RESEARCH PAPER

Modelling impact of early vigour on wheat yield in dryland regions

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Abstract

Early vigour, or faster early leaf area development, has been considered an important trait for rainfed wheat in dryland regions such as Australia. However, early vigour is a genetically complex trait, and results from field experiments have been highly variable. Whether early vigour can lead to improved water use efficiency and crop yields is strongly dependent on climate and management conditions across the entire growing season. Here, we present a modelling framework for simulating the impact of early vigour on wheat growth and yield at eight sites representing the major climate types in Australia. On a typical soil with plant available water capacity (PAWC) of 147 mm, simulated yield increase with early vigour associated with larger seed size was on average 4% higher compared with normal vigour wheat. Early vigour through selection of doubled early leaf sizes could increase yield by 16%. Increase in yield was mainly from increase in biomass and grain number, and was reduced at sites with seasonal rainfall plus initial soil water <300 mm. Opportunities exists for development of early vigour wheat varieties for wetter sites. Soil PAWC could play a significant role in delivering the benefit of early vigour and would require particular attention.

Keywords: APSIM next generation, environment, establishment, genotype, management, Triticum aestivum.

Introduction

Early vigour or seedling vigour (i.e. the amount of leaf area produced early in the season) has been considered an important trait for rainfed (water-limited) wheat especially in Mediterranean climate regions such as southern Australia. In these regions, rainfall is winter dominant (Rebetzke and Richards, 1999; Richards and Lukacs, 2002; Rebetzke et al., 2007) and coincides with early wheat growth (planted in mid-autumn to early winter). Wheat yield is often limited by insufficient rainfall around anthesis with a terminal drought during grain-filling (Richards, 1991). More efficient use of soil moisture at early wheat growing stages (before canopy closure) is considered crucial for higher grain yields. Greater early vigour leads to faster leaf area development, reduces soil water loss via soil evaporation, increases competition with weeds (López-Castañeda et al., 1995), and improves nutrient uptake (Liao et al., 2004; Ryan et al., 2015). Consequently, it has been shown that genotypes with higher early vigour produced higher biomass and grain yield (Whan et al., 1991; Turner and Nicolas, 1998; Rebetzke and Richards, 1999; Botwright et al., 2002). However, greater early growth and water use may also reduce available soil water later in the season to worsen terminal drought, leading to reduced yields. Whether early vigour leads...
to increased or decreased yield will depend on local climate conditions. Despite the promise of benefits through greater vigour (e.g. Botwright et al., 2002), there is a lack of systematic quantification of the impact of early vigour across a range of climate conditions.

Numerous morphological factors of moderate-to-high heritability contribute to increased early vigour in wheat (Richards, 2000; Rebetzke et al., 2008). Phenotypic differences in early vigour in wheat have largely been associated with variation in grain or embryo size, rate of seedling emergence, leaf dimensions (leaf width and leaf length) and specific leaf area (SLA) of seedling leaves, coleoptile length (for improved crop establishment), as well as coleoptile tiller production (López-Castañeda et al., 1996; Richards and Lukacs, 2002). Despite moderate heritability, all are influenced by strong environmental covariates through the maternal parent (e.g. Rebetzke et al., 2008) and potentially large genotype×environment (G×E) interactions. Besides this, the global deployment of gibberellin (GA)-insensitive dwarfing genes has been implicated in reductions in early vigour in modern cultivars (Calderini et al., 1996; Ellis et al., 2004; Ellis et al., 2007). These genes not only reduce plant height but also decrease cell size to reduce leaf size during early growth (Botwright et al., 2005).

Agronomic improvement on early vigour is mainly through selection of larger seed size targeting bigger embryos and larger leaves (a wider and longer leaf) and longer coleoptiles. Research efforts have also focused on better understanding of the genetic basis of these phenotypic differences in early vigour and their interactions with the environment, with targeted breeding for more genetic improvement in cereal improvement programmes in Australia. The screening for increased vigour mainly includes the selection of larger embryo and greater specific leaf area progeny to increase the width of seeding leaves (Richards and Lukacs, 2002; Zhang et al., 2015), selection of longer and larger coleoptiles (Rebetzke et al., 2008), and using alternative GA-sensitive dwarfing genes (e.g. Rht8) to reduce plant height while avoiding the reduction effect from GA-insensitive genes on the coleoptile length (Richards, 1992; Botwright et al., 2001; Rebetzke et al., 2004b, 2007, 2012a,b).

Early vigour is a genetically complex trait (Moore and Rebetzke, 2015). Despite significant breeding efforts on genetic improvement of early vigour targeting increased water use efficiencies and yield, results from field experiments have been highly variable from site to site and from growing season to growing season (e.g. Botwright et al., 2002; Richards et al., 2002). Experimental approaches aimed at interpreting the genotype-by-environment-by-management (G×E×M) interactions are costly and time-consuming due to the need in capturing the potential impact of long-term climate (Asseng and Turner, 2007; He et al., 2017). Opportunities exist to investigate the effect of early vigour through process-based crop modelling that integrates crop physiology, climate, and soil process interactions and their impact on crop growth and yield. Such modelling approaches allow a quick assessment of the consequences of early vigour across different climate, soil, and management conditions.

In this paper, we present a modelling framework for simulating the potential impact of early vigour on wheat growth and yield. We integrate this modelling approach into the Agricultural Production Systems sIMulator (APSIM) next generation Plant Modelling Framework (Brown et al., 2014) and parameterize the model using published data from literature. We then use the parameterized model together with historic climate data to simulate and quantify the contribution of improved early vigour on grain yield across seasons for representative climates (rainfall) in Australia.

Materials and methods

Quantification of traits and genes related to early vigour of wheat

Early vigour is characterized by rapid early growth of wheat, reflected in enhanced emergence capability and larger size of the first leaves (Richards and Lukacs, 2002; Rebetzke et al., 2008). The former may lead to earlier emergence or an ability to emerge with deep sowing. Higher early vigour was associated with larger embryo size that was closely related to seed size or seed weight (Richards and Lukacs, 2002; Rebetzke et al., 2008), and greater SLA (Rebetzke et al., 2004a). Larger seed may also increase coleoptile length (to improve crop establishment) and the likelihood of producing coleoptile tillers. However, some of the reducing height (Rht) genes are known to reduce the early vigour of wheat.

Size of embryo and first leaves

The area of embryo and the size (length and width) of the first two leaves were found to be linearly related to seed weight (Fig. 1A, C; Botwright et al., 2002; Richards and Lukacs, 2002):

\[
\text{Embryo size (mm}^2\text{)} = 0.03 \times \text{Seed weight (mg)} + 0.8 \quad (r^2 = 0.57) \quad (1)
\]

\[
\text{Leaf 1 Length (mm) = 0.28 \times Seed weight (mg)} + 62.7 \quad (r^2 = 0.90, \quad P < 0.05) \quad (2)
\]

\[
\text{Leaf 1 Width (mm) = 0.035 \times Seed weight (mg)} + 2.54 \quad (r^2 = 0.98, \quad P < 0.01) \quad (3)
\]

\[
\text{Leaf 2 Length (mm) = 0.55 \times Seed weight (mg)} + 112.3 \quad (r^2 = 0.93, \quad P < 0.01) \quad (4)
\]

\[
\text{Leaf 2 Width (mm) = 0.035 \times Seed weight (mg)} + 3.01 \quad (r^2 = 0.98, \quad P < 0.01) \quad (5)
\]

In addition, genetic variations in the size of first leaves (e.g. SLA) exist among germplasms showing different early vigour independent of seed size (Zhang et al., 2015), with some high vigour ones having first leaf sizes twice as big (observation by G. J. Rebetzke).

Time to emergence

Larger seed size has also been shown to be associated with faster emergence in wheat (Richards and Lukacs, 2002; Rebetzke et al., 2008). There are only limited data available, and based on these data a significant linear relationship was found between seed weight/size and time to emergence (Fig. 1E; Richards and Lukacs, 2002):

\[
\text{Time to emergence (d)} = -0.028 \times \text{Seed weight (mg)} + 6.45 \quad (r^2 = 0.91, \quad P < 0.05) \quad (6)
\]
Frequency of the coleoptile tiller

Increases in coleoptile tiller frequency and mass were correlated with larger embryo size and wider seedling leaves to increase seedling leaf area (Rebetzke et al., 2008). Emergence of the coleoptile tiller typically coincides with emergence of the second or third main stem leaf. The coleoptile tiller produces its own leaf area, which is positively correlated with total plant leaf area (Rebetzke et al., 2008). In wheat, lines selected for larger coleoptile tiller size produced 24–30% greater leaf area and dry weight than lines selected to produce small or no coleoptile tillers (Liang and Richards, 1994). Significant yet repeatable differences among generations for coleoptile tiller frequency and growth (numbers of leaves, leaf area, and biomass) reflected strong additive genetic control.

Impact of dwarfing genes

The GA-sensitive dwarfing genes such as Rht8 were found to have no influence on leaf dimensions. However, the widely used green revolution dwarfing genes Rht1 (syn. Rht-B1b) and Rht2 (syn. Rht-D1b), which are GA-insensitive are widely established to reduce the seedling vigour of wheat (Richards, 1992; Rebetzke et al., 2001) through reductions in cell size to reduce leaf dimensions (Keyes et al., 1989). Presence of the GA-insensitive dwarfing genes reduced leaf length by approximately 15% (Miralles et al., 1998) and leaf width by about the same (G. J. Rebetzke unpublished data). Based on this, a reduction factor on leaf length ($f_L(Rht_{1,2})$) and leaf width ($f_W(Rht_{1,2})$) can be used to quantify the reduction in leaf sizes in the presence of Rht1 and/or Rht2:

$$f_L(Rht_{1,2}) = \begin{cases} 1, & rht \\ 0.85, & Rht1 \text{ or } Rht2 \\ 0.80, & Rht1 + Rht2 \\ 1, & Rht8 \text{ or } Rht13 \end{cases}$$  \hspace{1cm} (7)

$$f_W(Rht_{1,2}) = 0.8 \sim 0.9$$  \hspace{1cm} (8)
The above equation implies that existence of *Rht1* and/or *Rht2* genes will lead to 10–20% reduction in potential leaf sizes.

The GA-insensitive dwarfing genes also result in shorter coleoptiles (*Whan, 1976a*) that may lead to poor emergence (*Whan, 1976b; Bush and Evans, 1988*), particularly with deep-sowing (>30 mm sowing depth) (*Rebetzke et al., 2004b*). Wheat containing the *Rht1* or *Rht2* GA-insensitive dwarfing genes produced significantly (P<0.01) shorter coleoptiles than both *Rht8* GA-sensitive gene and tall (rht) wheat (*Rebetzke et al., 2004b*). It was found that coleoptile length was reduced ca. 1.1–1.3 mm for each 1 cm reduction in plant height with selection of *Rht1* and/or *Rht2* (*Rebetzke et al., 2012b*). The presence of these dwarfing genes and their impact on coleoptile length can be quantified using a reduction factor on coleoptile length (*fc*): 

\[
fc(Rht) = \begin{cases} 
1, & \text{rht} \\
0.75, & \text{Rht1 or Rht2} \\
0.5, & \text{Rht1 + Rht2} \\
1, & \text{Rht8} \\
1, & \text{Rht13} 
\end{cases} 
\]

### Specific leaf area

Greater seedling leaf area, is partly associated with a larger SLA (the fresh leaf area divided by its dry mass; mm² leaf g⁻¹ DM; *Rebetzke et al., 2004a*). Although SLA is strongly influenced by environmental conditions (*Rebetzke et al., 2004a*), strong genetic associations between width of first leaf and SLA indicates the potential for indirect selection of high SLA through selection of wider leaves (*Rebetzke et al., 2004a*). Australian wheat cultivars also ranked low for SLA in various field studies (*Rebetzke et al., 2004a*).

Other maternal seed factors including seed mineral content can influence early vigour in wheat and may complicate any breeding program. For example, phosphorus content of the seed is related to seedling growth (*Marco and De Marco, 1990*).

### The APSIM next generation wheat model

We used the APSIM next generation crop simulation model to explore the potential impact of early vigour on wheat yield across different climatic regions in Australia. A brief description of the wheat model in the APSIM next generation is given here and how the impact of early vigour was captured in the model is described in the next section. APSIM next generation uses the Plant Modelling Framework (*Brown et al., 2014*) to simulate growth and yield of wheat, which is a further development of the APSIM modelling framework (*Holzworth et al., 2014*) and the crop models developed based on the earlier concept of 'generic crop template' (*Wang et al., 2002*). A detailed description of APSIM next generation can be found at the website [http://www.apsim.info](http://www.apsim.info).

APSIM next generation simulates wheat development, growth (as biomass), and grain yield in response to inputs of temperature, radiation, soil water, and nitrogen conditions with a daily time step. Wheat phenology is simulated as development progress from sowing to harvest ripe, with 10 sequential phases: (i) germinating, (ii) emerging, (iii) vegetative, (iv) early reproductive, (v) stem elongation, (vi) grain development, (vii) grain filling, (viii) maturing, (ix) ripening, and (x) ready for harvesting. After sowing, germination is only affected by soil water content and commences when the seed imbibles water from the soil. Phenological development of wheat from emergence towards terminal spikelet is determined by requirement of vernalization and sensitivity to photoperiod of the cultivar, which also determines the final leaf number. The duration from terminal spikelet to flag leaf is directly linked to leaf phyllochron and the number of leaves left to emerge at terminal spikelet. The duration from flag leaf to anthesis is thermal time driven, but also responds to photoperiod (*Brown et al., 2013*). Phenological development from flowering to maturity is driven by accumulation of thermal time.

Crop growth (as biomass) is simulated using stage-dependent radiation use efficiency (RUJE) together with intercepted radiation in the released version of APSIM next generation. Here we replaced the RUJE approach with a canopy photosynthesis model combined with the simulation of maintenance and growth respiration approaches as parameterized by *Wang and Engel (2000, 2002)* to calculate daily biomass growth. Impact of temperature on photosynthesis and maintenance respiration was simulated using the recently derived relationships of *Wang et al. (2017)*. Leaf area development and biomass growth are also modified by stresses of water and nitrogen if the water and/or nitrogen supply is not sufficient to meet the crop demand, with leaf area growth having a higher sensitivity to stresses. The response to stresses is process-dependent, not stage-dependent.

The length of the emergence phase, i.e. the thermal time requirement (*T*<sub>emerg</sub>), is composed of an initial lag period (*T*<sub>lag</sub>) of fixed thermal time (40 °C d), and a phase dependent on sowing depth (*D*<sub>seed</sub>) and the rate of seedling shoot elongation towards the soil surface (*r<sub>s</sub> = 1.5 °C d⁻¹ mm⁻¹) (Eq. 10). For example, at a sowing depth of 30 mm, seedling emergence occurs 85 °C d after germination (40 + 1.5×30):

\[
T_{\text{emerg}} = T_{\text{lag}} + r_s D_{\text{seed}}
\]

APOSIM next generation simulates the development of wheat leaves and tillers using a cohort approach based on the coordination of leaf and tiller appearance on main stem and tillers (*Brown et al., 2014*). Leaves and tillers that appear at the same time belong to the same leaf or tiller cohort and grow following the same pattern. The maximum area of each individual leaf is dependent on the leaf position/rank, and is defined using two parameters: the maximum leaf area for all leaves (with default value 2600 mm² per leaf) and a stage-dependent age factor. It is assumed that the maximum area of each individual leaf increases linearly with leaf rank from emergence to terminal spikelet, and all leaves appearing after terminal spikelet have the same maximum leaf area (Fig. 2A). Potential leaf area growth is calculated based on leaf appearance rate and the potential size of individual leaves, while the actual leaf area growth rate is the potential rate reduced by any water and nitrogen constraints (for cell division and elongation), and further limited by available assimilate partitioned to leaves as constrained by changes between maximum and minimum specific leaf area (*SLA<sub>max</sub>, SLA<sub>min</sub>*) and are maintained constant thereafter.

Maximum leaf size for each cohort is set with appearance of the leaf tip and a relative leaf size parameter (the age factor) is calculated as a function of development stage. The age factor increases from 0.1 at stage 3.0 (emergence) to 0.5 at stage 3.45 (when crop has progressed 45% of the way to terminal spikelet) and 1 at and beyond stage 4.0 (terminal spikelet) (*Brown et al., 2018*). Thus, the two to three leaves that emerge after terminal spikelet may all reach the maximum size. If the genotype develops quickly it will go from stage 3 to stage 3.45 quickly, at which time leaf size will increase linearly (e.g. in the case of spring wheat). If it is a slower developing crop, it will go from stage 3 to stage 3.45 slowly, and more leaf cohorts will be produced in this phase, resulting in a slower increase in leaf size (e.g. in the case of winter wheat).

Tillering (branching) is simulated with leaf number and a potential rate following the pattern of a Fibonacci series between emergence and terminal spikelet (Fig. 2B, orange line). The actual tillering rate is the potential rate of tillering reduced by water and nitrogen stresses, and further constrained by carbon assimilate supply. Tillering stops at terminal spikelet and tiller death occurs thereafter. Later appearing tillers with slower growth rate and the smallest tillers will die first, with the final tiller number (stem population) determined at the time of anthesis. At the terminal spikelet, all tillers with less than four leaves stopped growing new leaves.

### Modelling impact of early vigour in APSIM next generation

Modelling the impact of early vigour on wheat growth and yield was captured by integrating the relationships and data described in the section ‘Quantification of traits and genes related to early vigour of wheat’ in...
APSIM next generation. We used seed weight/size and existence of Rht genes, together with genetic variations in leaf size to simulate differences in vigour and their subsequent effects on growth and yield. The modifications include: (i) the rate of seedling emergence, (ii) the leaf size profile, (iii) the likelihood of coleoptile tiller, and (iv) the potential impact of Rht dwarfing genes on coleoptile length and leaf size (Figs 2, 3).

**Rate of emergence**
A threshold seed weight of 40 mg (which was typically used in the field) was chosen to standardize the relationships described in the section ‘Quantification of traits and genes related to early vigour of wheat’. The rate of shoot elongation towards soil surface was linked to seed weight with the relationship derived based Eq. (6) as shown in Fig. 1F. This will mean that increased seed size will lead to slightly early emergence time (Fig. 1F).

**Presence of coleoptile tiller**
Coleoptile tiller presence was simulated using a probability approach (Eq. 11). It was assumed that no coleoptile tiller would be present when the seed weight was less than the threshold weight (i.e. 40 mg in this study). If seed weight is larger than the threshold weight, coleoptile tiller can be produced with 30% probability:

\[
\text{Probility}_{\text{Coleoptile tiller}} = \begin{cases} 
0, & \text{if seed weight} \leq 40 \text{ mg} \\
0.3, & \text{if seed weight} > 40 \text{ mg}
\end{cases} \tag{11}
\]

The total number of coleoptile tillers was calculated using the above equation together with the total plant population (plants m\(^{-2}\)). Once a coleoptile tiller is formed, leaves and tillers develop on it following the coordination of leaf and tiller appearance between the main stem and tillers (Fig. 2B). Leaves on coleoptile tillers have the same size as the main stem leaves appearing in the same cohort. Presence of coleoptile tillers will therefore lead to increased stem population and leaf numbers, and thereby potentially greater leaf area development.

For a plant population of >100 plants m\(^{-2}\), the total number of coleoptile tillers should be close to 30% of the plant population:

\[
\text{Total coleoptile tiller no.} = \frac{\Sigma_{\text{PP}} \text{Coleoptile tiller}}{\text{Plant population}} = 0.3
\tag{12}
\]

where PP is plant population.

**Fig. 2.** Maximum leaf area of individual leaves in response to development stage (A) and new tiller numbers per plant with and without coleoptile tiller (B).

**Fig. 3.** Schematic representation of the linkage between main morphological traits and genetic background related to early vigour and how they are simulated.
Maximum leaf size and its profile with leaf rank
Assuming improvement on early vigour only affects the maximum leaf area for all leaves and did not change the age factor. For a wheat leaf, its area ($L_A$) can be calculated using length and the maximum width of the leaf:

$$L_A = \alpha L_l \times f_l (Rht, 2) \times L_w \times f_w (Rht, 2)$$  (13)

Where $L_l$ is the maximum leaf length, $L_A$ is the maximum leaf width, and $\alpha$ is a coefficient with a typical value of 0.8 (Rebetzke and Richards, 1999). The two factors $f_l(Rht,2)$ and $f_w(Rht,2)$ account for the reduction in leaf length and width due to the existence of the $Rht1$ or $Rht2$ dwarfing genes (Eqs 7, 8).

Initial leaf area at emergence
An initial leaf area per plant is needed to start the APSIM simulation. The current default value of initial leaf area per plant is 200 mm$^2$ (Zheng et al., 2015). Assuming emergence is defined as occurring at the same length of first leaf appearance, seedlings with greater early vigour will lead to increased leaf width (Eq. 3). The increase in leaf width was then applied to the initial leaf area per plant assuming that the increase in leaf area is the same as the increase in leaf width.

Leaf phyllochron
The phyllochron may also be affected by the length of leaves (Rebetzke and Richards, 1999) as longer leaves tend to take longer to emerge. This would imply that changes in early leaf sizes as a result of seed size variation or genetic variations would affect phyllochron. However, other studies found no difference in phyllochron between isogenic lines with Rht (Youssefian et al., 1992; Caldera et al., 1996). Due to these inconsistencies, we did not include the impact of early vigour on phyllochron in this study.

The SLA was not modified due to the high variance associated with environment (Rebetzke et al., 2004a). Coleoptile length was assumed to be unaffected by plant density for a normal sowing depth (i.e. less than 50 mm soil depth).

Impact of early vigour
We used 30 mg seed as the baseline to simulate the impact of increased early vigour due to the following.

(i) Increase in seed size from 30 mg to 40 mg. Compared with the baseline of 30 mg seed, 40 mg seed weight will increase the leaf area of the first leaf by ca 14% (Fig. 2A).
(ii) Doubling the sizes of leaves from (i). We assume that the increase in leaf area can be potentially doubled and independent of seed size (e.g. for the same seed size of 40 mg). The increase in the first leaf area was applied to the maximum leaf area assuming that the increase in maximum leaf area is the same as the increase in the first leaf area (Fig. 2A).
(iii) Impact of $Rht$ genes. This aims to explore what would have happened if the widely used green revolution dwarfing genes $Rht1$ and $Rht2$ were introduced, but would not have reduced leaf sizes and phyllochron (Fig. 2A). The impact would be equivalent to that if $Rht8$-type genes had been introduced, instead of $Rht1$ and $Rht2$.

**Results**

**Model performance**

Testing of the newly configure model indicated that the model was able to capture the changes in the dynamics of LAI and biomass as well as the final grain yield in response to variations in early leaf area (Fig. 5). Simulated LAI, biomass and grain yield of the three lines well matched the observed values, mostly within 1 standard deviation of the measurement data.

**Impact on wheat phenology, LAI and early biomass growth**

The effect of increased seed size (from 30 mg to 40 mg) on simulated phenology was small compared with the baseline wheat (data not shown). Wheat with 40 mg seed size emerged on average 0.2 d earlier. The slightly faster emergence did not have significant ($P>0.05$) impact on simulated flowering and maturity time.
At the time of terminal spikelet stage, the simulated LAI for wheat with 40 mg size was on average 20–24% higher ($P<0.001$) across the eight sites, compared with the baseline wheat (Fig. 6A). Doubling the sizes of early leaves (based on 40 mg seed size) resulted in 100–137% more LAI compared with baseline. This translated to on average 25–29% more biomass due to increased seed size, and 106–141% more biomass due to doubled leaf sizes (Fig. 6B). At flowering stage, the simulated biomass was on average 10–14% higher for wheat with 40 mg seed size, and 31–42% higher for wheat with doubled leaf sizes, compared with baseline (Fig. 6C).
The increase in early leaf area and biomass growth with early vigour (Fig. 6) did not translate into a similar amount of increases in final biomass (Fig. 7A) and yield (Fig. 7B). The simulated increase in biomass at maturity was much less than the increase in early biomass.

For wheat with 40 mg seed size, compared with baseline wheat, final biomass was simulated to be 7–10% greater across sites (Fig. 7A), with an increase in grain yield by 7%, 5%, 6%, 1%, 3%, −6%, 1%, and 5% \((P>0.05)\) at Young, Temora, Ardlethan, Griffith, Yanco, Merredin, Emerald, and Narrabri, respectively (Fig. 7B). The larger seed size led to yield decline at Merredin.

However, wheat with doubled leaf sizes resulted in significant increase in final biomass and yield for most of the sites (Fig. 7A, B). Compared with the baseline wheat, simulated biomass at maturity increased by 21–31% across sites, with corresponding increase in grain yield by an average of 24%, 22%, 22%, 10%, 15%, −4%, 7%, and 16% at Young, Temora, Ardlethan, Griffith, Yanco, Merredin, Emerald, and Narrabri, respectively (Fig. 7B).

The simulation results revealed that the increased early biomass growth before anthesis contributed to increase in grain number (Fig. 7C), while the impact of terminal drought in most years resulted in relatively smaller grain sizes for wheat with higher early vigour (Fig. 7D), as compared with baseline. The simulated increase in grain yield was mainly through an increase in grain number rather than grain size. The interannual variability of simulated above-ground biomass and grain yield were greater for more vigorous wheat, especially at wetter sites such as Young, Temora, and Narrabri, implying that inter-annual climate variability interacts strongly with the influence of early vigour on biomass and yield.

**Effects on total biomass and yield**

The average yield benefit from early vigour was strongly related to rainfall amount and seasonal rainfall distribution. On average, the benefit seemed to disappear at sites if the seasonal water supply (rainfall in the growing season plus initial plant available water in soil) was less than 300 mm (e.g. Griffith, Merredin, and Emerald) (Fig. 8). The higher outliers at the

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**Fig. 6.** Simulated ranges of leaf area index (LAI) (A), above-ground biomass at terminal spikelet stage (B), and above-ground biomass at flowering stage (C) at the eight study sites. The box plots show the 25, 50, and 75% percentiles, and the whisker caps indicate the 5th and 95th percentiles, with the average shown by a red circle. The black circles are the outliers.
Fig. 7. Simulated ranges (1957–2017) of aboveground biomass (A), grain yield (B), grain number (C), and grain size at maturity stage (D) at the eight study sites. For box plots details, see Fig. 6.

Fig. 8. Simulated ranges of yield change (1957–2017) caused by early vigour in wheat. The numbers below site names are in-season rainfall plus initial plant available water in soil. For box plots details, see Fig. 6.
low rainfall sites (Griffith and Merredin) were caused by either higher in-season rainfall or higher soil water at sowing time, or both in individual years.

For any given site, simulated yield change due to increase in either seed size or leaf sizes was positively correlated to seasonal rainfall plus the initial available soil water at sowing (Fig. 9). In general, no benefit of early vigour was simulated in years with less than 300 mm water supply (seasonal rainfall plus initial soil plant available water at sowing) (Fig. 9) or when yield of the baseline wheat was less than 2500 kg ha$^{-1}$ (Fig. 10).

**Likely impact of the green revolution dwarfing genes Rht1 and -2**

Based on our simulation results, if the green revolution dwarfing genes *Rht1* and -2 were introduced without the reduction effect on leaf size, more final biomass would have been produced. The final biomass would have been 8–15% higher, with yield change around 13%, 9%, 9%, 1%, 4%, −14%, 0%, and 6% at Young, Temora, Ardlethan, Griffith, Yanco, Merredin, Emerald, and Narrabri, respectively) (Fig. 11B). This effect

![Figure 9](image-url)  
*Fig. 9.* Simulated yield change in relation to seasonal rainfall plus initial plant available water content (PAWC) in soil at the eight study sites (1957 to 2017). Yield change is the difference in yield between early vigour wheat and baseline wheat.
should be similar to that if $Rht8$-type of genes were introduced, instead of $Rht1$ and $-2$.

**Discussion**

*Interactions of early vigour with environments*

This study combined crop modelling and current knowledge and data to assess impact of early vigour traits on final wheat yield across different climatic (rainfall) regions (sites). Our results clearly demonstrate that the contribution of early vigour to yield was strongly affected by environment (e.g. rainfall). Due to the complex physiological processes and their interactions during the whole growing period for yield formation, the average yield benefit from early vigour may not be promising when all seasons or sites are considered, but becomes significant in wetter seasons or sites. This was consistent with findings from a 2-year field experiment by Botwright *et al.* (2002) that translation of early vigour improvement through breeding programmes to higher yields was highly dependent.

![Simulated yield change (1957–2017) in relation to baseline wheat yield at the eight study sites. Yield change is the difference in yield between early vigour wheat and baseline wheat.](image)
on environment. On a typical soil with PAWC of 147 mm, at wetter sites and in wetter years (seasonal rainfall plus initial soil water storage >300 mm), early vigour traits were simulated to result in up to 4% (via larger seed) to 16% (via lines with doubled early leaf size) yield benefit. However, in dry years, particularly at drier sites (seasonal rainfall plus initial soil water storage <300 mm), early vigour growth could lead to considerable yield reduction (Figs 9, 10), due to limited seasonal rainfall and more rapid depletion of soil water (Wilson et al., 2015), leading to more severe water stress during grain filling from earlier onset of terminal drought and consequently lower grain yield. For such dry regions, other traits such as high harvest index (Richards et al., 2002) may lead to higher yield than those early vigour related traits.

The work presented in this paper was our first step to assess impact of early vigour on wheat yield across different climate regions. In our simulations we used a soil with representative water holding capacity (PAWC=147 mm). Soils with significantly larger (or smaller) PAWC may hold more (or less) water from rainfall for plants to use, leading to subsequently higher (or lower) yields. This was confirmed by the simulation results with soils with a lower PAWC (95 mm) and a higher PAWC (216 mm) (Fig. 12). A full analysis with a range of PAWCs across all the sites will be addressed in a separate paper.
Agronomic improvement versus genetic improvement of early vigour

Our results show that agronomic improvement of early vigour through selection of larger seed size led to an average of 4% increase in yield. While the average increase seemed to be relatively small, the yield increase could be significant in wetter years and at wetter sites. A much larger yield increase of 16% was simulated with early vigour through selecting larger first leaves, with much greater yield increase in wetter years and sites. This implies that selection of genetically vigorous lines would offer much greater potential as compared with using larger seeds for yield increase.

Our results also show that if the green revolution dwarfing genes (Rht1 and –2) had not caused the reduction in leaf size, the modern semi-dwarf cultivars would have had a yield level slightly higher compared with the current yield level only at wet sites. This further justifies the use of GA-sensitive dwarfing genes to reduce plant height while avoiding the reducing effect from GA-insensitive genes on coleoptile length, leading to maintained vigour and increased yield.

There have been some inconsistencies in the results of previous studies with regard to early vigour impact on leaf phyllochron. While some found that phyllochron was positively related to leaf length (Rebetzke and Richards, 1999), others found no difference in phyllochron on wheat phenology and yield was small and could be negligible. Therefore, phyllochron was not modified in the current study.

Impact on grain number versus grain size

The quicker leaf area growth of early vigour wheat contributed to more rapid canopy development during the early growing stage (Fig. 6). The higher ground coverage reduced soil water loss via evaporation while enabling more plant water use via transpiration, leading to more efficient use (data not shown) and higher biomass production at early stages (Richards and Lukacs, 2002). This translated to greater biomass production at anthesis as well as at maturity (Figs 7, 11) to increase grain yield in years with less terminal drought. Because grain number is strongly correlated to the stem and/or spike dry weight at flowering (Slafer et al., 1990; González et al., 2005; Beche et al., 2014), greater aboveground biomass before or around anthesis of higher early vigour wheat significantly increased grain number per unit area as compared with baseline scenario. Our modelling results show that the contribution of early vigour to yield increase is largely through increased grain number rather than grain size, similar to contributions of other yield-increasing traits (Foulkes et al., 2009). In wetter years or sites, this increased number of grain will have better chance to be filled, leading to more yield benefits. However, in general, the genotypes with high early vigour would have smaller grains due to more grains being produced, which could be a grain quality factor to consider.

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Fig. 12. Impact of plant available water holding capacity (PAWC) on the average of simulated wheat yield (1957–2017) for the baseline wheat and vigorous wheat (doubled leaf sizes).
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