The impact of selection and breeding for above-ground vigour on below-ground traits associated with weed competitiveness in wheat

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Summary Weeds are a critical pest management issue for wheat producers. The weed competitiveness of wheat has typically been reduced through a century of selection for dwarf genotypes to prevent lodging and increase the harvest index. Many of the cultural and chemical strategies employed to manage weeds are costly and some may lead to the development of herbicide resistance. Therefore, novel and cost-effective integrated approaches for weed management in cereals are needed. One approach to enhance competitiveness without reducing harvest index is through selection for early shoot vigour. However, the impact of above-ground vigour on below-ground root traits and competitiveness has not been well characterised to date.

Competitive root traits in wheat were evaluated against commercial cultivars and parent genotypes using a collection of wheat genotypes generated by recurrent selection at CSIRO. In field and controlled environments, shoot and root traits were evaluated in a series of experiments. Historic cultivars, triticale or cereal rye were included as positive weed suppressive controls for enhanced competitiveness. Genotypic differences in root traits and the allelopathic potential from root exudation were noted among selected early vigour and commercial lines. Their weed suppressiveness was quantified in field and controlled environments.

Keywords Root architecture traits, metabolomics, weed suppression, early vigour

INTRODUCTION

Wheat (*Triticum aestivum* L.) is one of the world's most cultivated crops and is grown across more than 215 million hectares every year (FAO, 2022). As a food crop, wheat accounts for ~20 % of the global human calorie intake (Savary *et al.* 2019). Weeds are considered the leading biotic limitation to wheat production (Oerke 2006), potentially reducing yields by as much as 23%, as they compete for resources that would otherwise be used by the crop (Gallandt and Weiner 2015).

Historically, crops competed with weeds by smothering and shading through increased plant height (Murphy *et al.* 2008). The introduction of the dwarfing genes (*Rht*) during the "Green Revolution" improved yields but reduced weed competitiveness (Vandeleur and Gill 2004), relying on primary tillage and pesticides to control weeds (Evers and Bastiaans 2016). While successful, these practices among other issues caused the emergence of herbicide-resistant weeds through increased selection pressure (Broster *et al.* 2013; Heap 2018). Improving the competitive ability of cereals would be a valuable and cost-effective alternative strategy for suppressing weeds above-ground (Lowry & Smith 2018) without compromising the harvest index (Bertholdsson 2005; Zerner *et al.* 2016).

However, interference occurring between the roots of crop species and weeds may be even more important than above-ground competition (Kiær *et al.* 2013). Traits that increase soil volume occupation (Craine and Dybzinski 2013), nutrient exploitation (Giehl *et al.* 2014), as well as the exudation of secondary phytotoxic metabolites (Weston 2005) generally enhance below-ground competitiveness. In this study, we analysed the effect of enhanced shoot vigour traits on root traits and assessed their contribution to the overall competitiveness of wheat. We measured growth parameters in a set of breeding lines selected for high shoot vigour and compared them with commercial and historic wheat cultivars and triticale, in a series of replicated controlled environment and field experiments.

MATERIALS AND METHODS

Genetic material High shoot vigour and weed-competitive wheat lines (W lines), generated from top-crosses between germplasm from a recurrent selection for increased shoot vigour (Zhang *et al.* 2015) and Australian commercial cultivars were evaluated. Genotypes included

: W400203 and W470201 derived from a cross with cv. Yitpi, and W010709 and W670704 derived from a cross with cv. Wyalkatchem (Zerner et al. 2016). Reference genotypes included commercial cultivars Condo, Yitpi, Wyalkatchem and Mace. Triticale (cv Chopper) was a vigorous and weed-suppressive control (Beres *et al*. 2010). Seeds were sourced from a previous glasshouse experiment and standardised by seed weight assessment.

Controlled environment experiments Root growth and competitive interaction were assessed both in hydroponics using root pouches as well as in 35cm tall PVC tubes filled with field soil collected from Wagga Wagga, NSW, Australia, characterised as a red clay-loam kandosol. The experiments were performed in growth chambers at 12 h (day/night) with 20 °C/15 °C and light 600 μmol.m^{-2}s^{-1}. Six replicates of each genotype were sown per experiment, and the experiments were performed three times.

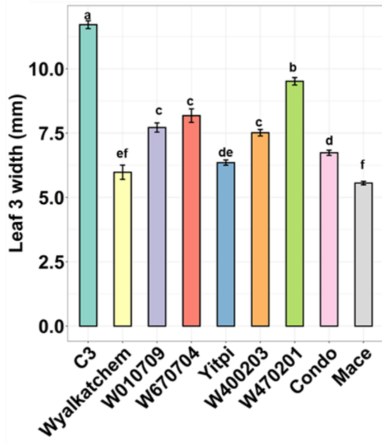
Field experiments Field trials were conducted from May to December in 2018 through 2020 at the Graham Centre (now Gulbali Centre) research field site in Wagga Wagga (35°03S, 147°36 E; 227 m altitude; NSW, Australia). 2018 and 2019 experienced below average rainfall, while in 2020 it was above average. Each cereal genotype was sown in six replicated plots with dimensions 12.0 x 1.8 m, arranged in a randomised complete block design. Above-ground wheat and weed growth was assessed over the growing season, along with ground cover, light interception, leaf area and crop and weed biomass.

RESULTS

In the controlled environment experiment, the commercial wheat control for high vigour (cv. Condo) had significantly wider leaves than the control for low vigour (cv. Mace). The vigour lines had significantly increased leaf width than Condo (Figure 1).

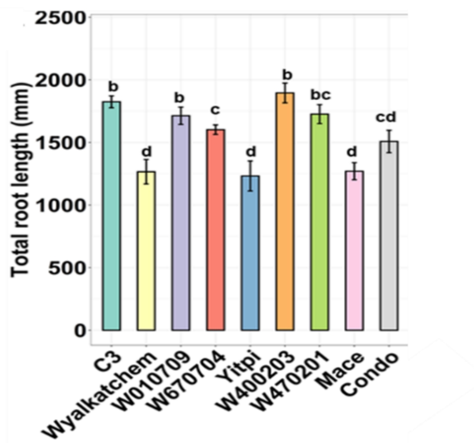
Early on (at second leaf expansion), total root length differed among genotypes (Figure 2). Triticale cv. Chopper, selected as the control for enhanced vigour and competitiveness, showed the longest total root length of all entries. The more vigorous Condo had a significantly longer root system than the low vigour Mace cultivar. Federation, a historic cultivar, exhibited a longer root system than all the commercial wheat cultivars, as did early vigour genotypes in contrast to their commercial parents (Figure 2). The vigour lines also exhibited more and longer root hairs than did commercial cultivars.

Figure 1. Leaf width measured on the third leaf (n=36 for C3 and n=24 for the other entries). Error bars represent standard errors. Letters identify



significant differences between means (P≤0.05) as determined by one-way ANOVA

Figure 2. Total root length at early growth (two-leaf stage) in selected wheat and triticale genotypes. The error bars represent standard errors (n=24). Letters identify significant differences between means



(P≤0.05) as determined by one-way ANOVA.

In the field, the high vigour lines closed the canopy earlier and intercepted more photosynthetically active radiation than did the commercial cultivars (P<0.05, Figure 3). A random forest regression performed on the complete set of measured above-ground traits identified that light interception at early tillering and ground cover at the end of tillering were key parameters in the model that explained the variability associated with weed suppression among the wheat entries (data not shown). Indeed, the vigour lines suppressed weeds by up to 200% more than their commercial cultivar parents ($P<0.05$, Figure 4).

Figure 3. Interception of photosynthetically active radiation over the growth of the HV lines and parental lines in the 2020 Wagga Wagga field experiment (Hendriks *et al.*, 2022)

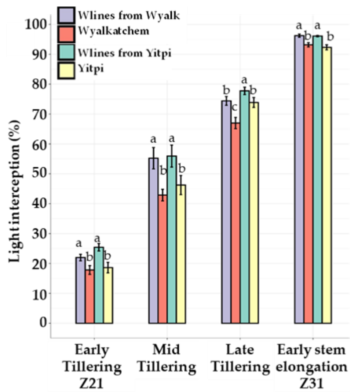
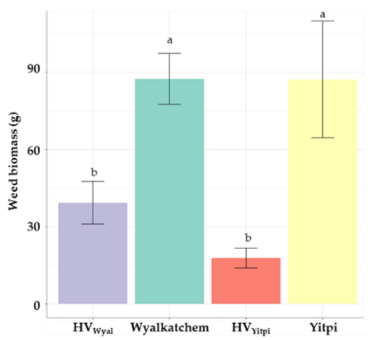


Figure 4. Weed biomass measured under each plot at anthesis (n=24). Letters identify significant differences between means ($P\leq0.05$) as determined by one-way ANOVA

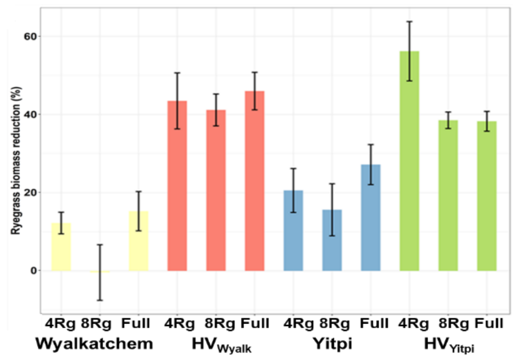


Controlled environment experiments that separated above and below-ground interaction suggest that the competition below-ground was more intensive as there were no significant differences between the weed suppression for plants that were allowed to compete above and below-ground and plants that could only compete below-ground (Figure 5).

DISCUSSION

Our results demonstrated that the incorporation of shoot vigour into commercial wheat cultivars was associated with significant modifications of root traits related to competitive ability. The progeny of crosses between commercial cultivars and genotypes resulting from recurrent selection for early shoot vigour exhibited longer root systems with longer root hairs than their commercial cultivar parents. Experiments designed to evaluate interference with weeds in hydroponics and in field soil suggest that both weed tolerance and weed suppressive ability of early vigour lines was significantly enhanced. These differences were observed as early as the second leaf formation in the controlled environment experiment, at a developmental stage where competition for light may not yet be limiting. In contrast, differential weed suppression was noted by early tillering in the field, approximatively 30 days after sowing. Our findings clearly demonstrate that early vigour is associated with weed competitiveness at growth stages considerably earlier than previously described (Mwendwa *et al.* 2020).

Figure 5. Weed suppression measured as the reduction of ryegrass biomass. Wheat was allowed to interact below ground against four (4Rg) or eight (8Rg) ryegrass plants or to interact above and below-ground (Full) with 4 ryegrass plants



Our findings also demonstrate the importance of below-ground root interaction on the outcomes of crop and weed interference, and are in agreement with results of several studies where above- and below-ground interference were separated. We and others have repeatedly shown that below-ground competition may impact crop growth to a greater degree than above-ground competition (De Lucas and Froud-Williams 1994; Exley and Snaydon 1992; Stone *et al.* 1998).

Soil volume occupation allows plants to access more resources, including soil water and nutrients, and can improve efficiency of their utilisation by crops (Craine *et al.* 2005). We show that high vigour lines exhibit enhanced root growth that allows increased soil volume occupation. Our results also demonstrate that introgressing enhanced early shoot vigour into commercial wheat cultivars resulted in root traits that increased the ability of wheat to successfully interfere with developing populations of weeds under field and controlled environment conditions.

New early vigour lines generated from more advanced recurrent selection and current commercial cultivars are being assessed by private industry. The competition with weeds is a synergy of multiple traits and for a better understanding of the below-ground interactions further studies remain to be conducted.

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