSM})$, where cumph(istage) is the cumulative phyllochron within a growth stage, optfr is stress factor (minimum of water, nitrogen or temperature stress), TPSM is tiller number per area and *ti* is daily phyllochron fraction, which is a function of daily thermal time and phyllochron interval (DTT/PHINT). The potential rate of tiller formation depends on the thermal time after emergence. The number of tillers per square meter (TPSM) is calculated as TPSM = Plant population * tillering per plant.

Nwheat calculates potential daily biomass production based on radiation-use efficiency and light interception (as a function of incoming direct radiation and a diffused light component, which increases with lower radiation). The equation used in Nwheat model for simulating biomass production for a given day is:

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