

Original Research

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

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Handling Editor: Stephen P. Long

Abstract. Tillering affects canopy leaf area, and hence crop growth via capture of light, water and nutrients. Depending on the season, variation in tillering can result in increased or decreased yield. 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 model of the dynamics of tillering in sorghum incorporating 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 commenced at 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. Cessation of tiller emergence could occur before TTN depending on extent of competition from neighbours. Subsequent cessation of growth of emerged tillers was related to the extent of internal competition for assimilate among plant organs, resulting in prediction of final fertile tiller number (FTN). The model predicted tillering dynamics well in an experiment with a range in plant density. Plausibility simulations of FTN conducted for diverse field conditions in the Australian sorghum belt reflected expectations. The model is able to predict FTN as an emergent property. Its utility to explore GxMxE crop adaptation landscapes, guide molecular discovery, provide a generic template for other cereals and link to advanced methods for enhancing genetic gain in crops were discussed.

KEYWORDS: Adaptation; dynamics; model; tillering; simulation; sorghum.

1. 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 maximized, 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 (Borrell *et al.* 2014; Hammer *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; Bidinger and Raju 2000; Zhong *et al.* 2002) to low-tillering species such as sorghum and maize (Kim *et al.* 2010b; 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 (MS) 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 (Kim et al. 2010b; Alam et al. 2014a). 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. 2020). 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 and Hammer 2002; Lafarge et al. 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 hypothesize 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.

2. 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. 2010a, 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. 2020), 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 plants respond to sensing neighbouring plants, a process dictated by variation in light quality (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 realized. Fourthly, after tiller emergence cessation, some emerged tillers experience cessation of continued

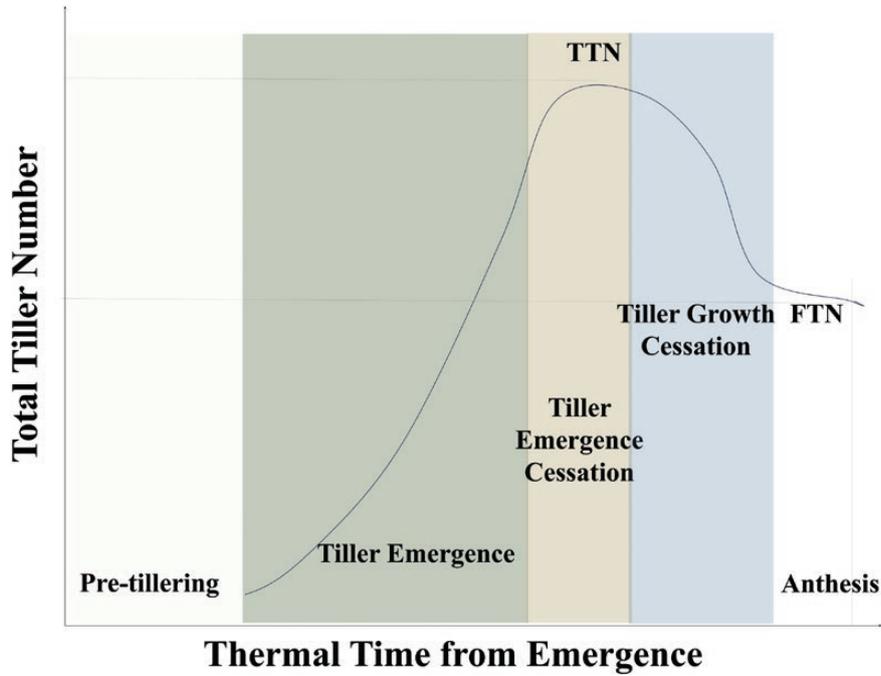


Figure 1. Exempler schematic showing phases defining the dynamics of tillering through the life cycle of sorghum. TTN is the number of tillers initiated by outgrowth of tiller buds, whereas FTN is the subset that continue to grow and develop, to ultimately flower and set grain (after Lafarge and Hammer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

growth so that not all progress to reproductive development and flowering to become fertile tillers. It is the ultimate 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.

3. 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 (LN) on an axis (numbered from the base) and the fully expanded leaf area of individual leaves using the equation (Dwyer and Stewart 1986)–

$$Y = Y_o \exp[a(X - X_o)^2 + b(X - X_o)^3] \quad (1)$$

where Y is the mature leaf area of an individual leaf, X is the leaf number, Y_o is the mature leaf area of the largest leaf, X_o is the leaf number of the largest leaf and a and b are empirical constants controlling the breadth and skewness, respectively, of the

resultant bell-shaped leaf size profile curve. More negative values for ‘ a ’ result in a sharper peak of the profile. Negative values for ‘ b ’ result in the profile being skewed towards earlier leaves and positive values result in the profile being skewed towards later leaves.

The parameters X_o , Y_o , a and b have each been generalized via associations with TLN in sorghum (Carberry *et al.* 1993), maize (Keating and Wafula 1992; Birch *et al.* 1998) and pearl millet (van Oosterom *et al.* 2001a). Although parameter values differed across these crops, in their comprehensive analysis van Oosterom *et al.* (2001a) observed that estimates for X_o , a and b based on associations with TLN had sufficient similarities to suggest that differences in leaf area profiles between sorghum and millet were predominantly associated with differences in Y_o . Hence, the general associations of X_o , a and b with TLN as reported by van Oosterom *et al.* (2001a) were used here –

$$X_o = 3.58 + 0.60 \times \text{TLN} \quad (2)$$

$$a = 0.00955 + \left(\frac{0.0608}{1 - 0.1293 \times \text{TLN}} \right) \quad (3)$$

$$b = 0.00144 + \left(\frac{0.0025}{1 - 0.1100 \times \text{TLN}} \right) \quad [4]$$

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

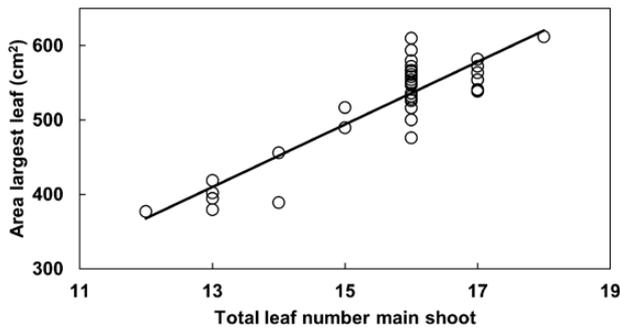


Figure 2. Association between the area of the largest leaf on the main culm (Y_0 , cm^2) and total leaf number (TLN) on that culm for the elite sorghum hybrid 'Buster'. Each data point is an individual plant.

$$Y_0 = -137.4 + 42.1 \times \text{TLN} \quad n = 38 \quad R^2 = 0.79 \quad (5)$$

The leaf size profile Equations (1–5) was 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 MSs and tillers (Carberry et al. 1993; van Oosterom et al. 2001a), but the possibility to derive tiller parameters from those of the MS 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 LN from which they emerged. While values for the distribution shape 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 so that tiller leaf size distributions had fewer initial small leaves than the MS. 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.

4. MODELLING THE PHASES OF TILLERING DYNAMICS

To predict the ultimate 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). This involves capturing the complex physiological network responsible for generating FTN and the interactions of genotypic and environmental factors on relevant aspects of plant growth and development, along with their influences on the key phases of tillering (Fig. 4). Initially, prediction of the potential leaf size distribution is required. This depends on prediction of TLN and the size of the largest leaf, which can vary among genotypes (G largest

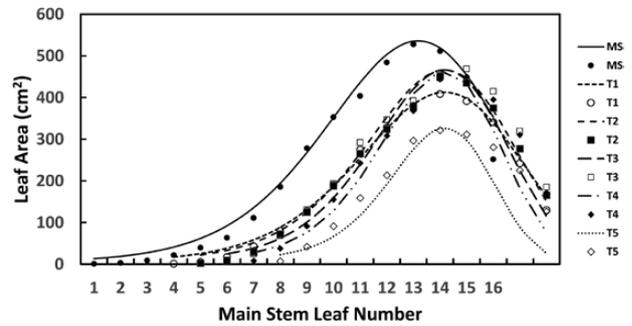


Figure 3. Average individual leaf area versus leaf position for leaves on the MS (●), tiller 1 (T1, ○), tiller 2 (T2, *), tiller 3 (T3, □), tiller 4 (T4, ◆) and tiller 5 (T5, ◇) for 16-leaf plants of the sorghum hybrid 'Buster' in the low-density treatments of the experiments of Lafarge et al. (2002). Lines represent fitted curves. Lines for each tiller are displaced so that leaf size of each tiller leaf is plotted against LN 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.

Leaf in Fig. 4). TLN estimates further depend on prediction of plant development, which can vary among genotypes based on their responses to photoperiod and temperature (G Phenology in Fig. 4), combined with the leaf appearance rate, which can also vary among genotypes (G Phyllo in Fig. 4). Subsequently, progression through the phases of tillering can be modelled -

4.1 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 synchronized 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 LN from which they emerged. Hence, if the main culm produced 16 leaves, T3, which emerged from the axillary bud of leaf 3 at full expansion of leaf 6, 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 2 phyllochrons after the main culm.

The total number of tillers that would emerge (Potential TTN—Fig. 4) was calculated at the time of full expansion of leaf 5 based on the 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)–

$$\text{Potential TTN} = \text{PTT} + c \times \frac{S}{D} \quad (6)$$

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

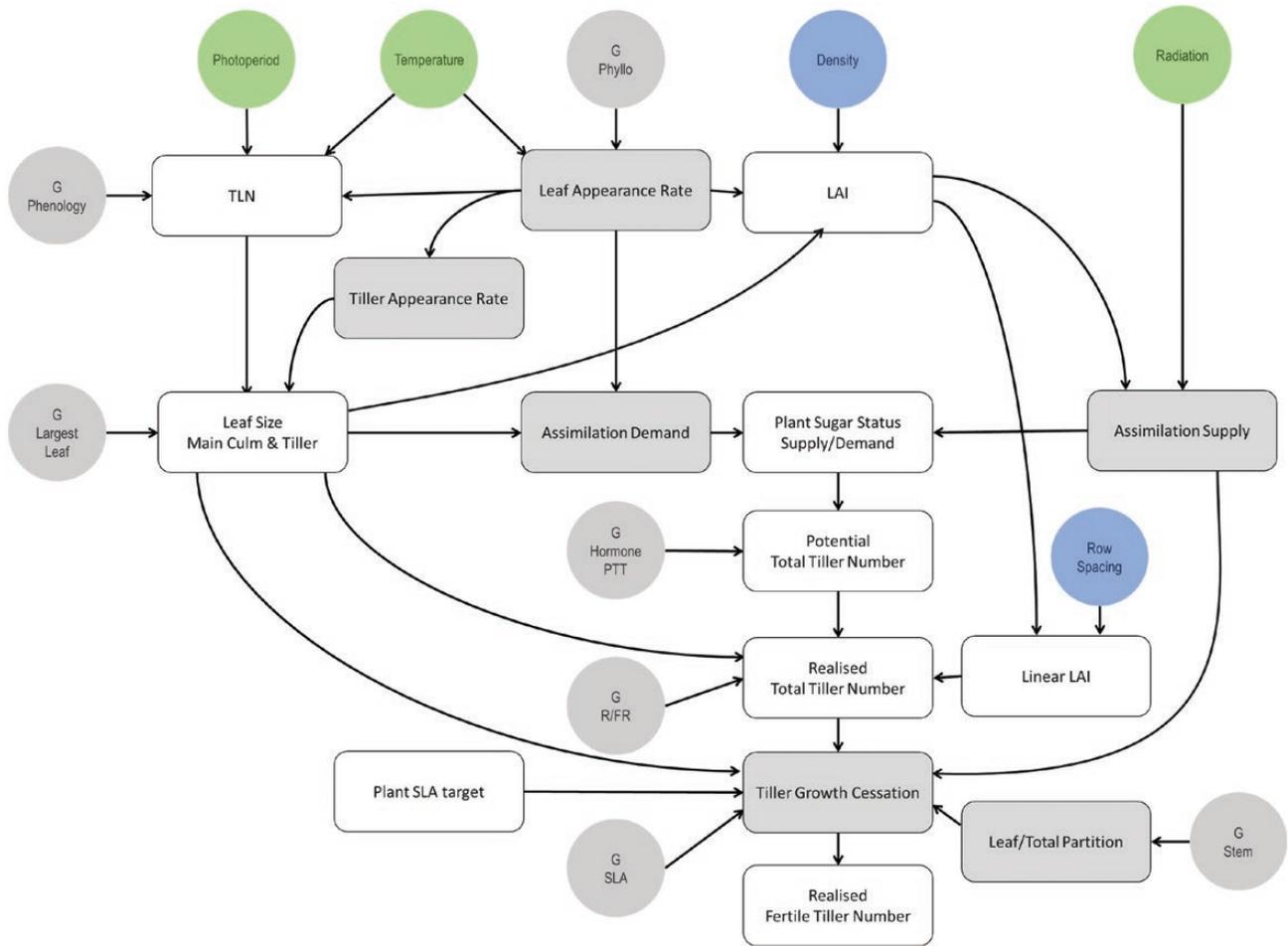


Figure 4. Schematic of the model of the physiological network responsible for generating FTN in sorghum. Open boxes indicate state variables (TLN, total leaf number; LAI, leaf area index; S/D—supply/demand ratio for available assimilate; TTN, total tiller number; SLA, specific leaf area). Grey-shaded boxes indicate key rate variables and filled circles indicate influence of E (green), M (blue) and G (grey) factors (PP, photoperiod; Temp, temperature; Radn, radiation; Phyllo, phyllochron; PTT, propensity to tiller; R/FR, Red/Far Red light ratio). Arrows indicate interrelationships captured in the model (see text).

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 –

$$S = \text{PTQ}_{3-5} \times \text{LA}_5 \times \text{phyllochron}_5 \quad (7)$$

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 3 to full expansion of leaf 5, LA_5 is the size of leaf 5 (cm^2), and phyllochron_5 is the duration from full expansion of leaf 4 to that of leaf 5 (°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 phyllochron_5 was used as previously ([Alam et al. 2014a](#)). LA_5 is an indicator of plant size and photosynthesizing surface area, and phyllochron_5 represents the time interval involved. D was determined as –

$$D = \text{LA}_9 - \text{LA}_5 \quad (8)$$

which captures the difference in size between leaves 9 and 5 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 potential TTN and the slightly modified S/D index across genotypes and experiments ([Fig. 5](#)) 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 (G-PTT, [Fig. 4](#)).

[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 $\text{TTN} = 2$ only T_3 and T_4 emerged, if $\text{TTN} = 4$ then T_2 and T_1 also emerged, and if $\text{TTN} = 6$ then T_5 and T_6 also emerged.

4.2 Cessation of tiller emergence

At the time of tiller emergence cessation, the TTN that occur is realized. [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 0.5 m row spacing. Sorghum is

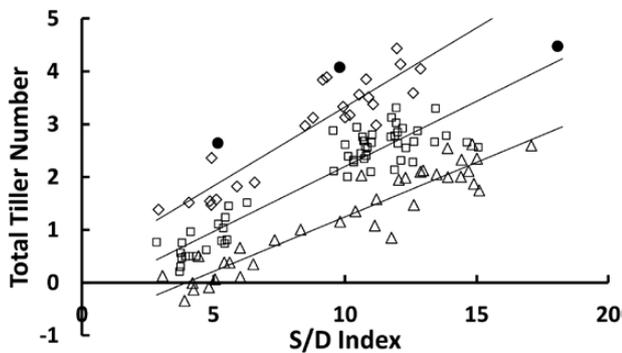


Figure 5. Total number of tillers emerged for individual genotypes grouped by those showing consistently high (\diamond), medium (\square) or low (Δ) tillering versus S/D index for data from experiments of Alam et al. (2014a). Data are Best Linear Unbiased Estimates from each of three experiments. The 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: $y = 0.21x - 0.82$ $R^2 = 0.89$.

commonly grown on wider row spacings (0.75–1.0 m) 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 (Fig. 4). Given Lafarge et al. (2002) used 50 cm 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 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 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. Further, crops with similar potential TTN can have differing realized TTN based on their linear LAI. For example, if the crop grown at 16 plants m^{-2} was on 1 m rows, it will have plant spacing of 6.25 cm and will reach the critical ‘linear LAI’ sooner than the crop grown on 0.5 m rows, leading to a lesser realized TTN.

4.3 Tiller growth cessation

The ultimate 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 (Figs 3 and 4).

Whether the potential leaf area growth per plant could be realized was calculated from estimates of plant growth rate, allocation of assimilate to leaf and stem and consequences on specific leaf area (SLA, cm^2g^{-1}) (Fig. 4). 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 (cm^2g^{-1}) for a sorghum plant with a given leaf number (LN) was derived from data for three hybrids reported by Reeves (1971) –

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

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 %.

5. MODEL TESTING

The dynamic of tiller number through the crop life cycle was predicted for each of the density treatments in the detailed water and nutrient non-limiting experiments of Lafarge et al. (2002) (Fig. 6). In all cases, there was an adequate prediction of the dynamics of tillering. The simulated pattern of the dynamic through the crop life cycle reflected well that was observed. Although simulated values were often not within the 95 % confidence interval of individual observed values, there was no bias in predictions and an overall robust goodness of fit (Fig. 7). The model predicted

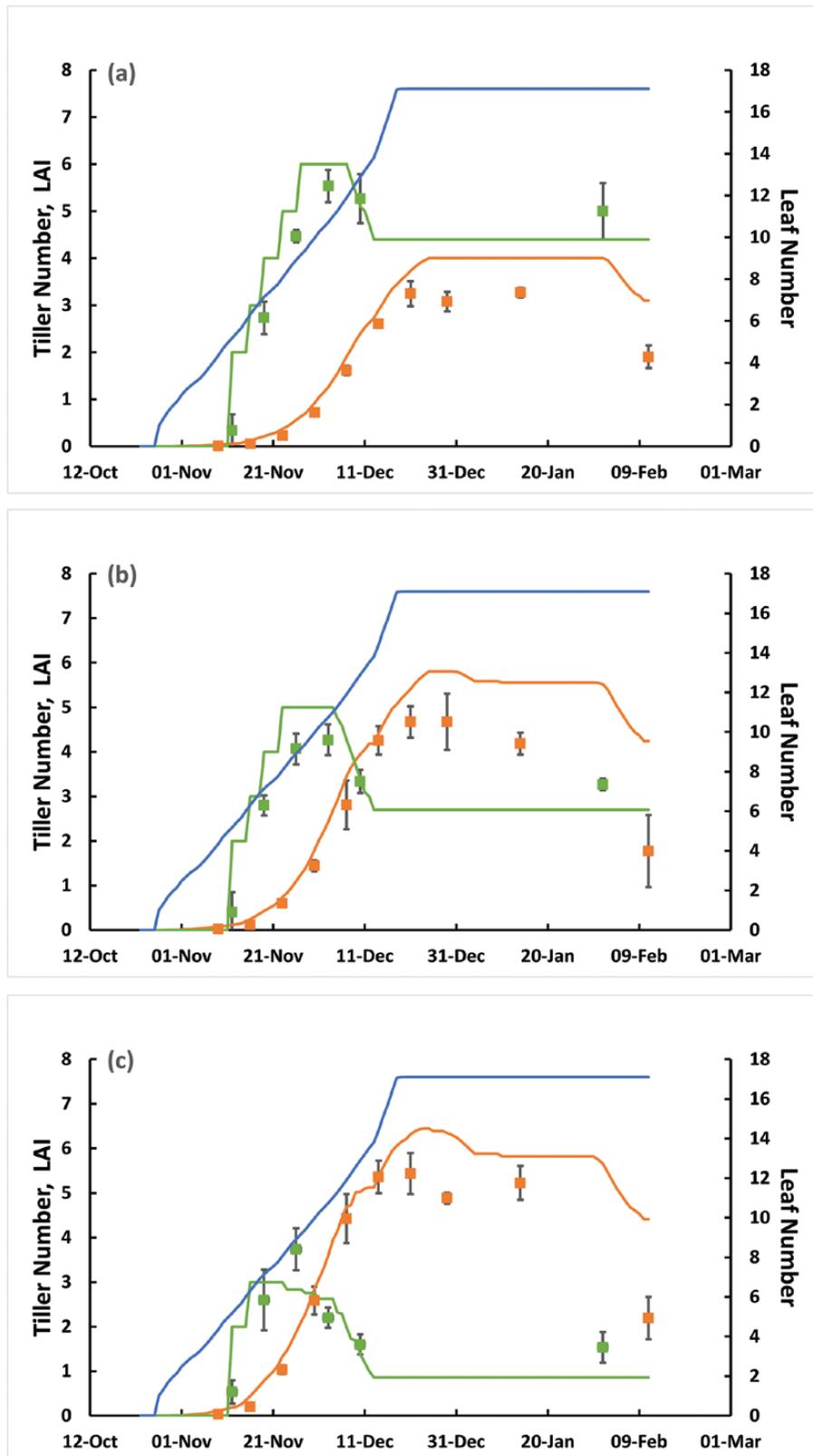


Figure 6. Simulated total and FTN (green), leaf number (blue) and leaf area index (LAI; orange) versus day of year for sorghum crops planted at Lawes (27.34 °S, 152.20 °E, 90 m altitude a.s.l.), in southeastern Queensland, Australia on 23 October 1998 at four levels of plant density: (a) 2 plants m^{-2} , (b) 4 plants m^{-2} , (c) 8 plants m^{-2} and (d) 16 plants m^{-2} . Data (filled squares) from [Lafarge et al. \(2002\)](#). Vertical bars are 95 % confidence intervals for observed tiller number and LAI.

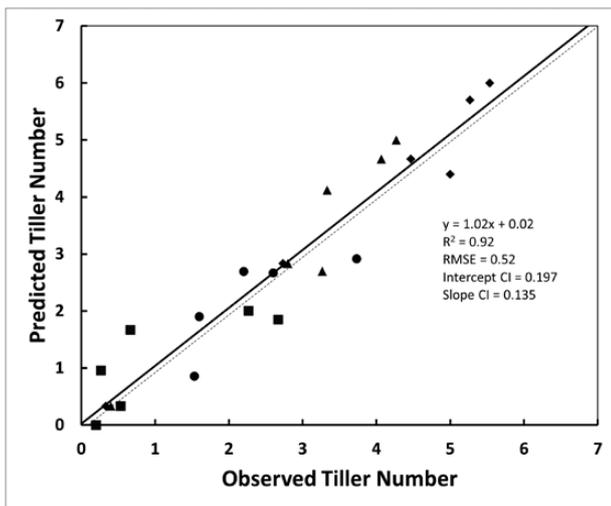


Figure 7. Predicted versus observed tiller number for sorghum crops planted on 23 October at four levels of plant density: 2 plants m^{-2} (diamonds), 4 plants m^{-2} (triangles), 8 plants m^{-2} (circles) and 16 plants m^{-2} (squares). Data from Lafarge et al. (2002). The solid line is the fitted regression, which is not significantly different from the 1:1 line (dashed).

the effects of density on both TTN produced, the resultant FTN and canopy LAI (Fig. 6). 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.

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 PTT. Model plausibility testing provides an effective means to test the broad generality of model algorithms and their capacity to regenerate qualitative responses expected from agronomic knowledge and experience. The simulated results were contrasted with the values that had been tabulated for use in APSIM v7.10 (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). Those values were based on observations over a broad range of on-farm and research trials combined with local knowledge of experienced agronomists involved in that research (e.g. Whish et al. 2005; Alam et al. 2017). The range of sites simulated formed a north-south transect of the Australian sorghum belt—from Emerald (central Queensland) in the sub-tropical north, to Dalby (southern Queensland), to Tamworth (northern New South Wales) in the more temperate south (Fig. 8). Seasonal variability was captured by simulating years from 1960 to 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 September) to summer (15 January) 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 m^{-2}) and row configuration (1.0 m solid row spacing, 1.0 m single skip row, 1.0 m double skip row) were simulated for each sowing as was the range in genetic tillering propensity (Fig. 5) to quantify high, medium and low tillering genotypes.

The plausibility simulations quantified the expected effects of environment (site, season), management (density, row configuration) and genetics (PTT) on extent and likelihood of tillering across the sorghum production zone in Australia (Fig. 9). 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 (Figs 4 and 5). Increased planting density diminished FTN 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 PTT, 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 a grower innovation to reduce tillering and canopy leaf area in this way as a means to manage crop water use (Whish et al. 2005).

6. 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 FTN for diverse GxExM situations, it provides an avenue for advance in several areas.

6.1 Capturing genetic variation and guiding molecular discovery

The architecture of the dynamic tillering model developed exposes potential quantitative links to molecular mechanisms and underpinning genetic regulation. Differences in tillering were generated by genetic, management and environmental factors via effects on tiller outgrowth and tiller cessation (Fig. 4). In addition to genetically regulated hormonal factors controlling tiller emergence (G Hormone Fig. 4), which were captured by PTT (Fig. 5), for tiller cessation, this likely reflects differences in plant morphology and their consequences on source-sink

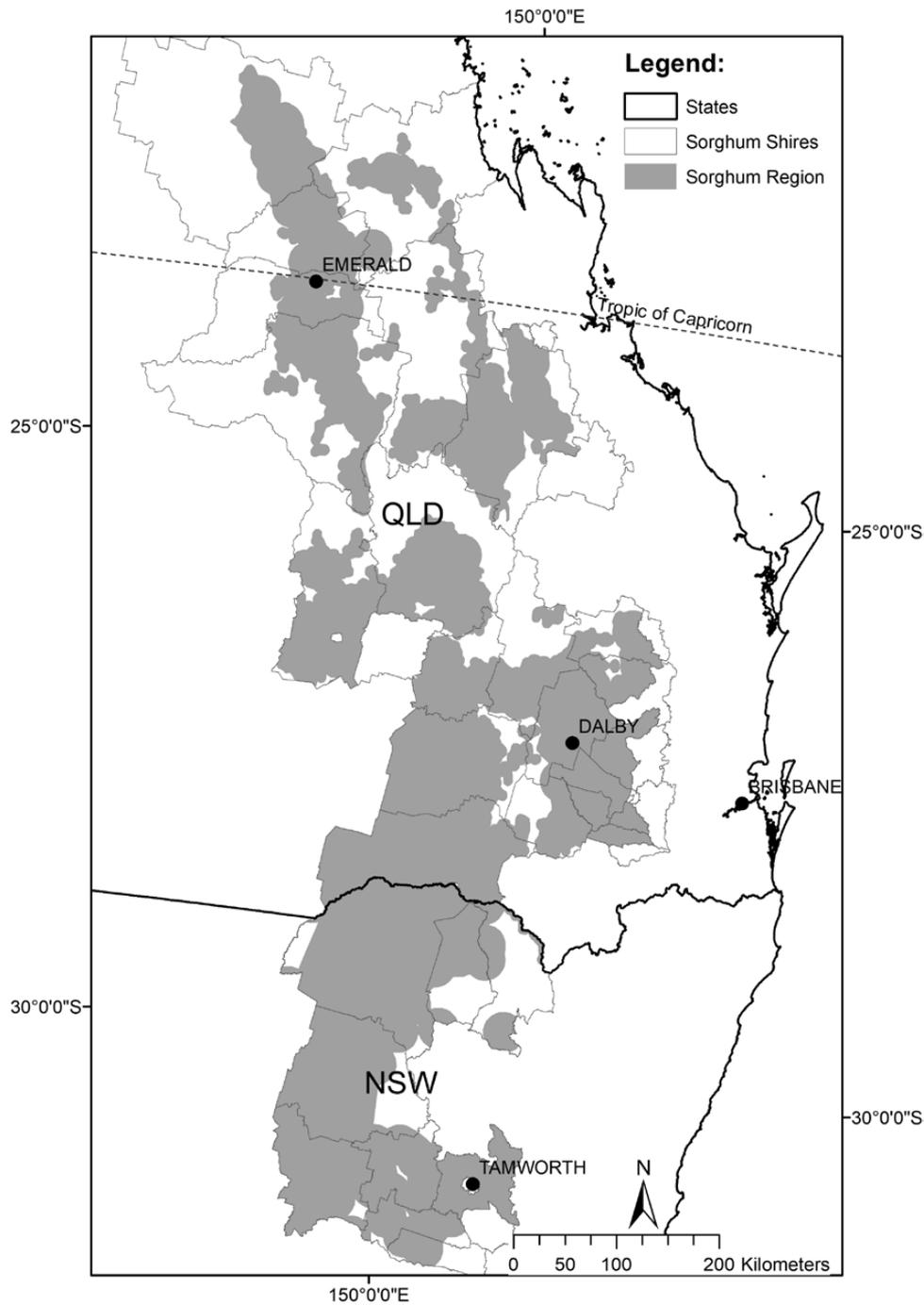


Figure 8. Sorghum growing areas in NE Australia showing location of key sites used for model plausibility testing (after [Hammer et al. 2014](#)).

dynamics via interactions with environmental conditions that determine assimilate availability surplus to the needs of the main culm and established tillers. While the hormone-assimilate availability interaction has been well studied for tiller/bud outgrowth ([Mason et al. 2014](#); [Barbier et al. 2015, 2019](#); [Bertheloot et al. 2020](#)), the results here suggest that in canopy situations, effects on tiller emergence cessation and tiller growth cessation may be equally, or more, important. However, the molecular basis of tiller emergence and growth cessation has not been subject to the same depth of study as bud outgrowth. Here, tiller emergence cessation was related to extent of inter-plant competition via canopy LAI ([Lafarge et al. 2002](#)), and the likely effect

on light quality by a decrease in red light to far-red light ratio (R:FR) that is known to reduce branching ([Ballare and Casal 2000](#)). The extent of genetic variation in this sensitivity of sorghum to neighbouring plants via variation in light quality is not known. 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](#)), so genetic variation is plausible and potentially manifest in the model via variation in the critical LAI for cessation of tiller emergence (G R/FR in [Fig. 4](#)).

Beyond tiller emergence cessation, given the ability in this study to predict the extent of tiller growth cessation from internal

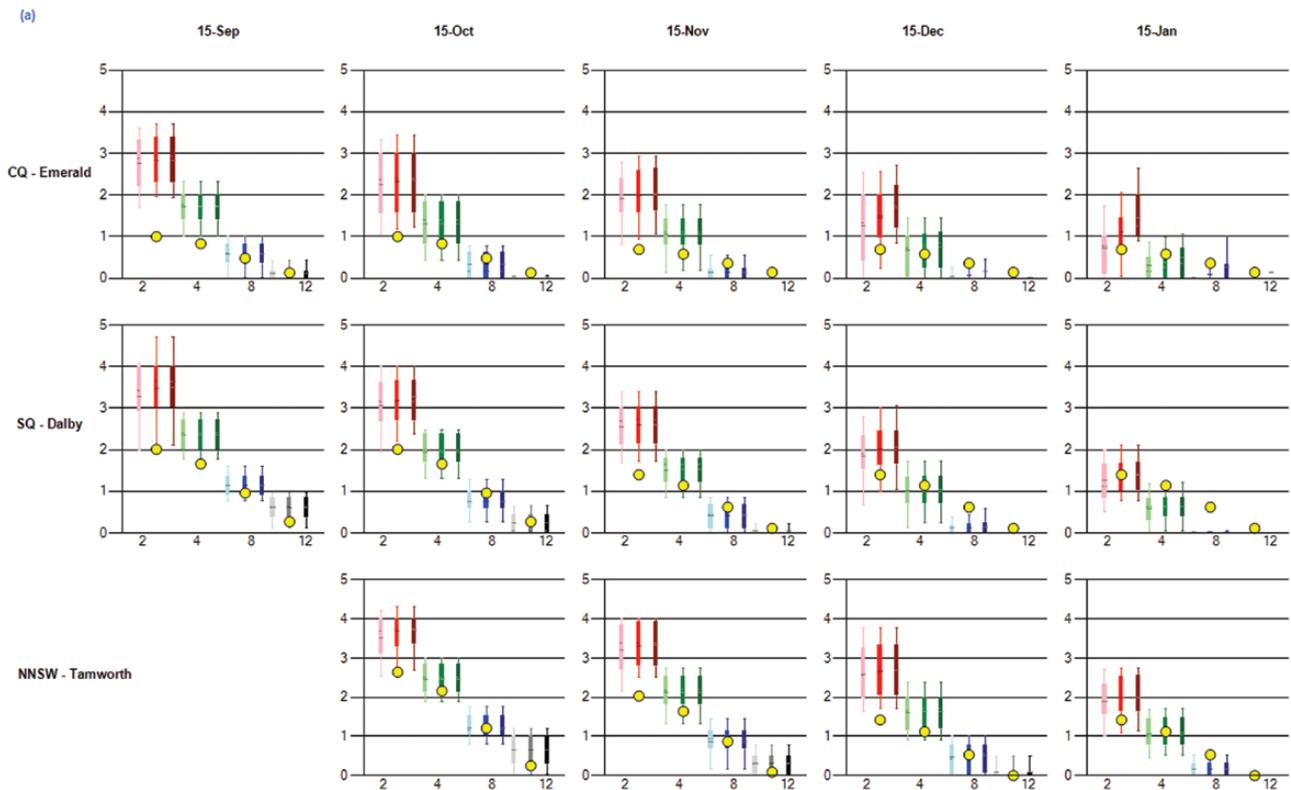


Figure 9. Simulated FTN per plant (y -axis) versus plant density (plants m^{-2}) (x -axis) for a N–S transect of sites (Emerald (CQ), Dalby (SQ), Tamworth (NNSW)) across the Australian sorghum belt for a range of sowing dates and genotype propensity to tiller for—(a) 1 m row solid planting configuration, (b) 1 m row single skip-row planting configuration and (c) 1 m row double skip-row planting configuration. Shaded bars (left-to-right) show probability distributions of FTN 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 10th and 90th percentiles. The median is indicated by a solid horizontal line. The yellow dots indicate values used in APSIM v7.10, based on generalized observations from on-farm research and experienced local agronomists (see text).

plant competition effects on surplus assimilate availability via sensitivity to change in SLA, sugar signalling effects on branch apical meristem activity and potential for genetic variation in those effects (G-SLA in Fig. 4), become a prime candidate for discovery research. This is reinforced by recent findings on the role of Tre6P, a regulatory sugar-phosphate that serves as a signal of plant sucrose status and is crucial for sucrose homeostasis, growth promotion and developmental progression (Fichter and Lunn 2021), along with studies that indicate sugar signalling modulation of shoot apical meristem (SAM) function (Lopes et al. 2023). However, how such signalling might generate the observed hierarchy of cessation of outgrowth of branch SAMs, and the basis of potential genetic variation, remains unclear. In this situation, exploratory *in silico* experimentation may assist understanding of the basis of phenotypic dynamics and generate testable hypotheses about molecular scale mechanisms in a manner similar to that demonstrated by Dun et al. (2009b). The putative genetic variation is potentially manifest in the model via variation in the association of change in SLA with extent of tiller growth cessation (G SLA in Fig. 4).

The concept of internal plant competition for available assimilate and the moderation of the 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. (2014a, 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 (G Pyllo in Fig. 4), have not been studied. Other potential effects, such as those associated with differences in stem size, have not been considered in the current model and may account similarly for potential genotypic difference in FTN not related to PTT (G Stem in Fig. 4). 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.

6.2 Exploring crop adaptation ($G \times M \times E$) landscapes

The capacity to predict the interactive dynamics of tillering with crop growth throughout the crop life cycle allows the

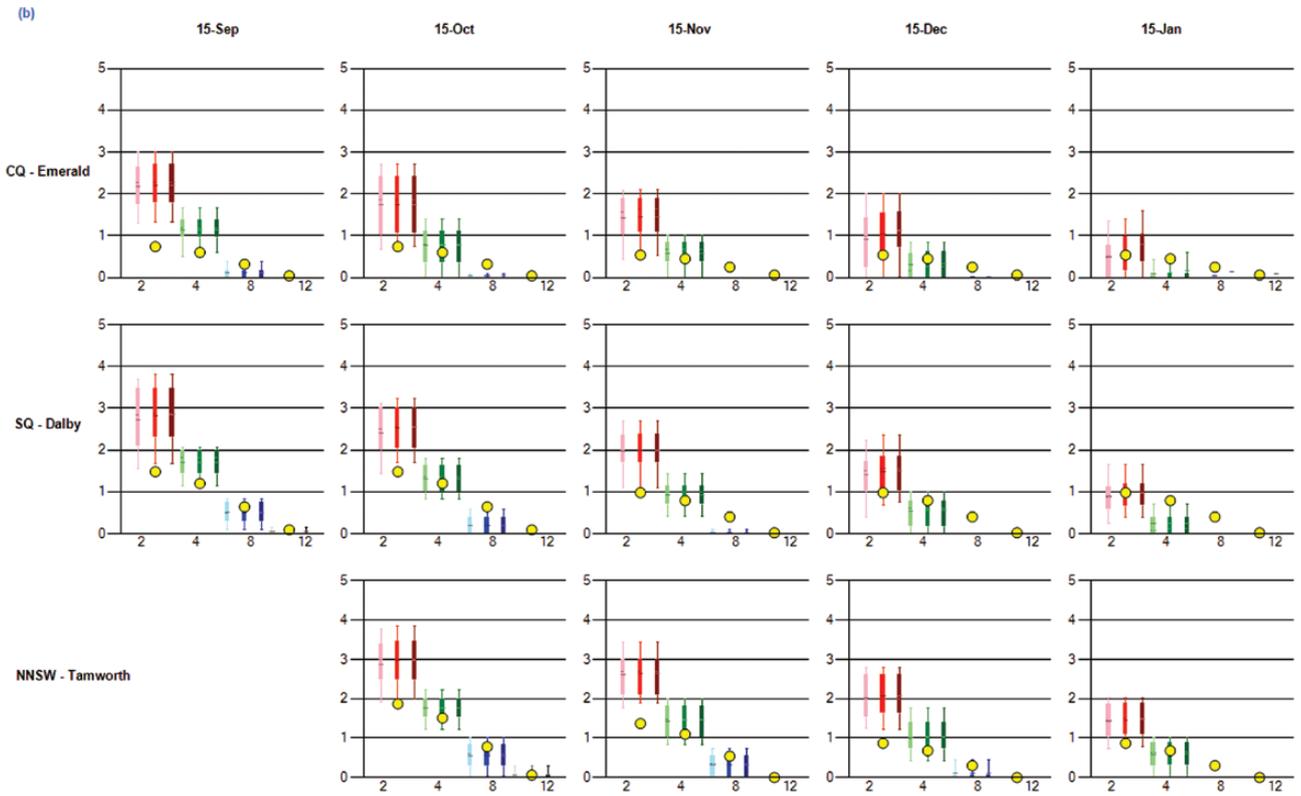


Figure 9. Continued

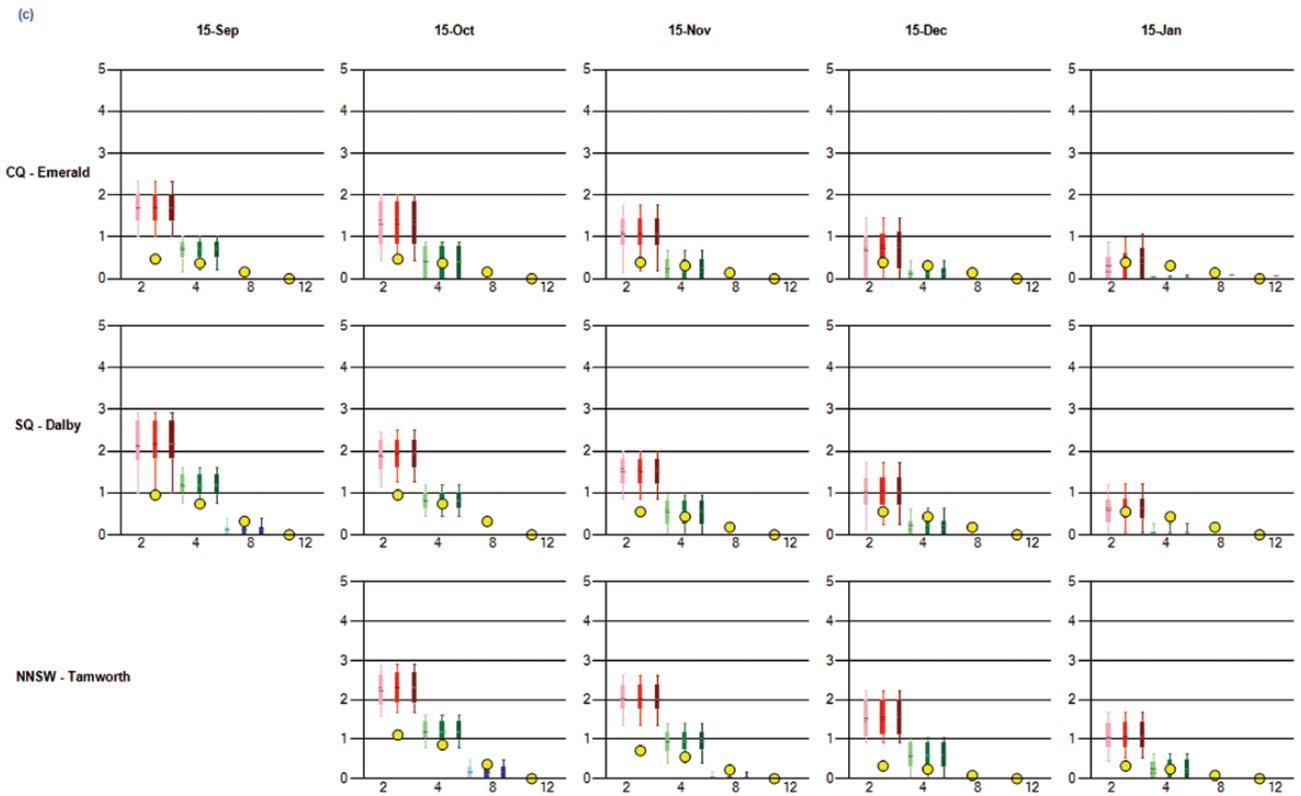


Figure 9. Continued

possibility to simulate crop adaptation landscapes associated with variation in genetic and management factors across production environments. Previous studies that explored crop adaptation $G \times M \times E$ 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), LN (Ravi Kumar et al. 2009) and shoot growth (Craufurd 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. (2014a, 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 programmes to their use in combination with agronomic management strategies within on-farm production systems.

6.3 Generalizing across cereals

The dynamic tillering model developed for sorghum in this study provides a generic phenomenological framework that would be suitable as a basis 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 parameterization for other cereals. By parameterizing 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). In particular, in high tillering species with many secondary tillers, the clear distinction between main culm and tillers will not be as obvious and changes in the dynamics of partitioning to stem components would need to be considered. Nonetheless, the conceptual framework could be adapted across cereals and 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.

6.4 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) 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 (Lafarge and Hammer 2002; Alam et al. 2014a, b) 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). The authors thank Paula Demarco for Fig. 1 and anonymous reviewers for suggesting Figs 4 and 7.

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