

# 3D modelling of tillering behaviour and light interception of freely (*-tin*) and restricted (*+tin*) tillering wheat near-isolines

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## Abstract

A functional-structural plant model of wheat architecture was parameterised to simulate a pair of lines varying for a tiller inhibition (*tin*) gene. Effects of planting configuration were explored through red : far-red (R:FR) signalling on tiller production, final spike numbers, and light interception. Both increased plant density (125 to 200 plants/m<sup>2</sup>) and row spacing (20 to 30 cm) reduced the simulated tiller and spike numbers per plant in both lines. This reduction was greater in the free-tillering (*-tin*) than in the reduced-tillering (*+tin*) line. At wider row spacing of 30 cm, simulated radiation interception was less in the *+tin* line than in the *-tin* line from about 60 days after sowing onwards. In the *+tin* line, increased R:FR signalling between individual plants due to less within-row spacing at wider rows resulted in reduced spikes/m<sup>2</sup> irrespective of population density. Spikes/m<sup>2</sup> simulated for the *-tin* line were similar at either row spacing in a population of 125 plants/m<sup>2</sup>, but decreased with wider row spacing at the higher density of 200 plants/m<sup>2</sup>. For both lines, the greatest number of tillers and ultimately spikes per m<sup>2</sup> was simulated at a density of 200 plants/m<sup>2</sup> and 20 cm row spacing (*-tin*: 820 spikes/m<sup>2</sup>; *+tin*: 570 spikes/m<sup>2</sup>). The simulations indicated that growing *+tin* wheat at an increased density of 200 plants/m<sup>2</sup> and 20 cm row spacing can produce similar, or greater, spikes/m<sup>2</sup> compared to *-tin* wheat grown at a density of 125 plants/m<sup>2</sup>.

## Keywords

Functional Structural Plant Model, wheat, tillering, canopy architecture, plant density, row spacing

## Introduction

Tillering is an important element of the canopy architecture in grasses such as wheat (*Triticum aestivum* L.). About 40 years ago, wheat with limited tillering was discovered in a farmer's field in North Africa (Atsmon & Jacobs, 1977). Since then, the tillering trait has been associated with a major gene named *tin* for tiller-inhibition. Genotypes with the *tin* gene (*+tin*) produce fewer tillers compared to genetically similar (near-isogenic) wheat lines without the gene (*-tin*). The reduced tillering trait is associated with an earlier cessation of tillering, reduced frequencies of later primary and higher-order tillers, and reduced leaf area. This behaviour may conserve soil moisture early in the season for later use when soil-water supply is frequently limiting in Australian growing environments. Because of their smaller canopies, *+tin* lines often intercept less photosynthetically active radiation (PAR) than freely tillering sisterlines (Mitchell et al., 2013; Moeller et al., 2014), which can limit productivity under favourable growth conditions.

Tillering plasticity is an adaptive mechanism by which individuals in a crop stand modify their architecture and physiological functions thereby responding dynamically to the availability of resources, chiefly light, water and nutrients. In conventionally tillering wheat (*-tin*), up to 60% of tillers can die under field conditions (Stapper and Fischer, 1990). While spike numbers are typically lower in *+tin* lines, on average about 10% more tillers become grain bearing spikes in *+tin* lines compared to *-tin* lines (Mitchell et al., 2013; Moeller et al., 2014). However, this increase in tiller economy may only improve, or maintain, yield if grain numbers per unit area (Fischer, 2008) are similar to those of conventional wheats with their lower tiller economy but greater tillering plasticity. A core determinant of grain number is spike number. This raises the question whether spike numbers and PAR interception, as discussed above, could be increased with a planting configuration (defined by combinations of plant population density and row spacing) that better suits the 'communal' rather than 'competitive' phenotypes associated with the presence of the *tin* gene.

Tillers die prematurely as a consequence of plant internal competition for resources. An important environmental signal for increased competition in a plant population is a lowered red / far-red intensity ratio (R:FR) of the light reflected by neighbouring plants. Low R:FR signals sensed at the plant base by specific photoreceptors results in the suppression of tillering in favour of elongation growth, which is a core aspect of shade avoidance (Franklin and Whitelam, 2005). Moeller et al. (2014) reported that tillering in *+tin* lines

ceased at a greater R:FR ratio than in *-tin* lines, and that this was independent of the observation that plant bases of *+tin* lines received more radiation and were exposed to greater R:FR than free-tillering sisters over much of the growing season. The aspect of tillering control associated with the R:FR signal was integrated into a spatially-explicit 3D model of canopy architecture, growth, and development called a functional-structural plant (FSP) model (Evers et al., 2007, 2015), which allows for the simulation of the feedbacks between the expanding canopy and light interception and scattering at the plant organ level. Here, an FSP model was parameterised to simulate a pair of near-isogenic lines (NILs) contrasting in the *tin* gene to subsequently explore effects of planting configuration through R:FR signalling on tillering, spike numbers, and PAR interception.

## Methods

An existing FSP model of wheat architecture (Evers et al., 2007) was implemented in the simulation platform GroIMP (Hemmerling et al., 2008). The model simulates, on a daily time step, the development of the aboveground parts of the wheat plant in terms of leaf appearance, expansion, and senescence, tiller appearance and senescence, as well as geometrical properties such as leaf angle and curvature. Light interception by the canopy was simulated using the GroIMP stochastic path-tracer model, with direct and diffuse light coming from light sources arranged appropriately (Zhu et al., 2015). Further model stochasticity in the tillering response of individuals was caused by individual seed orientation. Tiller production was assumed to stop, and senescence was assumed to occur, at certain threshold R:FR values according to Evers et al. (2006, 2007) and Sparkes et al. (2006).

Details on architectural and physiological characteristics of the NILs 7770P (*+tin*) and 7770N (*-tin*) used for FSP modelling are given by Moeller et al. (2014). These NILs were developed by crossing a Silverstar-based, *+tin* line to the cultivar Wyalkatchem (*-tin*), and subsequent backcrossing to Wyalkatchem before inbreeding to produce BC<sub>1</sub>F<sub>5,6</sub> plants heterozygous for *tin*. Plants were then self-pollinated to develop lines that are genetically similar (near-isogenic) except for the presence or absence of the *tin* gene. Briefly, the NILs were grown under well-watered and adequately fertilised conditions at a population density of 125 plants/m<sup>2</sup> and 20 cm row spacing in 2013 at Canberra. Architectural parameters were derived from detailed measurements taken on individual plants, and included leaf blade width and length, sheath length, and internode length for each phytomer and tiller type. The phyllochron was 85°Cd. Threshold R:FR values were calibrated for 7770N and 7770P considering the tillering dynamics as observed on an area basis in the field at 125 plants/m<sup>2</sup> and 20 cm row spacing. Data on leaf area index (LAI) and the fraction of intercepted noon-time PAR (fIPAR) were also taken on an area basis, and used only for comparison with model output.

Subsequently, simulations of tillering and canopy light interception were done for the NILs at four contrasting planting arrangements (Table 1). Tillering of individuals in the plant population responded to the average R:FR ratio simulated at 20 virtual sensors arranged around the base of each plant. The maximum expansion of leaves and internodes was entirely based on empirical rules, hence the same for each canopy configuration, and therefore the light intercepted was not used to drive growth. To eliminate border effects, only model output from the central area of the virtual plots was used in the analysis.

**Table 1: Simulated planting configurations**

Population density (plants/m <sup>2</sup> )	Row spacing (cm)	Within-row spacing (cm)
125	20	4.00
125	30	2.67
200	20	2.50
200	30	1.67

## Results and discussion

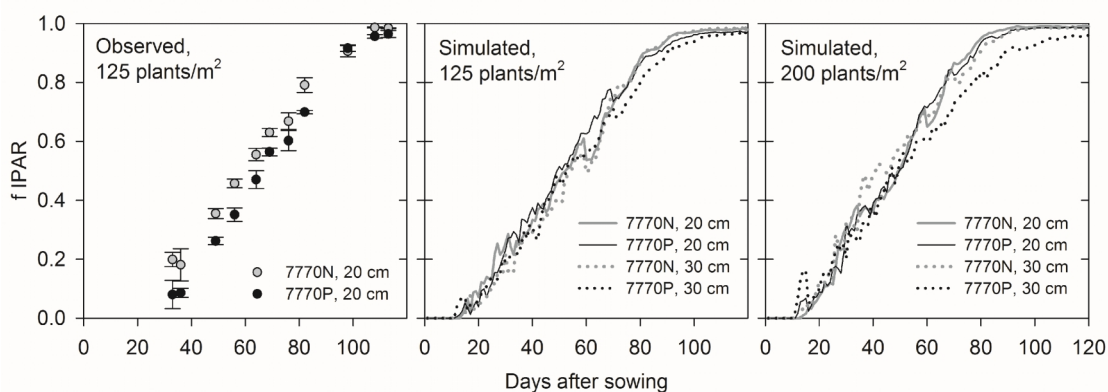
By integrating data describing the architecture of NILs contrasting in the *tin* gene and R:FR thresholds for the cessation of tillering and tiller senescence, the FSP model was able to dynamically simulate important differences in canopy structure between free- and reduced-tillering NILs as observed in the 2013 field experiment (Table 2). The simulated tillering dynamics deviated slightly from those observed in the field. The simulated tiller economy (calculated as the ratio of spike to maximum tiller number) was as a consequence the same for both NILs while the observed tiller economy of 7770P was 10% greater than that of 7770N (Moeller et al., 2014). The arguably small deviations from observed tiller numbers in the simulations, and possibly other characteristics (e.g. leaf angle) influencing optical properties that were not

considered in the model parameterisation, would affect the simulated light interception. This explains that at 125 plants/m<sup>2</sup> and 20 cm row spacing, the simulated PAR interception was similar for both NILs while observed PAR interception was 3-10% lower in line 7770P than in 7770N for much of the growing season (Table 2, Figure 1). In the simulations, light interception was similar for both NILs at narrower row spacing of 20 cm, while at wider rows of 30 cm the *+tin* line 7770P intercepted less PAR than the free-tillering line 7770N from about 60 days onwards (Figure 1).

**Table 2: Observed and simulated maximum tiller and spike number, leaf area index (LAI), and fraction of intercepted photosynthetic active radiation at the start of heading (fIPAR<sub>Z50</sub>) in free- (7770N) and reduced-tillering (7770P) wheat near-isolines at 125 plants/m<sup>2</sup> and 20 cm row spacing.**

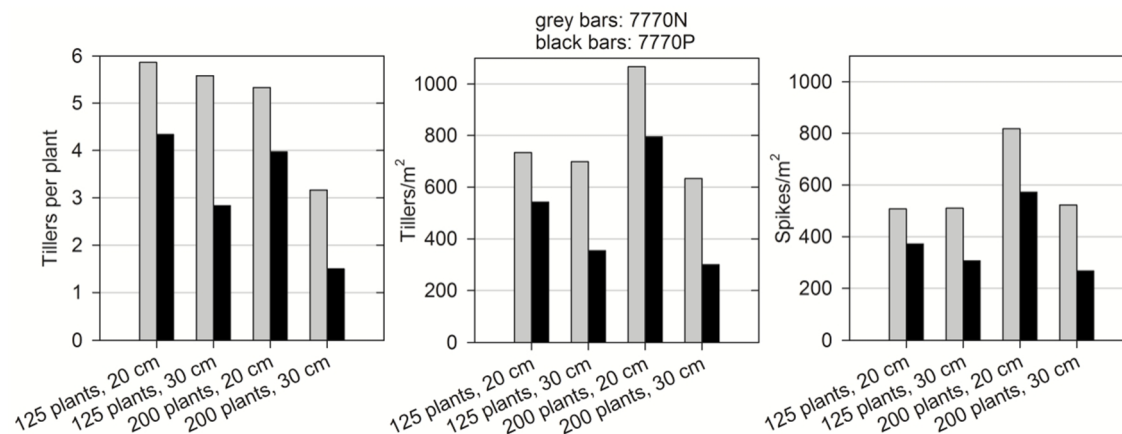
	7770N, <i>-tin</i>				7770P, <i>+tin</i>			
	Tillers/m <sup>2</sup>	Spikes/m <sup>2</sup>	LAI	fIPAR <sub>Z50</sub>	Tillers/m <sup>2</sup>	Spikes/m <sup>2</sup>	LAI	fIPAR <sub>Z50</sub>
observed	760 (20)	480 (21)	6.5 (0.3)	0.99 (0.02)	530 (19)	390 (25)	5.6 (0.6)	0.96 (0.06)
simulated	730	510	6.2	0.98	540	370	4.4	0.97

+/- one standard error of mean is given in parenthesis.



**Figure 1: Observed and simulated fraction of photosynthetically active radiation intercepted at noon-time (fIPAR) in free-tillering (7770N) and reduced-tillering (7770P) wheat near-isolines at different planting configurations (see text and table 1 for details).**

Both increased population density and row spacing are associated with plants within a row being closer together (Table 1) increasing the local low R:FR signalling, which acts as an environmental cue for future competition between neighbouring plants (Franklin and Whitelam, 2005). The increased R:FR signalling between individuals in the crop stand reduced the simulated tiller numbers, and ultimately spike numbers, per plant in both NILs (Figure 1). Similar responses in tiller and spike numbers to density and row spacing were previously reported for conventionally tillering wheat (Stapper and Fischer, 1990). At 20 cm row spacing, increasing the density from 125 to 200 plants/m<sup>2</sup> decreased the tiller numbers per plant by only 0.4-0.5 tillers in both NILs. However, at wider rows of 30 cm, this decline in tiller numbers per plant was 2.4 tillers in the free-tillering line 7770N compared to 1.3 tillers in line 7770P (Figure 2).



**Figure 2: Simulated maximum tiller and spike numbers of free-tillering (7770N) and reduced-tillering (7770P) wheat near-isolines at four planting configurations (see Table 1 for details).**

On a per area basis, the greatest number of tillers and ultimately spikes was simulated for both NILs at a population density of 200 plants/m<sup>2</sup> and 20 cm row spacing (Figure 2). In the +*tin* line 7770P, increased signalling between individual plants associated with wider rows resulted in reduced spikes/m<sup>2</sup> irrespective of population density. In other words, reduced tillering wheat performed better in terms of final spike numbers at narrower rows. In contrast, the final spike numbers of the free-tillering line 7770N were similar at either row spacing in a population of 125 plants/m<sup>2</sup>, and only decreased with wider row spacing at the higher density of 200 plants/m<sup>2</sup>. The simulation results also suggested that growing the reduced tillering lines 7770P at an increased population density of 200 plants/m<sup>2</sup> at 20 cm row spacing can produce similar, or greater, spikes/m<sup>2</sup> compared to the free-tillering line 7770N grown at a density of 125 plants/m<sup>2</sup>. Such information can inform the agronomy of *tin*-containing commercial cultivars, which are yet to be developed.

## Conclusion

The FSP model allowed for the simulation of the most important trends in the tillering response of reduced- and free-tillering wheat near-isolines as associated with changes in light quality. Other aspects such as water and nutrient effects on tillering were not included here. The simulation results suggest that +*tin* lines are less well adapted to wider rows than free-tillering -*tin* lines as indicated by large reductions in spikes/m<sup>2</sup> at wider rows. Fewer spikes can reduce grain numbers and ultimately yield. However, fewer spikes/m<sup>2</sup> associated with reduced tillers and ultimately spikes per plant in the +*tin* line can be compensated for by increasing the population density but only at narrower row spacing. Further work will consider factors such as leaf angles that influence the optical properties of the canopies and consequently simulations of light interception, and include additional planting configurations to further explore interactions between genotype and management.

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