Adapting APSIM to model the physiology and genetics of complex adaptive traits in field crops

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Abstract

Progress in molecular plant breeding is limited by the ability to predict plant phenotype based on its genotype, especially for complex adaptive traits. Suitably constructed crop growth and development models have the potential to bridge this predictability gap. A generic cereal crop growth and development model is outlined here. It is designed to exhibit reliable predictive skill at the crop level while also introducing sufficient physiological rigour for complex phenotypic responses to become emergent properties of the model dynamics. The approach quantifies capture and use of radiation, water, and nitrogen within a framework that predicts the realized growth of major organs based on their potential and whether the supply of carbohydrate and nitrogen can satisfy that potential. The model builds on existing approaches within the APSIM software platform. Experiments on diverse genotypes of sorghum that underpin the development and testing of the adapted crop model are detailed. Genotypes differing in height were found to differ in biomass partitioning among organs and a tall hybrid had significantly increased radiation use efficiency: a novel finding in sorghum. Introducing these genetic effects associated with plant height into the model generated emergent simulated phenotypic differences in green leaf area retention during grain filling via effects associated with nitrogen dynamics. The relevance to plant breeding of this capability in complex trait dissection and simulation is discussed.

Key words: APSIM, crop model, emergent property, gene-to-phenotype, sorghum, height, nitrogen, plant breeding, RUE, senescence.

Introduction

Progress in crop improvement and particularly in molecular approaches to plant breeding are limited by our ability to predict plant phenotype (P) based on its genotype (G), especially for complex traits like water productivity (Cooper et al., 2002, 2005). While there has been a long history of development and application of crop growth and development models for prediction in crop management (e.g. Sinclair and Seligman, 1996), the use of such modelling approaches for G-to-P prediction is in its infancy (Hammer et al., 2002; Hammer and Jordan, 2007). Recent studies suggest that while using crop models to tackle the G-to-P prediction problem for application in plant breeding has considerable potential, the adequacy of existing crop models for this task remains questionable (Chapman et al., 2002; Tardieu, 2003; Yin et al., 2004; Hammer et al., 2006; Messina et al., 2009).

Enhancing the crop modelling capability for G-to-P prediction requires algorithms that represent underlying processes and generate the phenotype of the plant as an emergent consequence of model dynamics. That is, crop models should explain complex phenotypic responses rather than relying on algorithms that simply describe them (Tardieu, 2003; Hammer et al., 2005; Chenu et al., 2008; Yin and Struik, 2008). This requires an iterative process of...
targeted experimentation and analyses based on process biology operating in concert with model development (Cooper and Hammer, 1996; Cooper et al., 2002; Messina et al., 2009). Recent studies on nitrogen (N) dynamics in field crops (Jeuffroy et al., 2002; Martre et al., 2006; Bertheloot et al., 2008; van Oosterom et al., 2010a, b) exemplify this link between experimentation and modelling in several species by quantifying N accumulation, allocation, and transfer patterns among plant organs based on their growth, composition, and activity. This contrasts with the descriptive functions of level of tissue N concentration through the crop life cycle used to model crop N dynamics in agronomic models (Jones and Kiniry, 1986). While crop models of this type have been applied successfully in support of agronomic practice (Robertson et al., 2000; Nelson et al., 2002), the response coefficients have no clear biological interpretation, such that their linkage to genetic variability is tenuous.

For robust G-to-P prediction the structure and coefficients underpinning the explanatory capability of the crop model must link effectively to the genomic regions associated with variability in the complex trait (Hammer et al., 2006; Chenu et al., 2009; Messina et al., 2009). Studies targeting specific component processes, such as aspects of phenology (Leon et al., 2001; Yin et al., 2005; Messina et al., 2006; Uptmoor et al., 2008) or leaf growth (Reymond et al., 2003; Tardieu et al., 2005; Sadok et al., 2007), have been more successful in this regard than those focused at the entire crop scale (Hoogenboom et al., 1997; Yin et al., 2003). The former have shown a credible capacity to predict phenotypic variation in the specific traits of interest for various genotypes and environments. The latter, however, have been unable to match this level of predictive capability across genotypes and environments for integrated targets like yield at crop scale. While G-to-P prediction at this integrated level is intrinsically more difficult, this outcome may also reflect the capacity of the model to capture and integrate the physiological basis of genetic variation (Hammer et al., 2002; Hammer and Jordan, 2007).

Ideally, the added generality and biological rigour required of crop models to improve their G-to-P prediction should not come at such a cost to model complexity that parameterization becomes problematic (Hammer et al., 2006) and restricts model utility. An objective of the effective and parsimonious modelling of physiological traits is central to this requirement (Tardieu, 2003; Messina et al., 2009) and underpins credible predictive extrapolation of effects onto target combinations of genotypes and environments. In their early discussions about crop modelling, de Wit and Penning de Vries (1983) aptly expressed the conceptual basis of this approach as ‘modelling hormone action without modelling the hormones’.

In this study, these principles are applied for parsimonious, biologically credible modelling to enhance the capability for modelling the physiology and genetics of complex adaptive traits in crops as a means to advance G-to-P prediction capacity. A specific case study for sorghum is used to exemplify the approach. First (i) the concepts and structure of the generic APSIM cereal template, and (ii) the associated experimentation to parameterize and test the template for diverse genotypes of sorghum grown in a wide range of environments, are presented. The concept of simulating complex phenotypic traits as emergent consequences of model dynamics is then demonstrated via an example showing how genetic differences in pre-anthesis growth associated with height can ultimately impact on post-anthesis leaf senescence via interactions with nitrogen dynamics.

### Model structure

**APSIM platform and generic cereal template**

The Agricultural Production Systems sIMulator (APSIM) is a cropping systems simulation model, designed to combine accurate predictions of economic product (e.g. grain, biomass, or sugar yield) for many crop species in response to climate and management conditions, with predictions of the long-term consequence of cropping systems on soil physical and chemical conditions (Keating et al., 2003). APSIM incorporates a generic crop model (Wang et al., 2002), which utilizes a library of routines for simulating crop growth and development processes.

A generic cereal template, programmed in object-oriented C++, has been developed based on the generic crop model. It is based on a framework of the physiological determinants of crop growth and development (Charles-Edwards, 1982) and is focused at the organ scale. It generates the phenotype of a crop as a consequence of underlying physiological processes (Fig. 1), using the concept of supply and demand balances for light, carbon, water, and nitrogen (Hammer et al., 2001). Demand for resources is defined by potential organ growth and potential supply by resource capture (Monteith, 1977, 1986; Passiourea, 1983) (Fig. 1). The sorghum module of APSIM, which was initially based on the fusion of earlier models and concepts (Sinclair, 1986; Rosenthal et al., 1989; Birch et al., 1990; Sinclair and Amir, 1992; Chapman et al., 1993; Hammer et al., 1994), has been adapted and redesigned into this template to enhance its capacity to deal with complex adaptive traits and G-to-P prediction.

There is considerable flexibility in the re-designed template. This includes scope to operate at the individual organ scale (e.g. individual leaf, grain, etc) by breaking organ pools down into cohorts. Allocation among organs within the plant is handled via an arbitrator, which contains rules and priorities that depend on plant status. This provides a platform to study individual processes while not unintentionally affecting the operation of others. This enables an examination of effects of variation in parameters of trait processes, which might reflect genetic differences, on overall performance of the crop under differing management or environmental scenarios. Further, the objects and sub-processes can be interchanged to test the effectiveness of alternate approaches to modelling specific processes, as done, for example, with alternative models of leaf area (Carberry et al., 1993; Chenu et al., 2008). Differences
between species and genotypes in the template are introduced through differences in input parameter values, rather than through differences in the underpinning crop physiological science for each species. The approach ensures scientific transparency, efficient use of code (Wang et al., 2002), and a more explanatory approach to the modelling of the underlying physiology (Hammer et al., 2006). The source code and details of the implementation for sorghum are provided as Supplementary information available at JXB online.

Process detail of implementation for sorghum

(i) Phenology, canopy development, and growth: Phenology is simulated through a number of development stages, using a thermal time approach (Muchow and Carberry, 1990; Hammer and Muchow, 1994), with the temperature response characterized by a base ($T_b$), optimum ($T_{opt}$), and maximum ($T_m$) temperature. Hammer et al. (1993) and Carberry et al. (1993) reported values of $T_b$, $T_{opt}$, and $T_m$ for sorghum of 11, 32, and 42 °C, respectively. The thermal time target for the phase between emergence and panicle initiation is also a function of day length (Hammer et al., 1989; Ravi Kumar et al., 2009) and its duration, when divided by the plastochron ($\text{Cd}$ per leaf), determines total leaf number (Fig. 1A). Total leaf number multiplied by the phyllochron ($\text{Cd}$ per leaf) determines the thermal time to reach flag leaf stage (Fig. 1A), which is thus an emergent property of the model. The duration of the phases between the stages of flag leaf, anthesis, and start and end of grain

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**Fig. 1.** Schematic representations of (A) crop growth and development dynamics, and (B) crop nitrogen dynamics, in the generic cereal template. Connections between the two schematics are shown by the shaded boxes.
filling are also simulated through thermal time targets (Muchow and Carberry, 1990; Hammer and Muchow, 1994; Ravi Kumar et al., 2009). Drought stress and N stress can both reduce the leaf appearance rate and hence delay phenology during the vegetative stages (Craufurd et al., 1993; van Oosterom et al., 2010a).

Canopy development is simulated on a whole plant basis through a relationship between total plant leaf area (TPLA) and thermal time. TPLA integrates the number of fully expanded leaves, their individual size, and tiller number, and includes an adjustment for the area of expanding leaves (Hammer et al., 1993). The object-oriented design of the crop template provides the flexibility to readily model canopy development using other options, such as via leaf size distribution (Carberry et al., 1993; van Oosterom et al., 2001), or from the extension rate of each leaf (Chenu et al., 2008). The number of fully expanded leaves is the product of thermal time elapsed since emergence, and the leaf appearance rate. Actual crop leaf area is the product of plant density and leaf area per plant. Green leaf area index is the difference between the total plant leaf area and the senesced leaf area. Under drought stress, the crop will initially cease expanding new leaves, thus reducing transpiration demand, and then commence senescing leaves until demand no longer exceeds supply (Hammer et al., 2001).

Above-ground biomass accumulation is simulated as the minimum of light-limited or water-limited growth (Fig. 1A). In the absence of water limitation, biomass accumulation is the product of the amount of intercepted radiation (IR) and its conversion efficiency, the radiation use efficiency (RUE). The fraction of incident radiation intercepted is a function of the leaf area index (LAI) and the canopy extinction coefficient (k), which is a measure of canopy structure (Lafarge and Hammer, 2002). The effects of N supply on crop growth are implicitly incorporated in this approach (Fig. 1A). Nitrogen limitation will reduce leaf area growth and hence LAI and IR. It can also reduce RUE, which is a function of the N-status of the leaves (Muchow and Sinclair, 1994; Sinclair and Amir, 1992). Sinclair and Muchow (1994) reviewed studies that had measured RUE in many crops and noted a consistent value of 1.25 g MJ⁻¹ for triple-dwarf sorghum under optimum growing conditions. The flexibility of the object-oriented template also allows the simulation of crop biomass accumulation via diurnal canopy photosynthesis models where this is required, as in the studies of Sinclair et al. (2005) and Hammer et al. (2009).

Under water limitation, above-ground biomass accumulation is the product of available soil water and its conversion efficiency, biomass produced per unit of water transpired, or transpiration efficiency (TE). It is necessary to adjust TE to allow for the prevailing vapour pressure deficit (VPD) (Fig. 1A) (Tanner and Sinclair, 1983; Kemanian et al., 2005). Numerous studies in sorghum (Tanner and Sinclair, 1983; Hammer et al., 1997) have found a standard value of 9 Pa for the TE coefficient in sorghum, so that at a VPD of 2 kPa a TE of 4.5 g m⁻² mm⁻¹ results. The water supply accessible to the plant depends on the effective rooting depth and the rate at which soil water can be extracted from the soil by the roots (Fig. 1A). The potential extraction rate is related to the soil water content via an exponential function, parameterized via an extraction decay constant (kl) that incorporates the effects of both soil hydraulic conductivity and root length density on water uptake (Passioura, 1983; Monteith, 1986; Robertson et al., 1993; Hammer et al., 2001). Water extraction occurs from multiple layers, and the total extraction is the sum of that calculated for individual layers. As RUE and TE are based on above-ground biomass only, root mass is not explicitly modelled, but is added to the above-ground biomass accumulation according to a root/shoot ratio that declines with successive growth stages of the crop.

Daily above-ground biomass accumulation is partitioned to plant parts in ratios that depend on the growth stage of the crop via functions that have been found to describe these ratios well (Jones and Kiniry, 1986). Prior to the flag leaf stage, new biomass is allocated to stem and leaves. Leaves are partitioned a fraction that decreases with increasing node number up to a maximum absolute allocation to the leaf that is set by the product of the new leaf area to be grown (described above) and a minimum specific leaf area (SLA, cm² g⁻¹). The remaining biomass is partitioned to stem and rachis. The stem fraction incorporates leaf sheaths, but a distinct allocation to rachis commences after panicle initiation. Between flag leaf and anthesis, accumulated biomass is allocated to the stem and rachis in a fixed ratio.

Grain yield is simulated as the product of grain number and grain size (Fig. 1A). Maximum grain number is a function of the change in plant biomass between panicle initiation and the start of grain filling (Rosenthal et al., 1989), while grain size is determined by grain growth rate, the effective grain-filling period, and the redistribution of assimilates post-anthesis (Heiniger et al., 1997b). If grain mass demand for a day exceeds the daily increase in biomass, the shortfall will first be met through translocation from the stem and, if that is insufficient to meet the demand of the grain, through translocation from leaves, accelerating their senescence. Conversely, if the daily increase in biomass exceeds the grain mass demand, the excess biomass production is allocated to the stem.

(ii) N dynamics: Crop N dynamics are modelled based on a physiological approach that accounts for the fact that the bulk of reduced N present in leaves is associated with photosynthesis structures and enzymes (Grindlay, 1997) (Fig. 1B). The rate of light-saturated net photosynthesis has been shown to be a linear function of the amount of leaf N per unit leaf area (specific leaf nitrogen, SLN), until a species-specific maximum rate of photosynthesis has been reached (Sinclair and Horie, 1989; Anten et al., 1995; Grindlay, 1997), apparently because the rate of CO₂ fixation under radiation-saturated conditions becomes limited by enzyme activity (Grindlay, 1997). Expressing crop N demand relative to canopy expansion thus provides a physiological link between crop N status, light interception, and
dry matter accumulation. In addition, the cardinal SLN values for new leaf growth and for leaf death in response to N deficiency are independent of growth stage (van Oosterom et al., 2010a).

During the pre-anthesis period, only stems (including rachis) and leaves are expanding and their N demand is met in a hierarchical fashion (van Oosterom et al., 2010a). First, structural N demand of the stem (and rachis) is met, as structural stem mass is required to support leaf growth. Structural stem N demand is represented by the minimum stem N concentration (Fig. 1B). If insufficient N has been taken up to meet structural stem N requirement, N can be translocated from leaves by dilution, or in extreme cases of early season N deficiency, from leaf senescence. Second, the N demand of expanding new leaves will be met, and this is represented by their critical SLN (Fig. 1B). Any additional N uptake will first be allocated to leaves to meet their target SLN and then to stem. For leaves, this N uptake represents ‘luxury’ uptake that can occur after full expansion of a leaf, and which does not affect growth and development (van Oosterom et al., 2010a). This hierarchical allocation of N is consistent with observations that under N stress a relatively larger proportion of N is allocated to the leaves (van Oosterom et al., 2010a). Hence, pre-anthesis N allocation ratios are a consequence of model dynamics, rather than a model input.

After anthesis, grain becomes the major sink for N and grain N demand is determined as the product of grain number and N demand per grain (Fig. 1B). During the first part of grain filling, N demand per grain is constant and independent of grain growth rate and N status of the crop (van Oosterom et al., 2010b). At this time endosperm cells are dividing, so that the accumulation of structural (metabolic) proteins in the grain is the key driver. During the second half of grain filling, grain N demand is linked with grain growth rate as cell division and simultaneous storage of carbohydrate and proteins assumes a greater role (Martre et al., 2006). Grain protein content can thus vary depending on the N supply–demand balance and the carbohydrate supply to the grain. Grain N demand is initially met through stem (plus rachis) N translocation, and if this becomes insufficient then N translocation from the leaf can occur. Maximum N translocation rates from stem and per unit leaf area are a function of the N status of these organs, so that sink demand determines the amount of leaf area that is senescing at any one time (van Oosterom et al., 2010b). The source regulation of N translocation follows a first-order kinetic relationship that is representative of enzyme activity. This approach allows a direct future link between the rate parameter in the model and genetic controls associated with N translocation processes.

The daily rate of crop N uptake is the minimum of demand for N by the crop and potential supply of N from the soil and senescing leaves, capped at a maximum N uptake rate (van Oosterom et al., 2010a). Potential N supply from the soil depends on the available soil N through the profile and on the extent to which roots have explored the soil. N supply from the soil is calculated from the combination of passive uptake, through mass flow of N taken up with the transpiration stream, and active uptake (van Keulen and Seligman, 1987). Soil N transformations and their modelling in APSIM have been detailed by Probert et al. (1998).

Model parameterization

Field experiments

A comprehensive set of field experiments (Table 1) was conducted to facilitate model parameterization and testing. The experiments were conducted at Lawes Experiment Station (latitude 27°34’ S, long. 152°20’ E, altitude 90 m asl)

<table>
<thead>
<tr>
<th>Location</th>
<th>Sowing date</th>
<th>Genotypes</th>
<th>Water regime</th>
<th>N rates (kg ha\textsuperscript{-1})</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hermitage\textsuperscript{a}</td>
<td>9 Jan 1997</td>
<td>Buster, M35-1, AQL41/RQL36</td>
<td>Irrig</td>
<td>240</td>
</tr>
<tr>
<td>Hermitage</td>
<td>9 Jan 1997</td>
<td>Buster, M35-1, AQL41/RQL36</td>
<td>Irrig</td>
<td>10</td>
</tr>
<tr>
<td>Hermitage</td>
<td>9 Jan 1997</td>
<td>Buster, M35-1, AQL41/RQL36</td>
<td>Rainout</td>
<td>120</td>
</tr>
<tr>
<td>Hermitage</td>
<td>9 Jan 1997</td>
<td>Buster, M35-1, AQL41/RQL36</td>
<td>Rainout</td>
<td>10</td>
</tr>
<tr>
<td>Hermitage\textsuperscript{b}</td>
<td>27 Nov 1997</td>
<td>Buster, M35-1, CSH13R</td>
<td>Irrig</td>
<td>240</td>
</tr>
<tr>
<td>Hermitage</td>
<td>27 Nov 1997</td>
<td>Buster, M35-1, CSH13R</td>
<td>Irrig</td>
<td>30</td>
</tr>
<tr>
<td>Hermitage</td>
<td>27 Nov 1997</td>
<td>Buster, M35-1, CSH13R</td>
<td>Rainout</td>
<td>120</td>
</tr>
<tr>
<td>Hermitage</td>
<td>27 Nov 1997</td>
<td>Buster, M35-1, CSH13R</td>
<td>Rainout</td>
<td>30</td>
</tr>
<tr>
<td>Lawes\textsuperscript{c}</td>
<td>11 Oct 1996</td>
<td>Buster, M35-1, AQL41/RQL36</td>
<td>Irrig</td>
<td>360</td>
</tr>
<tr>
<td>Lawes\textsuperscript{d}</td>
<td>6 Jan 1997</td>
<td>Buster, M35-1, AQL41/RQL36</td>
<td>Irrig</td>
<td>360</td>
</tr>
<tr>
<td>Lawes\textsuperscript{e}</td>
<td>4 Dec 1997</td>
<td>Buster, M35-1, CSH13R</td>
<td>Irrig</td>
<td>360</td>
</tr>
<tr>
<td>Lawes</td>
<td>11 Nov 1998</td>
<td>Buster, CSH13R</td>
<td>Irrig</td>
<td>0, 120, 240, 360</td>
</tr>
<tr>
<td>Lawes\textsuperscript{f}</td>
<td>2 Dec 1999</td>
<td>CSH13R, ATx642/RQL36, AQL39/RQL36</td>
<td>Irrig</td>
<td>0, 45, 360</td>
</tr>
</tbody>
</table>

\textsuperscript{a} Non-limiting water and N experiments for genotypic comparison of light extinction and RUE.

\textsuperscript{b} Post-anthesis data excluded due to damaging effects of severe storm at flowering.

\textsuperscript{c} Experiment on N responses of van Oosterom et al. (2010a, b).
and Hermitage Research Station (latitude 28°10' S, long. 152°02' E, altitude 480 m asl) in south-eastern Queensland, Australia. At Lawes, the soil was a deep alluvial, weakly cracking, clay loam vertisol (Powell, 1982) and at Hermitage a cracking, self-mulching, grey clay vertisol (McKeown, 1978). Daily solar radiation and maximum and minimum temperatures were recorded at the experimental sites.

A randomized block design with three replicates was used in all experiments, which included diverse triple- and single-dwarf sorghum genotypes and involved a range of N and water treatments. Overall, six genotypes were used in the experiments: AQL41/RQL36, Buster, ATx642/RQL36, and AQL39/RQL36 are well-adapted Australian triple-dwarf grain sorghum hybrids. M35-1 is the main variety grown in the Rabi (dry) season in India, and CSH13R is a high-yielding Indian hybrid. Both Indian genotypes are tall, single-dwarf, dual purpose sorghums that are grown for both stover and grain production. Plots measured 22×4 m (8 rows at 50 cm spacing) at Lawes and 20×4 m at Hermitage with stands thinned to 10 plants m⁻² two weeks after sowing. In all experiments weeds and pests were controlled as required and there was negligible pest damage to the photosynthetic leaf surface throughout growth. In the sowing at Lawes on 6 January 1997, severe lodging of M35-1 occurred on 27 February 1997 during a severe storm and grain-filling was affected.

Experiments were managed and sampled for growth and development regularly in a manner similar to that described in detail by van Oosterom et al. (2004) and Broad et al. (1998), except that only three samples (mid-vegetative, flowering, maturity stages) could be harvested from the rain-out shelter experiments at Hermitage due to experiment size limitations. In addition, radiation interception was measured in most non-limiting N and water treatments using tube solarimeters and the data collection system described by Muchow and Davis (1988), and canopy height was measured as height to the ligule of the last fully expanded leaf at the time of weekly leaf observations in most experiments.

The diversity of environments in the field experiments (Table 1), which ranged from non-limiting water and nutrient conditions to severe levels of water and N limitation across seasons and sites, combined with the diversity of genotypes, generated a wide range in crop growth and yield. Across all experiments and genotypes, total biomass at maturity ranged from about 500 to 2500 g m⁻², grain yield from 0 to about 1000 g m⁻², and LAI at anthesis from values below 2 to above 6. The data set collected provided a sound basis for parameterizing aspects of the model associated with genotypic differences, and for comprehensive model testing.

RUE but not the canopy light extinction coefficient varied among genotypes

Light interception and RUE were examined for the five field experiments conducted under non-limiting water and N conditions that included both Buster and M35-1 (Table 1). The fraction of incident radiation intercepted (RI) was plotted against canopy leaf area index (LAI) and a standard light extinction relationship (see Charles-Edwards, 1982) fitted -

\[
RI = 1 - e^{-kLAI}
\]

where \(k\) is the fitted canopy light extinction coefficient.

Analysis of covariance indicated no significant difference in \(k\) among the four genotypes grown in those experiments (Fig. 2) despite the large differences in height between the triple-dwarf (Buster, AQL41/RQL36) and single dwarf (M35-1, CSH13R) genotypes. The result suggests that aspects of canopy architecture likely to affect \(k\), such as leaf angle distribution, did not differ among these diverse genotypes.

\[\text{RUE} = \text{the maximum value found during the crop cycle prior to any possible decline in photosynthetic capacity during grain-filling or confounding effects of leaf senescence on light interception measurements. The maximum RUE was derived as the fitted slope of the linear relationship between net above-ground biomass and cumulative intercepted radiation using a step-wise regression procedure (Muchow and Sinclair, 1994) in which, starting at crop maturity, data points were progressively removed from the fit until no further improvement was gained in the proportion of variance accounted for by the regression. Analysis of covariance was used to test for differences among genotypes.}

Significant genotypic effects on RUE for above-ground biomass were found only for the experiments that included CSH13R (Fig. 3). This is the first study to find this effect for sorghum. A recent study has reported associations of biomass with height in sorghum (Salas Fernandez et al., 2009), but RUE was not measured and effects on biomass were confounded by differences in other factors, such as maturity. The values of RUE found in this study for the tall Indian hybrid CSH13R (1.6–1.8 g MJ⁻¹) are much higher than the commonly accepted range for sorghum
Fig. 3. Total biomass versus accumulated intercepted radiation for three sorghum genotypes grown in non-limiting water and N experiments at (A) Hermitage (H, 27 November 97) and (B) Lawes (L, 4 December 97). Circled symbols indicate data points excluded from the regressions to determine maximum radiation use efficiency (g MJ$^{-1}$) (see text). The non-zero intercept in (A) was due to light interception measurements not commencing until after crop establishment. For each regression the number in parentheses is the 95% confidence interval of the associated coefficient and $R^2$ is the proportion of variation explained: (A) CSH13R: $y=1.84(0.04)x+168$, $R^2=0.99$; M35-1: $y=1.34(0.05)x+136$, $R^2=0.99$; Buster: $y=1.19(0.06)x+216$, $R^2=0.99$. (B) CSH13R: $y=1.66(0.08)x$, $R^2=0.99$; M35-1: $y=1.34(0.10)x$, $R^2=0.98$; Buster: $y=1.43(0.10)x$, $R^2=0.95$.

(1.2–1.4 g MJ$^{-1}$) found in many previous studies as summarized in the review of Sinclair and Muchow (1999) and as found in this study for the tall Indian landrace line M35–1 and the short Australian hybrid Buster. The higher $RUE$ values found for CSH13R equate closely with those measured for maize (Sinclair and Muchow, 1999; Lindquist et al., 2005).

The reasons for this genotypic effect remain unknown, but may be associated with differences in net photosynthetic rate or root–shoot partitioning. Photosynthetic capacity is one of the main factors contributing to species differences in $RUE$ (Sinclair and Horie, 1989), but within species differences of this magnitude seem unlikely. However, the difference between the tall hybrid and tall landrace line may be associated with photosynthetic capacity. Inbred parent lines in maize have been shown to have lower photosynthetic rates than their associated hybrids during grain-filling (Ahmadzadeh et al., 2004) and under high N conditions this has been linked with lower $RUE$ in inbred lines during vegetative growth due to their reduced N uptake (D’Andrea et al., 2009), which was consistent with findings for M35-1 in this study (data not shown). In other crops, there is also some evidence indicating a reduction in $RUE$ associated with dwarfing. Miralles and Slafer (1997) observed 23% lower $RUE$ in dwarf lines of wheat compared with that of their near-isogenic taller counterparts. In a separate study they reported increased dry matter partitioning to roots associated with the dwarfing genes (Miralles et al., 1997). Hence, it is plausible that the lower $RUE$ of the short sorghum hybrid may have been associated with dwarfing genes per se. Four major dwarfing genes are known to regulate height in sorghum and most commercial grain sorghum hybrids have been developed by converting tall, native sorghums to short triple-dwarf types (Morgan and Finlayson, 2000). One of the major dwarfing genes, $dw3$, has been characterized (Multani et al., 2003) and found to modulate polar auxin transport, leading to reduced cell elongation and more compact internodes. If the reduced stem growth was associated with enhanced partitioning to roots, then this may explain the lower $RUE$ for above-ground biomass production in the short hybrid. This hypothesis might also be a basis for the $RUE$ differences found between sorghum and maize, which has been perplexing, since both species have $C_4$ photosynthesis and similar potential leaf photosynthetic rates, and so would be expected to have similar $RUE$ (Sinclair and Muchow, 1999). In the absence of most dwarfing genes, the $RUE$ of the tall sorghum hybrid (CSH13R) was similar to that of maize. It is clear that further study is required to unravel the factors causing this genotypic effect on $RUE$ in sorghum and its potential association with height. This is the subject of current ongoing research employing isolines for height (George-Jaeggli, 2009).

Canopy height was closely associated with node number for both single- and triple-dwarf genotypes

Data from experiments with non-limiting water and N conditions where height measurements were taken was used to fit potential canopy height ($Ht$) versus node number ($N$) relationships for each genotype. An exponential equation (Goudriaan and Monteith, 1990) was fitted –

$$Ht = \xi/\omega \ln \left\{ 1 + e^{\eta(N-\xi)} \right\}$$

where $\xi$, $\omega$, and $\eta$ were fitted coefficients, with $\xi$ being the maximum rate of height increase per node in the linear phase, $\omega$ the maximum relative rate of increase during the exponential phase, and $\eta$ an indicator of the node number at transition to the linear phase. Analysis of covariance was used to test for similarity of coefficients among genotypes as required.

This relationship fitted data well for all genotypes (Fig. 4). There were no significant differences among parameters for triple-dwarf genotypes so common values
were fitted. For the single-dwarf genotypes, there were no significant differences for \(\omega\) and \(\eta\), so common values were fitted. However, distinct values were required for the maximum rate of height increase in the linear phase \(\xi\) reflecting the difference in extension growth rate of stems for CSH13R and M35-1 (Fig. 4B). The similarity in values of the parameter \(\eta\) (9.3–9.4 nodes) across all genotypes indicated a common developmental timing of transition from exponential to linear growth in height. The single-dwarf types did not diverge greatly in height until after nine nodes. These responses suggest a linear increase in internode length up to a maximum at the ninth node, which is then maintained for subsequent internodes. This is consistent with the pattern of internode length found in studies on maize (Bennouna et al., 2004).

**Biomass partitioning between stem and leaf was closely associated with node number for both single- and triple-dwarf genotypes with increased partitioning to stem for single-dwarfs**

Available data from experiments with non-limiting water and N conditions was also used to fit a relationship between proportion of crop mass growth partitioned to leaves \(P_l\) and node number \(N\) for each genotype. The curvilinear relationship (Jones and Kiniry, 1986) fitted was –

\[
P_l = 1 / (1 + e^{N^2})
\]

where \(e\) was a fitted coefficient.

The relationship fitted data well for all genotypes (Fig. 5). As expected, the single-dwarf genotypes partitioned a lesser proportion of growth to leaf (and thus more to the stem) as node number increased, than the triple-dwarf genotypes. However, there were no significant differences among genotypes within each of those groups so common curves were fitted (Fig. 5).

**Genotypes differed in potential leaf area development and potential grain number**

Available data from experiments with non-limiting water and N conditions were used to fit sigmoid curves for total leaf area per plant \(TPLA\) as a function of thermal time from emergence \(TT\) (Hammer et al., 1993) for each genotype:

\[
TPLA = TPLA_{\text{max}} / \left(1 + e^{-(\frac{TT-\beta}{\alpha})}\right)
\]

\[
TPLA_{\text{max}} = (1 + \text{FTN})^{0.66} \times \text{TLN}^c
\]

where \(TPLA_{\text{max}}\) is the maximum value of \(TPLA\), \(TT\) was calculated from daily maximum and minimum temperatures as per Hammer and Muchow (1994), \(\alpha\), \(\beta\), and \(\gamma\) were fitted coefficients, \(\text{FTN}\) is fertile tiller number, and \(\text{TLN}\) is total leaf (node) number. On the occasions where tillering occurred, \(\text{FTN}\) was set at the value observed at flowering (data not shown). The value of \(\beta\) was set at 66% of the thermal time from emergence to flag leaf full expansion to allow for the wide range in \(\text{TLN}\) (Hammer et al., 1993).

**Fig. 4.** Canopy height (Ht, cm) versus fully expanded node number (N) for (A) triple- and (B) single-dwarf sorghum genotypes. The common fitted expolinear relationship for triple-dwarf genotypes was \(Ht = 7.8/0.277 \times \ln(1 + e^{0.277(N-9.3)}), n=63, R^2=0.96\). For the single-dwarf genotypes the fitted expolinear relationships were CSH13R: \(Ht = 25.1/0.557 \times \ln(1 + e^{0.557(N-9.4)}), n=25\), M35-1: \(Ht = 18.1/0.557 \times \ln(1 + e^{0.557(N-9.4)}), n=30\), combined \(R^2=0.98\).

**Fig. 5.** Proportion of crop growth partitioned to leaf \(P_l\) versus fully expanded node number \(N\) for triple- and single-dwarf sorghum genotypes. The fitted relationships were: Triple-dwarf genotypes (Buster, A35/QL36, QL39/QL36, QL41/QL36, dashed line): \(P_l=1/ (1+0.0073N^2), n=69, R^2=0.69\). Single-dwarf genotypes (CSH13R, M35-1, solid line): \(P_l=1/ (1+0.0106N^2), n=68, R^2=0.78\).
Fitted values for parameters ($\alpha$, $\gamma$) were consistent across experiments (data not shown) but differed among genotypes (Table 2). Greater/lesser values of $\gamma$ indicated greater/lesser maximum total plant leaf area for a given total leaf number, which reflected likely differences in potential leaf size. Differences in the value of $\alpha$ relate to the nature of the temporal change in plant leaf area and reflect likely differences in leaf size distribution.

Data from the same experiments were used to derive estimates for each genotype of the coefficient relating grain number to biomass accumulated during the period between panicle initiation and the start of grain-filling ($\omega$, g grain$^{-1}$) (Rosenthal et al., 1989; Heiniger et al., 1997a). The greater values of $\omega$ for the single-dwarf genotypes (Table 2) were consistent with fewer grain set by those types per unit of crop growth (van Oosterom and Hammer, 2008).

**Model testing**

*Simulating field experiments*

Genotypic parameters, relevant weather data, and details of soil N and water at sowing were collated so that all field experiments (Table 1) could be simulated. Parameters quantifying genotypic effects on phenology, canopy development, growth, and grain set were collated from analyses in this study and relevant other studies (Sinclair and Muchow, 1998; Ravi Kumar et al., 2009) (Table 2). Parameters defining genotypic differences in phenology (i.e. temperature and photoperiod responses) and leaf initiation rate were as reported by Ravi Kumar et al. (2009). Leaf appearance rate and thermal time from flag leaf full expansion to anthesis differed little among genotypes and so were set at standard values of 41 and 174 °Cd, respectively (Hammer et al., 1993; Ravi Kumar et al., 2009). Other parameters associated with genotypic differences in height growth, carbohydrate partitioning, total leaf area per plant, and $RUE$ were derived from values found in this study. As all genotypes other than CSH13R had $RUE$ values near the commonly accepted value of 1.25 g MJ$^{-1}$, that value was used for those genotypes. As CSH13R had an $RUE$ that was, on average, 0.4 g MJ$^{-1}$ greater (Fig. 3), its $RUE$ was set at 1.65 g MJ$^{-1}$ (Table 2).

Available N in the soil profile was measured prior to sowing for experiments with low N treatments. The values were 10.9 and 55.6 kg ha$^{-1}$ for the irrigated 9 January 1997 and 27 November 1997 sowings at Hermitage, and 55.1 and 60.5 kg ha$^{-1}$ for the 11 November 1998 and 2 December 1999 sowings at Lawes. The potential available water-holding capacity of the black earth soil at Hermitage was measured for the rain out experiments by determining the difference in water content of the soil profile when wet and drained (upper limit) with that after crop water use had ceased (lower limit) as per the method described by Dalgleish and Foale (1998) and Broad et al. (1998). The soil profile graded into decomposing basalt at a depth of 120 cm and held 225 mm of available water. In the rain out experiments, the profile was irrigated to maximum storage immediately prior to sowing and no further irrigation was applied. Soil water content was measured approximately weekly in rain out experiments via gravimetric sampling of the top 20 cm of the profile and via the neutron scattering technique for each subsequent 20 cm layer in the soil profile (503 DR Hydroprobe® Moisture Gauge, CPN International Inc., California, USA).

Each treatment of each experiment was simulated using the parameter estimates for each genotype (Table 2), and associated crop management, soil, and weather data. Soil characteristics and starting water and N conditions were set at measured values. Amounts and timing of water and N applications were included as per experimental procedures.

**Table 2.** Parameter values for relationships quantifying phenology, canopy development, growth, and grain set in the sorghum crop model for genotypes used in this study

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Genotype</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Buster</td>
</tr>
<tr>
<td>Thermal time to FI (°Cd)</td>
<td>160</td>
</tr>
<tr>
<td>PP effect (°Cd h$^{-1}$)</td>
<td>11.5</td>
</tr>
<tr>
<td>Thermal time A-PM (°Cd)</td>
<td>819</td>
</tr>
<tr>
<td>Plastochron (°Cd leaf$^{-1}$)</td>
<td>21.6</td>
</tr>
<tr>
<td>$\gamma$ (°Cd$^{-1}$)</td>
<td>2.90</td>
</tr>
<tr>
<td>$\alpha$ (°Cd$^{-1}$)</td>
<td>0.018</td>
</tr>
<tr>
<td>$\xi$ (node$^{-2}$)</td>
<td>0.0073</td>
</tr>
<tr>
<td>$\zeta$ (cm node$^{-1}$)</td>
<td>7.8</td>
</tr>
<tr>
<td>$\omega$ (node$^{-1}$)</td>
<td>0.277</td>
</tr>
<tr>
<td>$\eta$ (node)</td>
<td>9.3</td>
</tr>
<tr>
<td>$RUE$ (g MJ$^{-1}$)</td>
<td>1.25</td>
</tr>
<tr>
<td>$\kappa$ (g grain$^{-1}$)</td>
<td>0.00083</td>
</tr>
</tbody>
</table>
Simulated values of total, leaf, stem, and grain biomass and N, crop LAI, and available soil water and N were compared with measured values for each treatment. The time-course of simulated values through the crop cycle was plotted and compared with sequential measurements by inspection. Scatter plots of predicted versus observed values for all treatments of all experiments were constructed for total biomass (at physiological maturity), grain yield, LAI at flowering, total N uptake, grain N, and grain N%. Linear regressions were fitted to assess overall goodness of fit of the model.

Simulated crop growth and development throughout the crop life cycle accurately reflected observed genotypic effects and responses to water and N availability

The time-course of simulated values of crop attributes through the crop cycle showed generally good correspondence with measured values. The sample plots (Fig. 6) include a comparison of genotype effect (Fig. 6A, B), water limitation effect (Fig. 6A, C), and N limitation effect (Fig. 6B, D).

![Graphs showing simulated crop attributes throughout the crop life cycle compared to measured values](https://example.com/graphs)

The differences between the genotypes CSH13R (single-dwarf) and Buster (triple-dwarf) under potential growth conditions (Fig. 6A, B) were simulated credibly. CSH13R was predicted to accumulate more total biomass and allocate more to stem in line with its greater RUE, height (ξ), and partitioning coefficient (ε) (Table 2). The greater LAI of CSH13R, which was related to its slower rate of development and greater leaf number, was also predicted well, although total biomass was slightly underestimated during the grain-filling period. Both hybrids yielded similarly despite the large difference in total biomass arising from the greater RUE of CSH13R. This was simulated via the setting of fewer grain in CSH13R (data not shown) in line with its greater ξ, combined with its reduced duration of grain-filling. Hence, the simulation generated the reduced harvest index and larger grain size found for CSH13R under these conditions. The difference in N harvest index was also generated, as both hybrids accumulated similar amounts of total N, but a greater proportion of this was partitioned to stem in the taller CSH13R.

Water limitation severely restricted growth and yield of CSH13R and the effects were also simulated credibly.
The water-limited crop generated leaf area similarly to the non-limited crop up to a time just prior to flag leaf expansion, when available soil water became depleted and severe stress commenced, as simulated by the water supply–demand ratio. At this time, biomass accumulation slowed and ceased and leaves began to senesce. The crop failed to produce any viable grain, and the simulation predicted this failure of grain set. The depletion of available water in the soil profile was simulated well, although a small amount of water remained in the soil profile at the end of the simulation. This probably reflected a small difference in the actual soil water-holding capacity in this treatment compared with the average value used for the simulation.

N limitation severely restricted growth and yield of Buster and these effects were also simulated credibly (Fig. 6B, D). The N-limited crop was restricted in its leaf area development by its inability to meet the critical SLN requirement for new leaf area growth. The decline in SLN and depletion of available soil N were predicted well. The low LAI subsequently limited light interception, biomass accumulation, and grain set. The accurate prediction on N uptake in this case resulted in an accurate prediction of the timing and extent of leaf area senescence associated with N translocation to grain. The allocation of carbohydrate and N among organs was simulated well.

Simulated values of crop attributes reflected observations well across all experiments

The general adequacy of relationships between predicted and observed values for biomass, yield, LAI, and organ N across the diverse range of genotypes and environments found in these experiments indicated a robust predictive capability of the model (Fig. 7). The prediction of days to flowering was equally robust (\(y=0.87(0.14)x+12.4(10.3)
\) \(R^2=0.82\) \(\text{RMSD}=4.3\), data not shown). While some detailed data from some of these experiments was used to parameterize aspects of the genotypic responses, this does not significantly diminish the assessment of the overall ability to capture relatively faithfully the dynamics of organ mass and N throughout the crop life cycle for such a diverse set of conditions. Predictions of total biomass at physiological maturity and grain yield corresponded well with observed values over these conditions, although at high yield levels there was a tendency to over-predict grain yield. This related to over-prediction of grain number in some cases. Grain number in sorghum relates to panicle growth rate (Gerik et al., 2004; van Oosterom and Hammer, 2008), in a manner similar to that found for maize (Vega et al., 2001) and wheat (Miralles et al., 1998). However, initial attempts to implement this approach to grain number prediction by shortening the interval used for growth accumulation and excluding the non-panicle growth components, failed due to the sensitivities introduced. Hence grain number in the model was based on crop growth rate over the period between panicle initiation and the start of grain-filling (Rosenthal et al., 1989). This remains an area where further improvement is required.

Predictions of LAI at flowering and total and grain N showed good correspondence with observed values, although total N uptake was slightly under-predicted at high N levels. The prediction of grain N%, which is the ratio of independent predictions of grain N and grain mass, showed more scatter, but good overall correspondence. The under-prediction of grain N% in some cases was associated with the over-prediction of grain yield rather than with under-prediction of N partitioning to grain.

Simulating emergent consequences of differences in height

A simulation of hypothetical genotypes differing in height was conducted to examine emergent consequences on growth and development. The tall and short hypothetical genotypes were parameterized using values found for the single- and triple-dwarf hybrids in this study. It was assumed that the hypothetical genotypes differed only in height growth (\(\xi\), partitioning to stem (\(\phi\), and \(RUE\), and the contrasting values found for Buster and CSH13R were used (Table 2). All other factors, such as coefficients quantifying phenology, leaf area production, grain set, and responses to water and N limitation were assumed to be the same for both hypothetical genotypes and were set at the values found for Buster (Table 2). The simulated crop was sown on 15 December 1995 at Dalby, Queensland, with soil N of 25 kg N ha\(^{-1}\), and three applications of 50 kg N ha\(^{-1}\) (sowing, initiation, anthesis). The simulated crop was provided with non-limiting water supply. The time-course of simulated values of key variables through the crop cycle was plotted for both hypothetical hybrids to explore any emergent consequences on growth, yield, and LAI.

Simulating genotypic variation in height generated phenotypic differences in green leaf area retention during grain filling

As expected, the simulated taller hybrid accumulated more total and stem biomass, in line with its similar phenology and leaf area development but greater \(RUE\) and partitioning to stem (Fig. 8A). While total N uptake was similar for the two types, the taller hybrid partitioned more N to stem (Fig. 8B), because even though it had the same minimum stem N% requirement, it had more stem mass. As a consequence, the SLN of the taller hybrid was reduced during canopy development as a lesser amount of N was allocated to the same leaf area (Fig. 8D). As the taller hybrid had greater growth leading into anthesis due to its higher \(RUE\), it set more grain (data not shown). This generated a greater grain N demand in the tall hybrid, which could not be met from the increased N in the stem, as this was structural and not available for mobilization. Due to its greater stem mass and thus greater structural N requirement, the tall hybrid retained more N in the stem throughout grain-filling (Fig. 8B). As a consequence, the tall hybrid remobilized N earlier from leaves causing earlier
senescence and decline in leaf area (Fig. 8C). Hence, a senescent phenotype arose as an emergent consequence of the increase in height, with its associated increases in carbohydrate partitioning to the stem and $RUE$. This effect was consistent with the experimental observations of van Oosterom et al. (2010b). While this effect was associated with crop N dynamics, none of the coefficients regulating N responses were modified in the simulation of change in height. This outcome was only possible because of the advances implemented in modelling N dynamics by introducing the organ demand and supply approach to replace the conventional approach that used descriptive functions of critical tissue N concentrations throughout the crop cycle.

The APSIM framework provides a robust basis for further advance in modelling the physiology and genetics of complex traits

The modelling framework progressed here is robust and explanatory and provides a sound basis for ongoing exploration of the physiology and genetics of complex traits. It is grounded in sound process physiology, has evolved with appropriately structured and detailed experimentation on growth and development processes, and predicts the dynamics of phenotypic responses in crop growth and development well across a diverse range of environments and genotypes. It is capable of generating plausible phenotypic responses to hypotheses about the genetic regulation of
traits as emergent consequences of model dynamics, thus making it suitable as an integral part of G-to-P research. The APSIM framework has many design features that make it conducive to ongoing scientific model development. The design allows multiple instantiations of an object, which enables the simulation of cohorts and facilitates an easy ‘swap’ of individual plant parts or processes, without affecting the integrity of the remainder of the model. This capability has already been exploited in studies that have introduced a grain cohort capability for carbohydrate allocation and grain growth within the maize ear (Messina et al., 2009), leaf area development based on individual leaf expansion rate in maize (Chenu et al., 2008), radiation and soil water capture based on canopy and root system architecture attributes associated with leaf and root angles in maize (Hammer et al., 2009), and a simple gene network for predicting transition to flowering in sorghum (van Oosterom et al., 2006).

While the modelling framework presented is grounded in the concepts of organ initiation and growth, and arbitration of supply of major resources to those organs through the crop cycle, there remains a need for continual improvement in the explanatory capability of the model to meet the needs of G-to-P prediction better. In particular, the approach to carbohydrate partitioning between the stem and leaf remains empirical, root system growth is not linked directly with shoot growth, and grain number prediction lacks robustness. Modelling carbohydrate partitioning will probably be improved by better definition of organ demand (Dingkuhn et al., 2005; Luquet et al., 2006) as developed in modelling horticultural crops (Marcellis, 1993; Heuvelink, 1996; Génard et al., 2008). The developments made in modelling carbon allocation in the detailed functional–structural crop model GRAAL (Drouet and Pagès, 2003), which takes the approach of organ demand and supply and includes roots are instructive in this regard. However, parameterization requirements limit its general applicability. There also appears to be an acceptance of the notion that combining architectural models with functional process models is required for this purpose (Drouet and Pagès, 2003; Dingkuhn et al., 2005; Génard et al., 2008). While there may well be some issues where this combination is needed, as in horticultural crops where effects of pruning will depend on fruit position (Lopez et al., 2008), it is not obligatory for defining potential organ growth in field crops. The concept of phytomers and their size/mass (e.g. height, area, density) are often, or can be, accommodated in functional process models alone, so that the overhead of the architectural parameterization associated with organ position adds unnecessary detail. In essence, in a similar vein to the de Wit and Penning de Vries (1983) comment on hormone action, our approach is akin to modelling structural effects realistically without directly modelling the architecture.

For effective use of crop models in crop improvement, there remains the dilemma of enhancing the physiological robustness of the model while maintaining the parsimony needed. The quest for balance in modelling (Monteith, 1996) has not diminished in relevance. Model parameters are required that link more effectively to traits and their genetic control for G-to-P modelling, but does this imply that we need greater complexity? It has been argued elsewhere (Tardieu, 2003; Hammer et al., 2006; Messina et al., 2009) that models of relatively coarse granularity are suitable to integrate phenotypic and molecular approaches to plant breeding, provided they faithfully capture the physiological basis of adaptive traits and system dynamics. A recent study by Letort et al. (2008) employed a simulation of hypothetical genotypes to examine QTL associations with model parameters versus phenotypic traits. They argued that a functional–structural model was required to

![Fig. 8. Simulated crop attributes throughout the crop life cycle for two hypothetical sorghum hybrids differing in height (see text for details). In each panel, the solid line represents results for the tall hybrid. The panels show: (A) total and organ (stem, leaf, grain) biomass, (B) total and organ (stem, leaf, grain) N mass, (C) canopy specific leaf nitrogen (SLN) (D) crop leaf area index (LAI). Values for stem include simulated mass of rachis.](https://academic.oup.com/jxb/article-abstract/61/8/2185/490569)
achieve satisfactory associations for model parameters. However, while their study showed that the associations with model parameters were indeed superior, it was instructive to note that the main model variables involved were related to the supply-demand ratio for carbohydrate by specific organs – aspects that are already included in functional organ-level process models (such as the formalism presented here) in the absence of architectural detail.

While the development of G-to-P modelling capability into the future will undoubtedly be informed by more detailed models, the quest for balance dictates that they may not necessarily be incorporated per se within that capability. For example, improved approaches on modelling root systems might be based on concepts of resource supply, organ demand and transport resistance (Thornley, 1998), and on learning from models that account for hydraulic properties of roots and root system architecture in determining patterns of water uptake (Doussan et al., 1998; de Dorlodot et al., 2007), without incorporating their complete detailed formalisms. Similarly, lessons derived from quantitative approaches to model plants (Christophe et al., 2008) and to understanding hormone action (Dun et al., 2009) will also aid the task of understanding and quantifying plant/crop functional dynamics in the manner most useful to crop improvement. In other instances, direct incorporation of more detailed organ level modelling may be feasible and the best way forward, as in the case of leaf growth in maize (Chenu et al., 2008).

Relevance of an enhanced crop modelling capability for complex trait dissection and plant breeding

An improved explanatory and parsimonious crop modelling capability suitable for G-to-P prediction offers many advantages to plant breeding and crop improvement.

(i) Better connection of complex traits to their genetic regulation

Dissecting and understanding the physiological basis of complex traits can identify putative causes that are not intuitively obvious, such as the association of height with leaf senescence suggested in this study via links with N dynamics (Borrell et al., 2001; van Oosterom et al., 2010b). A robust modelling capability provides a dynamic biological framework to analyse and quantify component traits. This can generate improved connection to the genetic architecture that controls the trait of interest by identifying model parameters that link more stably to genomic regions than direct phenotypic measures (Tardieu, 2003; Dingkuhn et al., 2005; Hammer et al., 2006; Letort et al., 2008). To date, the best examples are at the sub-model level for issues such as leaf growth (Reymond et al., 2003; Tardieu et al., 2005; Sadok et al., 2007) and transition to reproductive growth (Leon et al., 2001; Welch et al., 2005; Yin et al., 2005; Messina et al., 2006; Uptmoor et al., 2008). This may well be the preferred way to proceed, with the whole plant/crop model helping to identify suitable target traits and possible avenues for their rapid phenotyping in breeding populations. This approach has been demonstrated in the studies on adaptation to water limitation in wheat and its likely association with root system architecture (Manschadi et al., 2006, 2008; Christopher et al., 2008).

(ii) Phenotypic prediction of trait value

A robust crop modelling capability provides the ability to predict phenotypic consequences and generate the adaptation landscape associated with the genotype–management–environment (G*M*E) system, as conceived by Cooper and Hammer (1996). This provides estimates of the phenotypic value of specific traits or genomic regions on productivity (e.g. yield) in specific management systems and environments for potential combinations well beyond what is possible experimentally. The G-to-P prediction process is often characterized by partitioning into gene-to-trait and trait-to-phenotype components (Messina et al., 2009) in the simulation studies reported to date (Chapman et al., 2003; Hammer et al., 2005; Chenu et al., 2008; Letort et al., 2008). Chenu et al. (2009) have reported the first G-to-P modelling study that derives estimates of the effects on grain yield in target production environments of known quantitative trait loci (QTL) controlling a specific adaptive trait—leaf and silk elongation in maize. Their study highlighted the value of the G-to-P modelling approach in interpreting the genetic control of yield and, hence, its relevance to plant breeding.

It has been inviting to physiologists to view G-to-P predictive capability as a way to design optimal crop ideotypes (Boote et al., 2001; Letort et al., 2008), but this can be misleading in the absence of knowledge of the genetic architecture of complex traits. The study of Chenu et al. (2009) highlights the points that genetic architecture limits the feasible combinations of model parameter values and pleiotropic effects may have major consequences. Hence, while it is instructive to undertake simulations of the adaptation landscape to assess the relative value of an anticipated variation in traits and their associated model parameters, this can only be exploratory and hypothesis-generating. Sinclair et al. (2005) adopted this approach in considering the likely value of limiting maximum transpiration rate in sorghum. Linking phenotypic prediction of trait value with breeding programmes and their understanding of the germplasm is likely to be more useful to crop improvement (Hammer and Jordan, 2007). In this context, the explanatory power of G-to-P modelling based on knowledge of trait physiology can aid the accumulation of favourable alleles in breeding programmes by helping to unravel some aspects of unexplained phenotypic variation in target environments (Messina et al., 2009).

Adding value to plant breeding/selection methods

Credible simulation of the complex G*M*E crop adaptation landscape can be utilized to add value to plant
breeding. Beyond the use in defining environment types in the target population of environments (Chapman et al., 2000) and using that quantification to weight selection decisions to improve the rate of genetic gain (Podlich et al., 1999), simulated landscapes can be used as a test-bed for statistical techniques for QTL detection (Chapman, 2008; Letort et al., 2008; van Eeuwijk et al., 2010), to aid design of breeding strategies by linking with breeding system simulation capability (Podlich and Cooper, 1998; Cooper et al., 2002, 2005; Chapman et al., 2003; Hammer et al., 2005), and to support operational molecular breeding (Messina et al., 2009).

These developments rely to varying degrees on the capability for modelling the physiology and genetics of complex adaptive traits and the associated G-to-trait-to-P predictions. While this capability continues to evolve with advances in knowledge, a framework suitable for current use in navigating complexity in crop yield improvement that can also serve the continuing evolution in capability has been presented.

**Supplementary data**

Supplementary information (The Sorghum Code Viewer) can be found at *JXB* online.

**Acknowledgements**

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