


*in silico* Plants

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Journal:	<i>In Silico Plants</i>
Manuscript ID	ISPLANTS-2023-021
Manuscript Type:	Original Research
Date Submitted by the Author:	09-Jun-2023
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Keywords:	tillering, sorghum, dynamics, model, adaptation, simulation

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**Modelling the dynamics and phenotypic consequences of tiller outgrowth and cessation in sorghum**

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Manuscript prepared for In Silico Plants

IDVII Special Issue - Modelling GxExM for drought adaptation and decision making in agriculture

**Abstract**

Tillering affects the development of canopy leaf area, thus influencing the dynamics of crop growth via the capture of light, water, and nutrients through the crop life cycle. Depending on the nature of the growing season, variation in tillering can result in increased or decreased yield outcomes. Reduced tillering has been associated with water-saving and enhanced yield in water-limited conditions. The objective of this study was to develop a generic phenomenological model that predicts the dynamics of tillering in sorghum throughout the crop life cycle and incorporates key genetic and environmental controls. The dynamic of tillering was defined in four key phases – pre-tillering, tiller emergence, cessation of tiller emergence, and cessation of tiller growth. Tillering did not commence until full expansion of leaf four and thereafter was synchronized with leaf appearance. The potential total number of tillers (TTN) was dependent on a genetic propensity to tiller and an index of assimilate availability dependent on the shoot source-sink balance, which aligned with known hormonal and sugar signaling controls. Cessation of tiller emergence could occur before TTN was reached if the canopy reached a critical size that was consistent with the known influence of neighboring plants through their effect on the red:far red ratio of light in the canopy. Cessation of growth of the emerged tillers was related to the extent of internal competition for assimilate among plant organs, employing potential specific leaf area (SLA) as an indicator of source-sink and plant sugar status. A tendency to increased SLA (i.e. more leaf area than could be sustained by available assimilate) invoked tiller growth cessation and resulted in the prediction of final fertile tiller number (FTN). The model predicted tillering dynamics well in a detailed controlled experiment with a range in plant density. Plausibility simulations of FTN conducted for a range of production environments and management conditions in the Australian sorghum belt reflected the general expectations of experienced agronomists. Hence, the study developed a robust and generic phenomenological model for tillering in sorghum incorporating key genetic and environmental controls. In addition to providing a means to predict the emergent fertile tiller number and explore GxMxE crop adaptation landscapes, the potential for its use in guiding molecular discovery, providing a generic template for the modelling of tillering across cereals, and linking to advanced methods for enhancing genetic gain in crops were considered.

## Introduction

Tillering in cereals has significant consequences on crop adaptation. It influences the development of canopy leaf area, which dictates crop growth and the dynamics of resource capture through the crop life cycle via the extent and timing of light interception, and demand for water and nutrient use. Hence, high tillering is advantageous to growth and yield in favourable environments as resource capture can be maximised, but the opposite occurs in adverse environments where resources, such as available water, can limit growth. In those situations, low tillering, with reduced canopy leaf area, and the associated metering out of available water to the post-anthesis phase of the crop cycle, can enhance crop yield (Hammer et al., 2014; Borrell et al., 2014). This trait-by-environment interaction confounds the role of tillering in cereal adaptation and breeding (Doust, 2007).

Tillers emerge from the outgrowth of axillary buds located in the leaf axil of each main culm phytomer (Schmidt and Theres, 2005), which is the repeated unit of main culm structure consisting of a leaf blade, leaf sheath, stem node, stem internode, and axillary tiller bud. Tillering is a common feature of many key cereal crops and varies in magnitude from the high-tillering species wheat, barley, rice, and millet (Kirby et al., 1985; van Oosterom and Acevedo, 1992; Zhong et al., 2002; Bidinger and Raju, 2000) to low-tillering species such as sorghum and maize (Kim et al., 2010; Rotili et al., 2021).

The outgrowth of tiller buds is regulated by a range of environmental and genetic factors. Kim et al. (2010a) showed that tiller appearance in sorghum was highly synchronized with main shoot leaf appearance. Further, a generalized index of internal plant competition for assimilate, which took account of plant assimilate supply and demand from the main culm (S/D index) during the critical period for tillering, explained most of the variation in maximum tiller number observed across their experiments for a specific genotype. The S/D index incorporated incident radiation and leaf size to index S during the period of tiller appearance, and potential leaf area growth of the main culm during that period to index D.

Studies on diverse sorghum genotypes demonstrated significant genetic variation in tillering (Alam et al., 2014a; Kim et al., 2010b). They showed that by considering variation in the assimilate S/D index to capture effects of surplus assimilate availability on tillering, the remaining genotypic differences in tillering could be explained by an independent propensity to tiller (PTT). Alam et al. (2014b) identified QTL for tillering from analysis of multiple sorghum populations that were associated with PTT and traits influencing S/D index, such as leaf size and leaf appearance rate. These factors (PTT and S/D index), which are capable of explaining phenotypic responses at

plant/crop scale (Alam et al., 2017), represent quantifications of hormonal effects and their interactions with sucrose availability operating at molecular scale (Dun et al., 2009a; Mason et al., 2014; Kebrom and Mullet, 2015; Bertheloot et al., 2019). Hence, the effects quantifying variation in tillering observed in sorghum align with the emerging understanding of gene networks and signalling controlling shoot branching (Barbier et al., 2019).

The total number of axillary buds that outgrow to form nascent tillers depends on the extent of inter-plant competition experienced (Lafarge et al., 2002). Lafarge et al. (2002) showed in sorghum that fewer axillary buds grew out to initiate potential tillers in higher density situations, which could be explained by the sensitivity of sorghum to neighbouring plants via variation in light quality. Ballare and Casal (2000) reported reduced branching as a consequence of a decrease in red light to far-red light ratio (R:FR) as would be experienced in situations of increased plant density. The low R:FR generated in these competitive situations is sensed by the phytochrome family of photoreceptors, including the major R:FR sensor phyB (Ballare et al, 1987). Signals perceived by phyB evoke a suite of adaptive responses, including reduced axillary bud growth, such as in clover (Casal et al., 1985) and Arabidopsis (Holalu and Finlayson, 2017).

Not all tillers continue to grow after bud outgrowth, with some ceasing to continue before becoming fertile and ultimately senescing (Lafarge et al., 2002; Larue et al., 2019). In sorghum, it is the ultimate fertile tiller number (FTN) that has greatest impact on canopy leaf area development (Hammer et al., 1993) as the initiated tillers that cease to grow out generally do so at an early stage in their development when their contribution to plant leaf area is minor (Lafarge et al., 2002). In the study on sorghum of Lafarge and Hammer (2002), at the higher density, in addition to fewer tillers initiating there was a more rapid rate of cessation of tiller outgrowth of the tillers that had initiated. This was consistent with findings in a detailed study of the dynamics of tiller production and continued growth in millet (van Oosterom et al., 2001b). These results are consistent with source-sink dynamics and assimilate balance in the plant, which can be related to the extent of internal plant competition via S/D index during tiller expansion, similar to that proposed for rice (Luquet et al., 2006) and as noted for initial tiller outgrowth at an earlier stage of development (Lafarge and Hammer, 2002; Larue et al., 2019).

Attempts to model the dynamics of tiller outgrowth and cessation in sorghum (Lafarge et al., 2002; Lafarge and Hammer, 2002; Larue et al., 2019) have suggested that approaches to quantifying source-sink dynamics and assimilate availability within a hierarchical framework of axes, from main culm to youngest tiller, perhaps offers the best prospects for prediction. This could incorporate environmental drivers and known avenues of genetic variation (Alam et al., 2017). However, the

ability to model tillering dynamics realistically across diverse environments and genotypes remains challenging given the difficulties of accurately capturing source-sink dynamics early in crop development. Much emphasis in molecular studies has been put on bud outgrowth and tiller emergence via hormonal drivers and their interactions with sucrose (Barbier et al., 2015; Fichtner et al., 2017), yet much of the variation in FTN at crop scale relates to cessation of initiated tillers (Lafarge and Hammer, 2002).

Here, we hypothesise that differences in tillering are generated by genetic, management, and environmental factors via effects on tiller outgrowth and tiller cessation. In addition to genetically regulated hormonal factors, this likely reflects differences in morphology and their consequences on source-sink dynamics via interactions with environmental conditions that determine assimilate availability surplus to the needs of the main culm and established tillers. The objective of this study is to develop a generic phenomenological model for sorghum that incorporates key genetic and environmental controls to predict dynamics of outgrowth and cessation of tillers throughout the crop life cycle.

### **Model Overview**

There are four key phases defining the dynamic of tillering through the life cycle in sorghum (Fig.1) and the model proposed quantifies each. Firstly, the pre-tillering phase occurring immediately after emergence is the period prior to any bud outgrowth when initial seedling growth and plant establishment is occurring. There are four leaf initials in the seed embryo in sorghum (Paulson, 1969) and the pre-tillering period extends until about the time of full expansion of the fourth leaf when the fifth leaf is expanding (Lafarge and Hammer, 2002). Secondly, tiller bud outgrowth commences at the end of the pre-tillering period with extent depending on both genetic and environmental factors (Kim et al., 2010 a,b; Alam et al., 2014a). As noted above, this could be quantified by PTT, likely associated with hormonal effects (Dun et al., 2009a; Bertheloot et al., 2019), in combination with genetic and environmental effects on source-sink balance and thus sucrose availability (Mason et al., 2014; Barbier et al., 2019) as quantified by the S/D ratio. The size of leaves on the main culm and their rate of appearance both influence the S/D ratio. Thirdly, tiller emergence ceases once sensing of neighbouring plants, via variation in light quality, dictates (Ballare and Casal, 2000). Lafarge et al. (2002) observed a common leaf area index of 0.65 across a wide range of plant density at the time of tiller emergence cessation in sorghum. This value reflects a situation where the canopy is still quite open and intercepting only approximately 20% of incident radiation (Hammer et al., 2010; George-Jaeggli et al., 2013). At the time of tiller emergence cessation, the total tiller number (TTN) that will occur is realised. Fourthly, after tiller emergence

cessation, some emerged tillers experience cessation of continued growth so that not all progress to reproductive development and flowering to become fertile tillers. It is the ultimate fertile tiller number (FTN) that has greatest impact on canopy leaf area development and hence, crop growth and yield (Hammer et al., 1993). The balance between capacity of an individual plant to maintain supply of assimilate to the increasing demand from leaf growth across the expanding leaves on the main culm and growing tillers provides an avenue to quantify the rate of tiller growth cessation (Lafarge and Hammer, 2002) using a source-sink S/D ratio context.

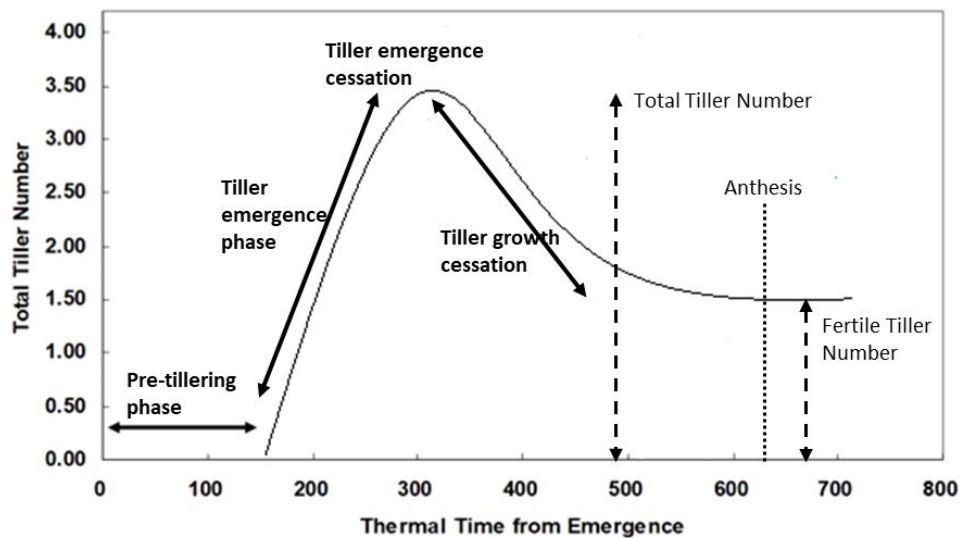


Figure 1. Exemplar schematic showing phases defining the dynamics of tillering through the life cycle of sorghum. Total tiller number is the number of tillers initiated by outgrowth of tiller buds, whereas fertile tiller number is the subset that continue to grow and develop, to ultimately flower and set grain (after Lafarge and Hammer, 2002).

### **Leaf size distribution on main stem and tillers**

To quantify plant leaf area, its potential increase, and the source-sink assimilate S/D ratio needed to model tillering dynamics, it is necessary to quantify the size (area) of individual leaves on the main stem and each tiller. Carberry et al. (1993) presented a robust empirical approach to model plant leaf area in tillering sorghum based on the leaf size distribution profile of individual leaves on each culm and their rate of appearance. The leaf size profile was estimated using a relationship between leaf number on an axis (numbered from the base) and the fully expanded leaf area of individual leaves using the equation (Dwyer and Stewart, 1986) –

184

$$Y = Y_o \exp[a(X-X_o)^2 + b(X-X_o)^3]$$

[1]

185 where Y is the mature leaf area of an individual leaf, X is the leaf number, Y<sub>o</sub> is the mature leaf area  
186 of the largest leaf, X<sub>o</sub> is the leaf number of the largest leaf, and a and b are empirical constants  
187 controlling the breadth and skewness, respectively, of the resultant bell-shaped leaf size profile  
188 curve. More negative values for ‘a’ result in a sharper peak of the profile. Negative values for ‘b’  
189 result in the profile being skewed towards earlier leaves and positive values result in the profile  
190 being skewed towards later leaves.

191 The parameters X<sub>o</sub>, Y<sub>o</sub>, a, and b have each been generalised via associations with TLN in sorghum  
192 (Carberry et al., 1993), maize (Keating and Wafula, 1992; Birch et al., 1998), and pearl millet (van  
193 Oosterom et al., 2001a). Although parameter values differed across these crops, in their  
194 comprehensive analysis van Oosterom et al. (2001a) observed that estimates for X<sub>o</sub>, a, and b based  
195 on associations with TLN had sufficient similarities to suggest that species differences in leaf area  
196 profiles were predominantly associated with differences in Y<sub>o</sub>. Hence, the general associations of X<sub>o</sub>,  
197 a, and b with TLN as reported by van Oosterom et al (2001a) were used here -

198

$$X_o = 3.58 + 0.60 \cdot \text{TLN}$$

[2]

199

$$a = 0.00955 + (0.0608 / (1 - 0.1293 \cdot \text{TLN}))$$

[3]

200

$$b = 0.00144 + (0.0025 / (1 - 0.1100 \cdot \text{TLN}))$$

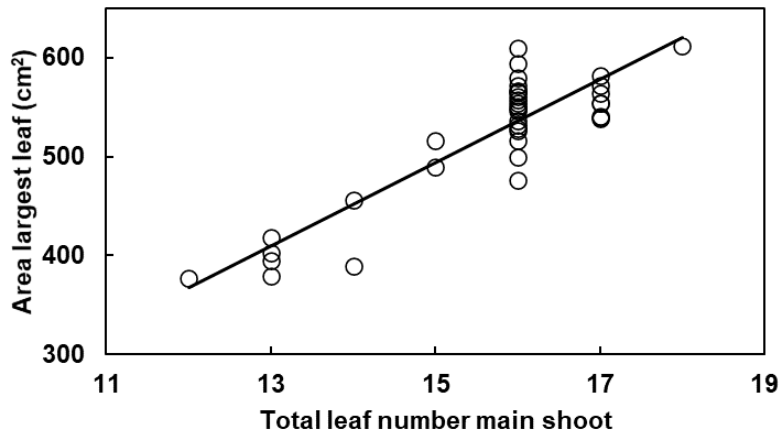
[4]

201 Leaf size profile data for the elite sorghum hybrid ‘Buster’ that covered a range in TLN from 12 to  
202 18 was collated from field and lysimetry experiments (Lafarge et al. 2002; van Oosterom et al.,  
203 2021). There was a linear association of Y<sub>o</sub> on the main culm with TLN over this range (Fig. 2) –

204

$$Y_o = -137.4 + 42.1 \cdot \text{TLN} \quad n = 38 \quad R^2 = 0.79$$

[5]



205 Figure 2. Association between the area of the largest leaf on the main culm (Y<sub>o</sub>, cm²) and total  
206 leaf number (TLN) on that culm for the elite sorghum hybrid ‘Buster’.



The leaf size profile equations ([1] – [5]) were fitted to the individual leaf size profile data on sorghum from the low density treatment of the detailed study on tillering of Lafarge et al. (2002). There was a good fit for the leaf size profile on the main culm and for the tillers (Fig. 3) for 16-leaf plants once adjustments were made for TLN and position and size of the largest leaf on each tiller. Previous studies for sorghum and pearl millet indicated that parameter values differed between main shoots and tillers (Carberry et al., 1993; van Oosterom et al., 2001a), but the possibility to derive tiller parameters from those of the main shoot has not been explored. Tillers were denoted by the MS leaf number from which they emerged – T1, T2, T3, T4, T5. TLN on each tiller was the TLN on the MS less the leaf number from which they emerged. While values for the coefficients  $a$  and  $b$  were determined from the consequent TLN of each tiller via equations [3] and [4], observed values for  $X_0$  and  $Y_0$  were related to main culm characteristics. For T1,  $X_0$  was two leaves sooner than for the main culm and for each subsequent tiller  $X_0$  was one leaf sooner. Relative to the main culm,  $Y_0$  was reduced by 23% for T1, 13% for T2, T3, and T4, and 39% for T5. For the fitted leaf size distributions using these relationships (Fig. 3),  $R^2$  values ranged from 0.99 (MS, T1) to 0.83 (T5). While there was an overall reasonable fit of leaf size profiles from this approach, there was some over estimation for early leaves on MS, T1 and T2, and some under estimation for late leaves on T4 and T5.

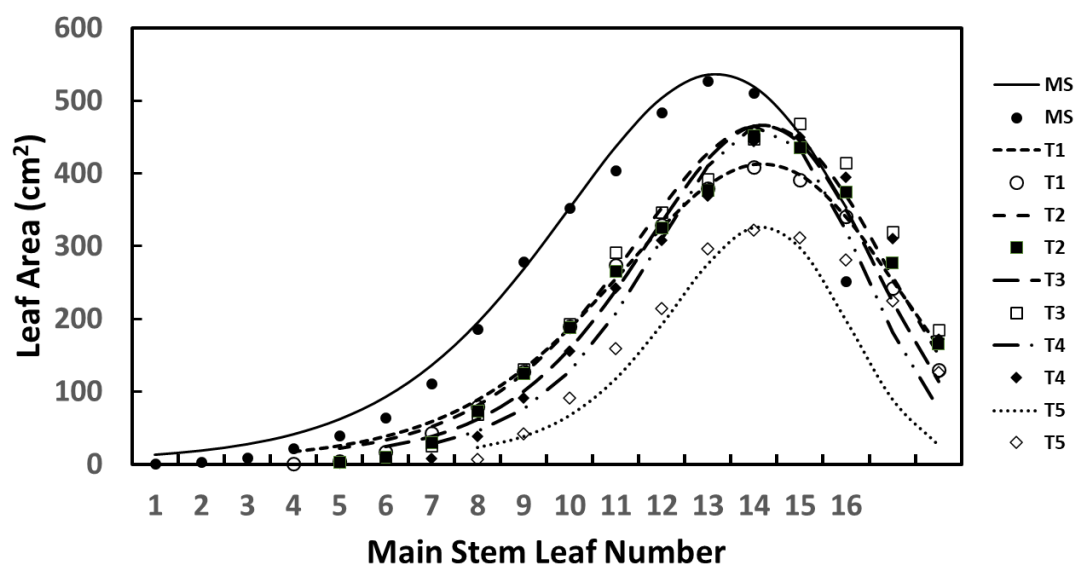


Figure 3. Average individual leaf area versus leaf position for leaves on the main shoot (MS, ●), tiller 1 (T1, ○), tiller 2 (T2, ■), tiller 3 (T3, □), tiller 4 (T4, ◆), and tiller 5 (T5, ◇) for 16-leaf plants of the sorghum hybrid 'Buster' in the low density treatments of the experiments of Lafarge et al. (2002). Lines represent fitted curves. Lines for each tiller are displaced so that leaf size of each tiller leaf is plotted against leaf number on the main culm at the time of full expansion of the tiller leaf. Hence, tillers proceed two phyllochrons beyond flag leaf full expansion on the main culm.

### Modelling the phases of tillering dynamics

To predict the ultimate fertile tiller number (FTN) per plant it is necessary to model passage through the four key phases defining the dynamic of tillering through the sorghum life cycle (Fig.1) -

*Pre-tillering and tiller emergence phases*

Over a range of experiments (Lafarge and Hammer, 2002; Kim et al., 2010a) for the elite sorghum hybrid 'Buster', no tillers emerged prior to about the full expansion of leaf four. The first tillers (if they occurred) emerged at around full expansion of leaf five and originated from the axillary buds of leaf two (so denoted T2) and leaf one (T1). If both T1 and T2 appeared they were simultaneous (Lafarge et al., 2002). Emergence of any subsequent tillers was synchronised with leaf appearance, with one newly emerged tiller for each additional fully expanded leaf.

Tillers produced the same number of leaves as the main culm less the leaf number from which they emerged. Hence, if the main culm produced 16 leaves, T3, which emerged from the axillary bud of leaf three at full expansion of leaf six, would produce 13 leaves, and so on. Given that tillers emerged with their first fully expanded leaf, each tiller reached full expansion of its flag leaf two phyllochrons after the main culm.

The total number of tillers that would emerge (TTN) was calculated at the time of full expansion of leaf five based on the propensity to tiller (PTT) and the plant assimilate supply/demand index (S/D), as found in the comprehensive study on tillering in sorghum across numerous genotypes and environments by Alam et al. (2014a) -

$$TTN = PTT + c \cdot S/D \quad [6]$$

where PTT is the intercept of the relationship between TTN and S/D and c is the slope. The S/D index employed was a slightly modified version of the index presented by Alam et al. (2014a). The index of plant assimilate supply, S, around the time of expansion of leaf 5 was determined as the product -

$$S = PTQ_{3-5} \cdot LA_5 \cdot \text{phyllochron}_5 \quad [7]$$

where  $PTQ_{3-5}$  is the average incident radiation per unit thermal time ( $\text{MJm}^{-2}\text{d}^{-1}(\text{°Cd})^{-1}$ ) for the period from full expansion of leaf three to full expansion of leaf five,  $LA_5$  is the size of leaf five ( $\text{cm}^2$ ), and  $\text{phyllochron}_5$  is the duration from full expansion of leaf four to that of leaf five ( $\text{°Cd}$ ).  $PTQ_{3-5}$  is an indicator of potential assimilation per unit crop development. The longer duration used for  $PTQ_{3-5}$  here avoided averaging this environmental quotient over a very short interval if only the period  $\text{phyllochron}_5$  was used as previously (Alam et al., 2014a).  $LA_5$  is an indicator of plant size and photosynthesising surface area, and  $\text{phyllochron}_5$  represents the time interval involved. D was determined as -

$$D = LA_9 - LA_5$$

[8]

which captures the difference in size between leaves nine and five on the main culm in a manner similar to, but simpler than, that proposed by Alam et al. (2014a). This difference indicates the rate of growth of the main culm.

There was a strong linear relationship between TTN and the slightly modified S/D index across genotypes and experiments (Fig. 4) as found in the original study (Alam et al., 2014a). By grouping genotypes it was possible to quantify relationships for high, medium, and low tillering types.

Lafarge et al. (2002) reported a common hierarchy of tiller emergence of  $T_3 > T_4 > T_2 > T_1 > T_5 > T_6$  across diverse density treatments. Hence, if  $TTN=2$  only  $T_3$  and  $T_4$  emerged, if  $TTN=4$  then  $T_2$  and  $T_1$  also emerged, and if  $TTN=6$  then  $T_5$  and  $T_6$  also emerged.

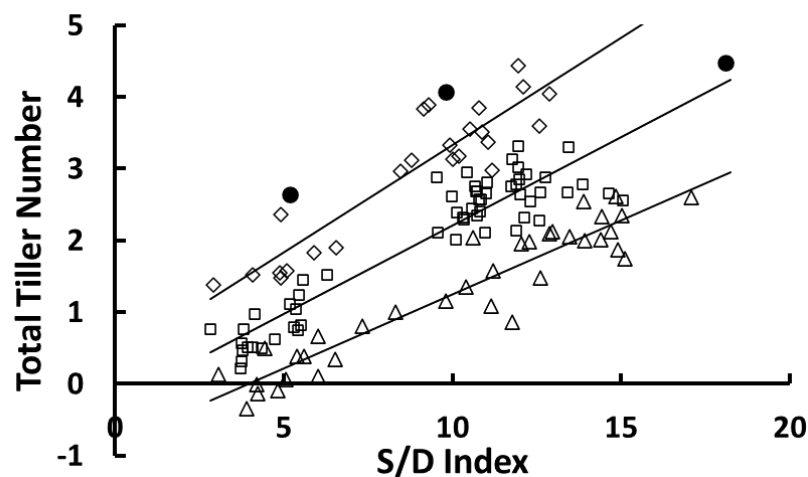


Figure 4. Total number of tillers emerged for individual genotypes grouped by those showing consistently high ( $\diamond$ ), medium ( $\square$ ), or low ( $\triangle$ ) tillering versus S/D index for data from experiments of Alam et al. (2014a). Data are Best Linear Unbiased Estimates (BLUEs) from each of three experiments. The sorghum hybrid 'Buster' ( $\bullet$ ) aligned best with the high tillering group.

Linear regressions:

High group:  $y = 0.30x + 0.33$   $R^2 = 0.85$

Medium group:  $y = 0.25x - 0.27$   $R^2 = 0.87$

Low group:  $y = 0.21x - 0.82$   $R^2 = 0.89$

*Cessation of tiller emergence*

At the time of tiller emergence cessation, the total tiller number (TTN) that will occur is realised. Lafarge et al. (2002) observed a common leaf area index of 0.65 across a wide range of plant density at the time of tiller emergence cessation in sorghum. Their experiment was conducted using 0.5m row spacing. Sorghum is commonly grown on wider row spacings (0.75 – 1.0m) and can be grown in even wider rows or skip-row configurations in more water-limited situations (Whish et al., 2005). Hence, the plant-plant spacing in the row is reduced for a given planting density, and this can have consequences on reducing tillering. To accommodate this configuration management effect, the concept of 'linear LAI' was introduced by calculating LAI from size of adjacent plants within a row. Given Lafarge et al. (2002) used 50cm row spacing, their critical LAI of 0.65 corresponds to a linear LAI of 0.325, which is invoked to model cessation of tiller emergence in this study. 'Linear LAI' calculated in this way is dependent on plant spacing within the row rather than plant density per unit area. For example, a crop grown on 1 m rows at a density of 8 plants  $\text{m}^{-2}$  will have a plant spacing of 12.5 cm in the row, and so will have the same 'linear LAI' as a crop grown at a density of 16 plants  $\text{m}^{-2}$  on 0.5 m rows. For a given genotype in these contrasting density situations, cessation of tiller emergence will be predicted to occur at the same time.

#### *Tiller growth cessation*

The ultimate fertile tiller number (FTN) produced is determined by the number of emerged tillers (TTN) that continue to develop and grow. Lafarge and Hammer (2002) found that the rate of decrease in potentially fertile tillers was related to the extent that the plant was able to achieve its potential leaf area growth if all remaining potentially fertile tillers were to continue to develop. This was consistent with the findings on the influence of extent of internal plant competition on rate of tiller cessation reported for millet (van Oosterom et al., 2001b). The potential leaf area growth per plant in an ensuing period can be calculated from the temperature experienced and the phyllochron, to determine the number of new leaves to potentially emerge, combined with the size of those leaves depending on their position on the axes involved (Fig. 3).

Whether the potential leaf area growth per plant could be realised was calculated from estimates of plant growth rate, allocation of assimilate to leaf and stem, and consequences on specific leaf area (SLA,  $\text{cm}^2\text{g}^{-1}$ ). Crop growth rate was determined from canopy radiation interception and radiation use efficiency using the algorithms in the sorghum model of Hammer et al. (2010). Plant growth rate was derived from crop growth rate by dividing by plant density. The proportion of assimilate allocated to leaf and stem is dependent on stage of development during the vegetative stage and was calculated using the relationship with total node number reported by

Hammer et al. (2010). The proportion allocated to leaf diminishes in a curvilinear fashion as node number increases.

Given estimates per plant of the potential leaf area growth and assimilate partitioned to leaf, the projected effect on canopy SLA can be generated from the model dynamics and used as an indicator of source-sink balance to determine if growth cessation of any tillers is required. An increasing SLA is indicative of the inability of assimilate supply to meet the demand for leaf area expansion. In essence, it is an indicator of plant sugar status that might be reflected in sugar signalling. The average canopy SLA ( $\text{cm}^2\text{g}^{-1}$ ) for a sorghum plant with a given leaf number (LN) was derived from data for three hybrids reported by Reeves (1971) –

$$\text{SLA} = \max \{150, \min \{400, 429.7 - 18.2 * \text{LN}\}\} \quad R^2 = 0.97 \quad n = 24 \quad [9]$$

Once plants have reached their projected TTN (equation [6]) and have at least seven fully expanded leaves, if SLA increased to within 15% of this canopy average, then tiller cessation was initiated at up to a maximum of 0.3 tillers per day to simulate the consequence of increased internal plant competition and restrict the rate of increase in canopy SLA. If these conditions were satisfied, tiller cessation was enabled up to the time of full expansion of the largest leaf on the main culm. After that time there is rapid stem expansion of active axes and progression to flowering. The common hierarchy of tiller emergence (Lafarge et al., 2002) was reversed to generate the order of tiller cessation. This approach reflects the finding of Larue et al. (2019) with a more detailed phytomer-based model (Luquet et al., 2006), that internal plant competition for assimilate and a tiller hierarchy provided the most effective means for predicting tiller cessation. Any continuing tendency to increase SLA after full expansion of the largest leaf results in reduced leaf size so that SLA does not exceed the canopy average by more than 10%.

### **Model Testing**

The dynamic of tiller number through the crop life cycle was predicted for each of the density treatments in the detailed experiments of Lafarge et al. (2002) (Fig. 5). In all cases there was an adequate prediction of the dynamics of tillering. The model predicted the effects of density on both total tiller number produced, the resultant fertile tiller number, and canopy LAI (Fig. 5). The appearance of tillers ceased earlier with increasing density, hence generating fewer tillers at higher density. Tiller cessation was also enhanced with increasing density, resulting in a decreasing number of fertile tillers as density increased. The slight but consistent over-estimate of LAI late in the vegetative phase suggests the need for a greater reduction of leaf size/leaf area growth associated with the limited assimilate supply per plant occurring at the higher densities at that time.

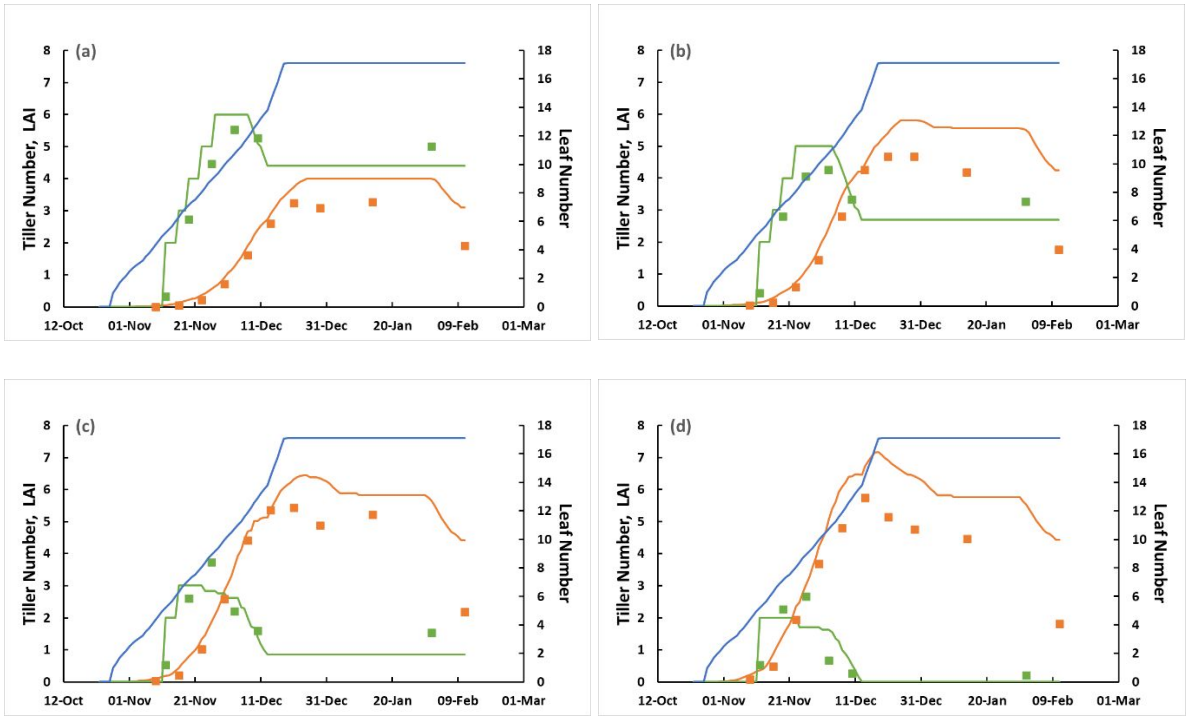


Figure 5. Simulated total and fertile tiller number (green), leaf number (blue), and leaf area index (LAI; orange) versus day of year for sorghum crops planted on 23 October at four levels of plant density: (a) 2 plants  $\text{m}^{-2}$ , (b) 4 plants  $\text{m}^{-2}$ , (c) 8 plants  $\text{m}^{-2}$ , and (d) 16 plants  $\text{m}^{-2}$ . Data (filled squares) from Lafarge et al. (2002).

Given that some of the model algorithms were derived from the results of the detailed experiments, the broad plausibility of model predictions was tested by conducting simulations of tillering across a range of environments in the Australian sorghum belt (seasons, sites and sowing dates), with a range of imposed management conditions (plant density and row configuration), and an assumed range of genetic propensity to tiller (PTT). The simulated results were contrasted with the expectations of local experienced agronomists (pers. comm.) that had been tabulated for use in APSIM v7.10 ([www.apsim.info](http://www.apsim.info)) to derive the value of FTN needed for input to the model in the absence of a dynamic tillering routine (Hammer et al., 2010). The range of sites simulated formed a north-south transect of the Australian sorghum belt - from Emerald (central Queensland (CQ)) in the sub-tropical north, to Dalby (southern Queensland (SQ)), to Tamworth (northern New South Wales (NNSW)) in the more temperate south (Fig. 6). Seasonal variability was captured by simulating years from 1960-2015 using historical weather data for the chosen sites. Soil characteristics (type, depth, water-holding capacity) at each location were as specified by Hammer et al (2014). A 75% full profile of soil water at sowing and N non-limiting conditions were assumed. Simulated monthly sowing dates ranged from spring (15 Sep) to summer (15 Jan) consistent with the known spread of sowing dates for the selected sites. All combinations of a broad range in plant density (2, 4, 8, 12 plants  $\text{m}^{-2}$ )

and row configuration (1.0m solid row spacing, 1.0m single skip row, 1.0m double skip row) were simulated for each sowing as was the range in genetic tillering propensity (Fig. 4) to quantify high, medium, and low tillering genotypes.

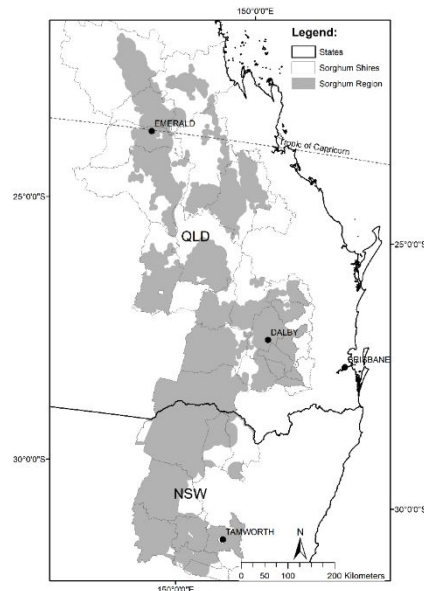
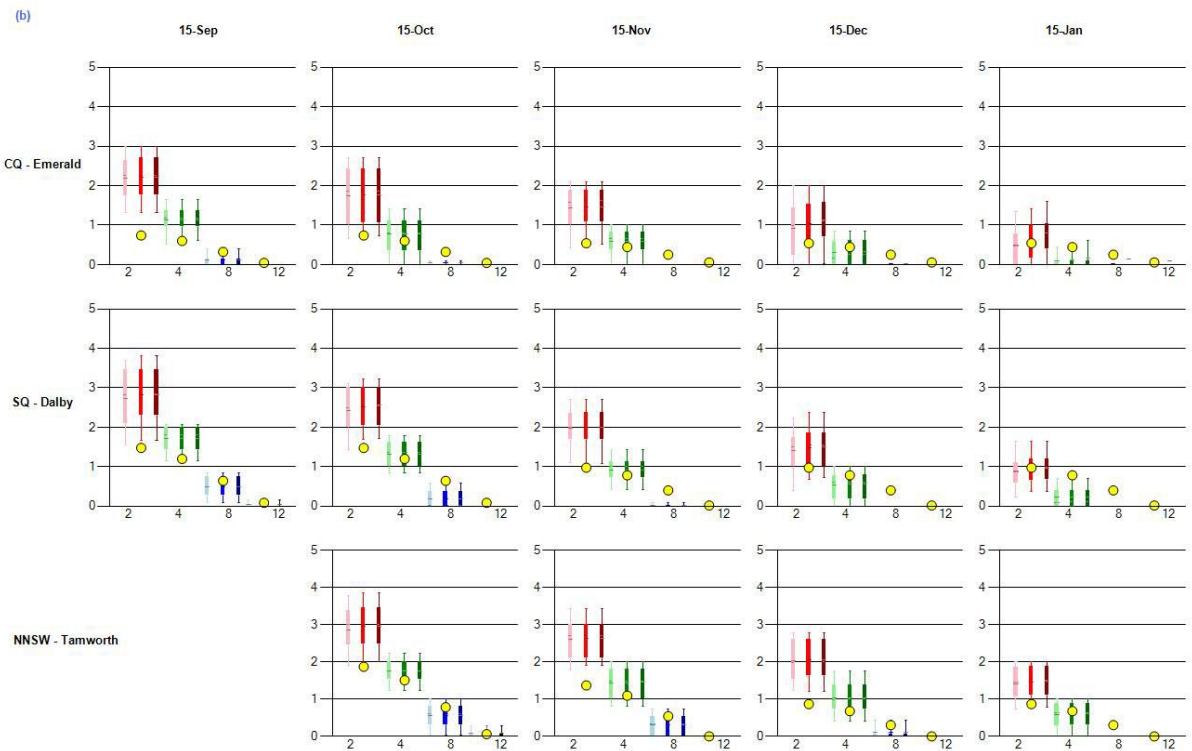
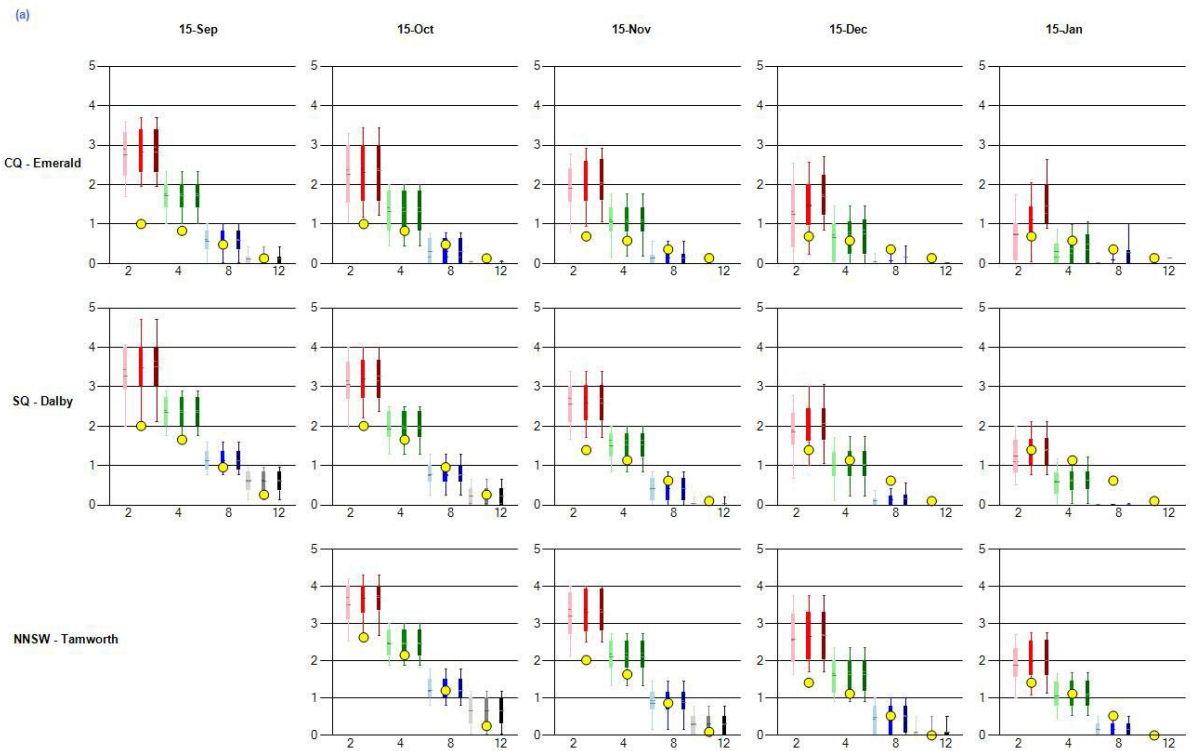


Figure 6. Sorghum growing areas in NE Australia showing location of key sites used for model plausibility testing (after Hammer et al., 2014).

The plausibility simulations quantified the expected effects of environment (site, season), management (density, row configuration), and genetics (propensity to tiller) on extent and likelihood of tillering across the sorghum production zone in Australia (Fig. 7). The simulated results reflected the expectations of local experienced agronomists, as used previously as input to APSIM, in relation to the site, season, and management effects. Tillering was enhanced with early sowing and in the more southerly locations, reflecting the influence of increased photothermal quotient (i.e., greater radiation per unit thermal time) and hence, increased S/D index generating greater tiller outgrowth (Fig. 4). Increased planting density diminished fertile tiller number in line with anticipated effects on cessation of tiller emergence and enhanced rates of tiller growth cessation. The model predicted more tillers at lower densities than anticipated by local agronomists, but such low density is rarely used in practice, so experience would be limited. There was only a small effect of genetic propensity to tiller, which suggested that effects on cessation of tiller emergence and tiller growth cessation dominated any effect on potential extent of tiller emergence. While tillering patterns were similar across management systems, the extent of tillering was reduced by single skip-row configuration and then further by double skip-row configuration, reflecting the reduced plant-plant spacing in the row at a given density and its effect on earlier cessation of tiller emergence. Skip-row systems were

394 a grower innovation to reduce tillering and canopy leaf area in this way as a means to manage crop  
395 water use (Whish et al., 2005).





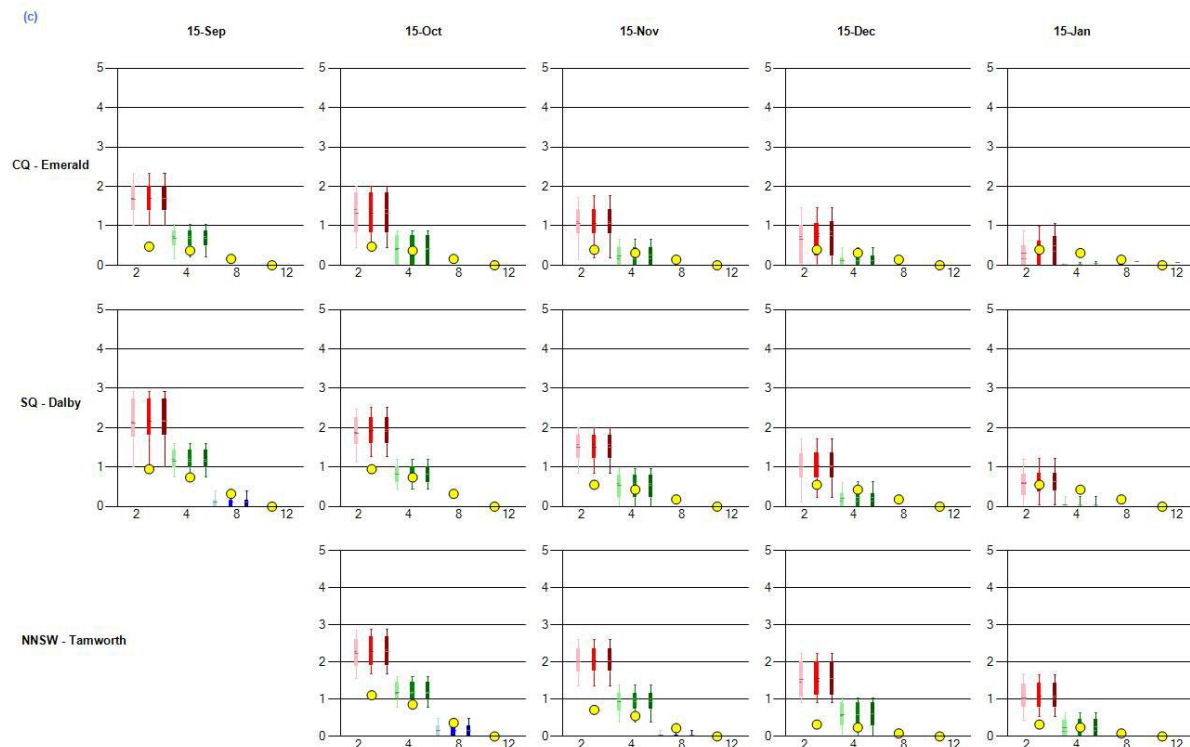


Figure 7. Simulated fertile tiller number versus plant density for a N-S transect of sites (Emerald (CQ), Dalby (SQ), Tamworth (NNSW)) across the Australian sorghum belt for a range of sowing dates, and genotype propensity to tiller for –

- (a) 1m row solid planting configuration,
- (b) 1m row single skip-row planting configuration, and
- (c) 1m row double skip-row planting configuration.

Shaded bars (left-to-right) show probability distributions of fertile tiller number for low, medium, and high tillering types based on simulation results over 55 seasons of historical weather (1960-2015). The solid bar indicates the central 50% of the distribution and the lines extend to the 10<sup>th</sup> and 90<sup>th</sup> percentiles. The median is indicated by a solid horizontal line. The yellow dots indicate expectations of experienced local agronomists (see text).



## Discussion

This study has developed a robust and generic phenomenological model for tillering in sorghum that incorporates key genetic and environmental controls to predict dynamics of outgrowth and cessation of tillers throughout the crop life cycle. In addition to providing a means to predict the emergent fertile tiller number for diverse GxExM situations, it provides an avenue for advance in several areas -

## 418 *Guiding molecular discovery*

419       The architecture of the dynamic tillering model developed exposes potential quantitative links  
420 to molecular mechanisms and underpinning genetic regulation. Differences in tillering were  
421 generated by genetic, management, and environmental factors via effects on tiller outgrowth and  
422 tiller cessation. In addition to genetically regulated hormonal factors controlling tiller emergence,  
423 which were captured by PTT, for tiller cessation this likely reflects differences in plant morphology  
424 and their consequences on source-sink dynamics via interactions with environmental conditions that  
425 determine assimilate availability surplus to the needs of the main culm and established tillers. While  
426 the hormone-assimilate availability interaction has been well studied for tiller/bud outgrowth  
427 (Mason et al., 2014; Barbier et al., 2015, 2019; Bertheloot et al., 2020), the results here suggest that  
428 in canopy situations, effects on tiller emergence cessation and tiller growth cessation may be  
429 equally, or more, important. However, the molecular basis of tiller emergence and growth cessation  
430 has not been subject to the same depth of study as bud outgrowth. Here, tiller emergence cessation  
431 was related to extent of inter-plant competition via canopy LAI (Lafarge et al., 2002), and the likely  
432 effect on light quality by a decrease in red light to far-red light ratio (R:FR) that is known to reduce  
433 branching (Ballare and Casal, 2000). The extent of genetic variation in this sensitivity of sorghum to  
434 neighbouring plants via variation in light quality is not known. The low R:FR generated in these  
435 competitive situations is sensed by the phytochrome family of photoreceptors, including the major  
436 R:FR sensor phyB (Ballare et al, 1987), so genetic variation is plausible.

437       Beyond tiller emergence cessation, given the ability in this study to predict the extent of tiller  
438 growth cessation from internal plant competition effects on surplus assimilate availability, sugar  
439 signalling effects on branch apical meristem activity, and potential for genetic variation in those  
440 effects, become a prime candidate for discovery research. This is reinforced by recent findings on  
441 the role of Tre6P, a regulatory sugar-phosphate that serves as a signal of plant sucrose status and is  
442 crucial for sucrose homeostasis, growth promotion, and developmental progression (Fichter and  
443 Lunn, 2021), along with studies that indicate sugar signalling modulation of shoot apical meristem  
444 (SAM) function (Lopes et al., 2023). However, how such signalling might generate the observed  
445 hierarchy of cessation of outgrowth of branch SAMs, and the basis of potential genetic variation,  
446 remains unclear. In this situation, exploratory in silico experimentation may assist understanding of  
447 the basis of phenotypic dynamics and generate testable hypotheses about molecular scale  
448 mechanisms in a manner similar to that demonstrated by Dun et al. (2009b).

449       The concept of internal plant competition for available assimilate and the moderation of the  
450 available surplus via source-sink balance considerations links tillering to the size of competing organs

and the prevailing environment. The studies of Kim et al. (2010b) and Alam et al. (2014 a, b) demonstrated the relevance of leaf size to genetic variation in tillering of sorghum through effects on source-sink balance that have been incorporated in the current model. However, other likely effects mediated by genetic differences in leaf appearance rate (van Oosterom et al., 2011), although incorporated, have not been studied. Other potential effects, such as those associated with differences in stem size, have not been captured in the current model and may account similarly for potential genotypic difference in FTN not related to PTT. Further, the central role of temperature in leaf expansion (Tardieu et al., 1999) and the potential for genetic variation in response of leaf expansion and appearance rates to temperature (Reymond et al., 2003; Tirfessa et al., 2023) also provides an avenue for indirect variation in tillering that is not accommodated in the current model. In this situation, it is also plausible that exploratory in silico experimentation would be useful to quantify putative effects on tillering of such genetic variation in a manner similar to that suggested by Wu (2023) and as demonstrated in the detailed study of Chenu et al. (2009). This provides another avenue to identify key trait targets for informing molecular discovery.

#### *Exploring crop adaptation (G\*M\*E) landscapes*

The capacity to predict the interactive dynamics of tillering with crop growth throughout the crop life cycle allows the possibility to simulate crop adaptation landscapes associated with variation in genetic and management factors across production environments. Previous studies that explored crop adaptation G\*M\*E landscapes in this way for current (Hammer et al., 2014) or future climates (Hammer et al., 2020) were limited by the need to consider tillering in a categorical manner. The potential now arises to incorporate trait-trait interactions with tillering in a dynamic way, enabling more credible simulation of trait combinations. For example, known effects of temperature and photoperiod on time to flowering (Hammer et al., 1989), leaf number (Ravi Kumar et al., 2009), and shoot growth (Crauford and Bidinger, 1988) will generate indirect effects on tillering via consequences on canopy development, emergent source-sink dynamics, and internal plant competition for assimilate.

The more robust modelling capability enables comprehensive simulation of QTL (and gene network) effects on tillering and their interactions with agronomic management and environment. There are numerous genomic regions known to influence tillering (Hart et al., 2001; Wang et al., 2020) and Alam et al. (2014 a,b) set out a preliminary framework to link these regions with component traits affecting hormonal or morphological factors controlling tillering. Further, there is an advancing capacity to model the dynamics of gene networks underpinning the hormonal control of branching (Dun et al., 2009a; Barbier et al., 2019; Bertheloot et al., 2020; Powell et al., 2022) so it

becomes feasible to connect this with the model for tillering advanced in this study to explore consequences of perturbations of the gene network at crop scale. Cooper et al. (2023) advance this “end-to-end” perspective to the development of  $G \times E \times M$  prediction methodology for sustainable crop improvement by discussing applications from the creation of new genotypes in breeding programs to their use in combination with agronomic management strategies within on-farm production systems.

#### *Generalising across cereals*

The dynamic tillering model developed for sorghum in this study provides a generic phenomenological framework for modelling tillering across cereal species. Its application to millet has already been progressed (Garin et al., 2023) and the biological functionality captured in modelling the key phases of tillering - tiller emergence, tiller emergence cessation, and tiller growth cessation (Fig. 1) – make it suitable for application by parameterisation for other cereals. By parameterising leaf and organ size it would be feasible to generate low tillering larger plant types (maize) and high tillering smaller plant types (rice). This may require consideration of differences in other interacting factors relevant to species differences, as demonstrated for radiation use efficiency in the comparative sorghum-maize study of van Oosterom et al. (2021). Application to other species in this way would underpin a simulation capability that could usefully extend experimental studies on tillering, such as in maize (Veenstra et al., 2021).

However, there are some limits to the generality of the tillering model developed in this study. Although the leaf size distribution functions fit well across maize, sorghum, and millet (van Oosterom et al (2001a)), their empirical nature limits their generality. Indeed, for sorghum in this study, the coefficients of the leaf size distribution function (i.e. ‘a’ and ‘b’) are stable only for TLN between 10 and 20, which explains the tendency towards a poorer fit for T5 in Fig. 3 as it approaches this boundary condition. It would be preferable to seek a more biologically robust and more broadly applicable method to predict leaf size according to leaf position, while retaining parsimony of the approach. Chenu et al. (2008) present a robust more detailed model for leaf size distribution in maize based on timing of individual leaf development and leaf length extension rate, which provides a template for this, but requires detailed data.

#### *Linking to advanced methods for genetic gain in crops*

Improved functionality in dynamic crop models opens possibilities for linking to advanced quantitative procedures, such as whole genome prediction (WGP), for enhancing genetic gain in crops (Cooper et al., 2021, 2023). In discussing the potential future of plant breeding and challenges

enabling prediction for breeding, Cooper et al. (2014) noted that crop growth and development models (CGM) structured to explicitly capture variation for the biophysical processes that determine yield and agronomic trait variation can be used to augment and extend the accuracy of genetic predictions for genotype performance. This requires sufficient resolution to produce predictions applicable to the large number of genotype and environment combinations necessary to support the plant-breeding advancement process (Messina et al., 2011; Cooper et al., 2014). The efficacy of this novel CGM-WGP approach has been demonstrated in initial studies on maize (Messina et al., 2018) and reinforced in more comprehensive recent studies (Diepenbrock et al., 2021).

The phenomenological model developed here for tillering in sorghum (code available in APSIM NextGen sorghum: [www.apsim.info](http://www.apsim.info)) provides the quantitative biological framework for connecting to gene networks associated with process control (Hammer et al., 2019). The emerging understanding and modelling of gene networks associated with regulation of tiller emergence through hormonal and sugar signalling (Beveridge, 2006; Dun et al., 2009a; Mason et al., 2014; Barbier et al., 2019; Bertheloot et al., 2020), tiller emergence cessation through interactive effects of R:FR light signalling (Casal et al., 1985; Dun et al., 2009a; Holalu and Finlayson, 2017), and tiller growth cessation through internal plant competition effects on sugars (Lopes et al., 2023) aligns with the models of genetic and environmental control of tillering reported from comprehensive field studies (Alam et al., 2014 a,b; Lafarge and Hammer, 2002) and the incorporation of morphological traits and environmental factors likely to affect plant sugar status. Hence, it is now possible to explore *in silico* the likely phenotypic consequences of perturbation of numerous interacting gene networks and the possibilities of the CGM-WGP approach for informing plant breeding in relation to tillering.

### **Acknowledgements**

The contributions of Graeme Hammer, Greg McLean and Erik van Oosterom were supported by the Australian Research Council Centre of Excellence for Plant Success in Nature and Agriculture (CE200100015). The contribution of Jana Kholova was supported by a grant of the Faculty of Economics and Management, Czech University of Life Sciences Prague, (grant no. 2023B0005; Oborově zaměřené datové modely pro podporu iniciativy Open Science a principů FAIR).

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