Symmetric competition between neighbours explains genetic gains in wheat yield

C. Mariano Cossani and Victor O. Sadras

South Australian Research and Development Institute, and The University of Adelaide, Waite Campus, Urrbrae (5064), Email: mariano.cossani@sa.gov.au

"...if several varieties of wheat be sown together, and the mixed seed be resown, some of the varieties which suit best the soil or climate, or naturally most fertile, will beat the others and so yield more seed, and will consequently in a few years quite supplant the other varieties…" Darwin (1859).

Abstract
We used mixtures of cultivars spanning five decades of selection for yield and agronomic adaptation to ask three questions. First, what is the degree of symmetry in the response of yield to neighbour; this is, if an older, more competitive cultivar increases yield by 10% with a less competitive neighbour in comparison to pure stands, would the newer, less competitive cultivar reduce yield by 10% when grown with older neighbours. Second, what are the yield components underlying competitive interactions. Third, to what extent are the responses to neighbour mediated by radiation, water and nitrogen. A focus on yield components and resources can help the interpretation of shifts in the crop phenotype in response to selection for yield. The rate of genetic gain in yield was 24 kg ha^{-1} yr^{-1} or 0.59% yr^{-1}. A strongly symmetrical yield response to neighbour indicates that a reduction in competitive ability has been the primary driver of yield improvement. Response to neighbour was larger for grain number and biomass than for grain weight and allocation of biomass to grain. Under our experimental conditions, competition for radiation was dominant relative to competition of water and nitrogen. Higher yielding, newer phenotypes had lower competitive ability for radiation but compensated with higher radiation use efficiency. Genetic and agronomic manipulation of the crop phenotype to reduce competitive ability can further improve wheat yield.

Keywords
nitrogen, water, radiation, phenotype, competition, radiation use efficiency

Introduction
The negative correlation between yield and competitive ability has been demonstrated experimentally in species of contrasting physiology and morphology, including cereals, pulses and oilseed crops (Hamblin and Donald, 1974). Theory and empirical evidence for traits underlying the negative correlation between yield and competitive ability are most advanced in maize. For example, high-yielding maize phenotypes sustain plant growth rate at flowering close to the threshold for suppression of ear growth and more erect leaves that allow for higher stand density. In wheat, phenotypes with reduced competitive ability and high yield feature more erect canopies with relaxed extinction of nitrogen relative to the extinction of radiation, and smaller root system with higher nitrogen uptake per unit root length (Aziz et al., 2017; Richards et al., 2019; Sadras and Lawson, 2013). Here we address three questions in mixtures of wheat cultivars spanning five decades of selection for yield and agronomic adaptation. First, what is the degree of symmetry in the response of yield to neighbour. Second, what are the main yield components underlying competitive interactions. Third, to what extent are the responses to neighbour mediated by radiation, water and nitrogen.

Methods
Two experiments were carried out at Roseworthy and at Riverton in 2019. Crops were sown on May 23 at Roseworthy and June 3 at Riverton, were fertilised with ammonium poly-phosphate liquid at 50 L ha^{-1} (23.8% P, 15.9% N), and managed to control of weeds, insects and pathogens. In each location, we established a full factorial combining (a) 16 stands, resulting from all mixtures of four cultivars and pure-stand controls (Fig. 1), (b) two stand densities d = 90 pl m^{-2} and D = 180 pl m^{-2} (high), (c) and two rates of urea fertiliser, n = 0 kg N ha^{-1} and N = 100 kg N ha^{-1}, which was split in two applications at two leaves and the beginning of stem elongation. Cultivars were Halberd (released in

1969), Spear (1984), Mace (2007) and Scepter (2015). Treatments were laid in a split-split-split block design with three replicates; locations were nested with target cultivar (main plot), neighbour (split plot), plant density (split-split plot), and nitrogen randomised. We monitored crop phenology weekly. Shoot biomass was sampled at tillering, anthesis and maturity. We measured NDVI regularly and calculated the fraction of absorbed photosynthetically active radiation (fAPAR) in pure stands using calibrations with NDVI. Radiation use efficiency was calculated as the ratio between biomass at maturity and seasonal APAR. At flowering, we measured the concentration of water soluble carbohydrates (WSC), the nitrogen nutrition index (NNI) to quantify crop nitrogen status, and carbon isotope composition ($\delta^{13}C$) to quantify crop water status. At maturity, shoots were threshed and grain yield and grain weight were determined. The absolute (kg ha^{-1} yr^{-1}) and relative (% yr^{-1}) rate of genetic gain in yield was calculated as the slope of the least square regression between yield in pure stand and year of release (Fischer et al., 2014). The same approach was used to calculate the rate of genetic change in other traits. We defined triads of the form "A**B**A", where B is the target cultivar, A is the neighbour and bold indicates the trait was measured in the target plant. For each trait, we calculated response to neighbour RN (%):

$$RN\ (\%) = 100\ x\ \frac{A\textbf{B}A}{B\textbf{B}B} \qquad \text{eq. 1}$$

We used linear least square regression to relate response to neighbour and the difference in year of release of target and neighbour. Significance of the quadratic term was used to test for departures from linearity.

Results

Yield in pure stands increased linearly with year of release (Fig. 1A) and there were not differences in the relative rate of genetic gain with stand density, nitrogen or their interaction ($p = 0.579$, $s = 0.8$). Genetic gain in yield associated with shorter plants, higher WSC, higher tiller fertility, more grains per m^2, heavier grains, more biomass at maturity and higher harvest index (Fig. 1B).

Halberd, the oldest cultivar in our set, increased yield by 17 ± 0.03 % with the newest cultivar neighbours in comparison to pure stands. Scepter, the newest cultivar, decreased yield by 13 ± 0.05 % with Halberd neighbours in comparison to pure Scepter stands. All 12-pairwise combinations of cultivars grown under 8 conditions aligned in a plot of yield of target cultivar relative to pure stand (eq. 1) and the difference in year of release between target and neighbour (Fig. 2). The fitted line passed through the (0, 100) coordinate ($p < 0.0001$, $s > 13.3$) supporting the conclusion of symmetry in the response of yield to neighbour. The scatter in Fig. 2 was associated with stand density and nitrogen, with slopes from close-to-zero with low density and low nitrogen to -0.36 % y^{-1} for high density and high nitrogen.
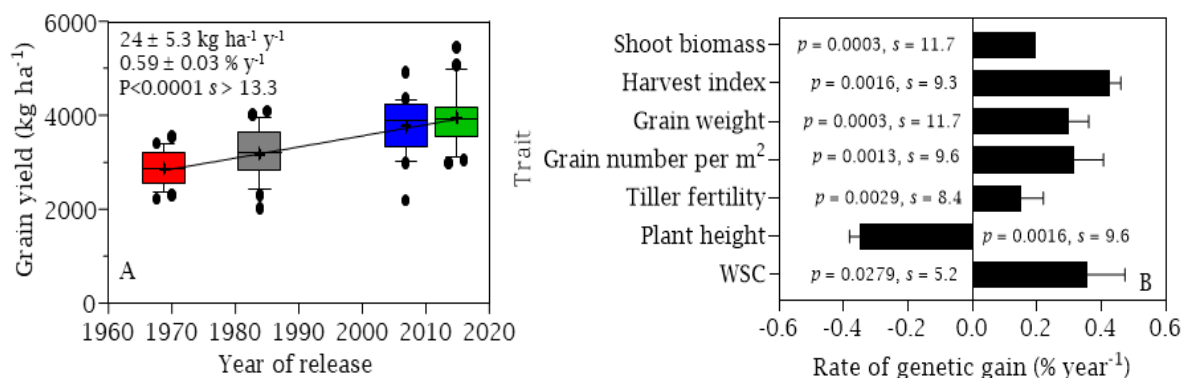

Figure 1. (A) Wheat grain yield in pure stands as a function of year of cultivar release in crops grown under two stand densities (90, 180 plants m^{-2}) and two nitrogen rates (0, 100 kg ha^{-1}) at two locations, (Roseworthy and Riverton) of South Australia. Solid line is the least square regression for data pooled across growing conditions. Absolute (kg ha^{-1} y^{-1}) and relative (% y^{-1}) rates ± s.e. are shown. (B) Relative rate ± s.e. of genetic change in crop traits for the data pooled across growing conditions.
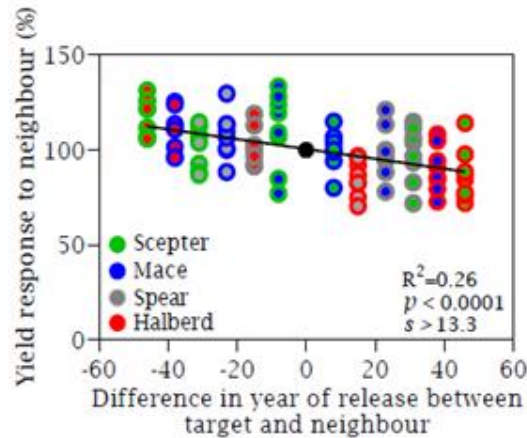
Figure 2. Yield response to neighbour as a function of the difference in year of release between target and neighbour cultivars for data pooled across two stand densities (90 plants m^{-2} and 180 plants m^{-2}), two nitrogen rates (0 kg ha^{-1} and 100 kg ha^{-1}) and two locations, Roseworthy and Riverton. The line is the least-square regression, that passes through the black point representing pure stands, thus emphasising the strong symmetry in response to neighbour.

Newer cultivars were shorter and plant height did not respond to neighbour, except for a slight response in high-nitrogen, low density stands. The area under the NDVI curve was higher for Halberd than for Scepter, and intermediate for the mixture with more marked differences in high-nitrogen, high-density stands (Fig. 3A and 3B). In pure stands, radiation use efficiency increased from older to newer varieties (Fig. 3C).
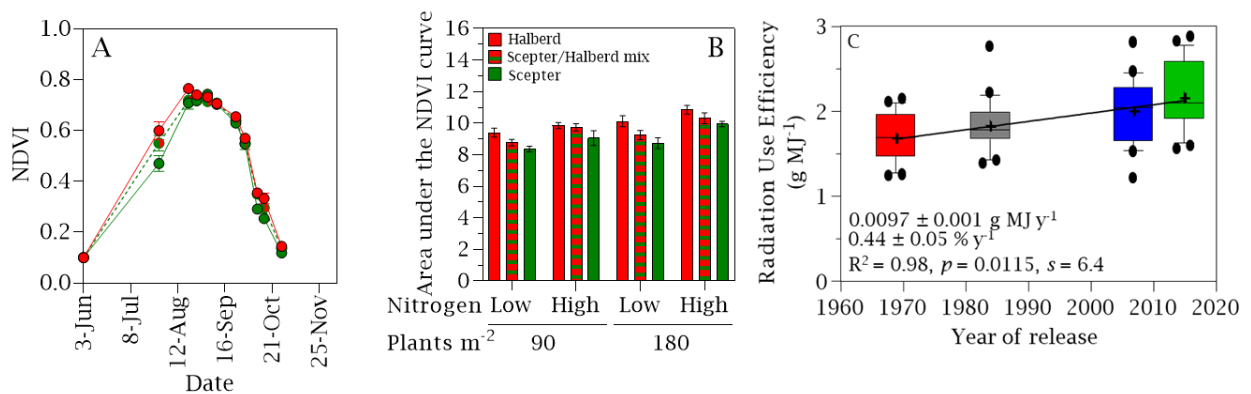

Figure 3. (A) Example of seasonal dynamics of NDVI for Halberd (red), the oldest cultivar; Scepter, the newest cultivar (green), and their mixture (red and green, dashed line). (B) Area under the curve of NDVI dynamics for stands with two population densities and two nitrogen rates, pooled for two locations. In both (A) and (B) error bars are two standard errors of the mean. (C) Radiation use efficiency in pure stands as a function of year of cultivar release.

The δ^{13}C ($0.15<p<0.82$, $0.3<s<2.7$) and the NNI ($0.23<p<0.58$, $0.8<s<2.1$) at anthesis did not respond to neighbour. Shoot biomass at anthesis increased in older cultivars with newer neighbours and decreased symmetrically in newer cultivars with older neighbours in high density stands irrespective of nitrogen supply (data not shown). WSC increased in older cultivars with newer neighbours and *vice-versa* in high nitrogen and high density stands ($p=0.0086$, $s=6.9$), and to a lesser extent in low nitrogen, high density stands ($p=0.09$, $s=3.5$). Low density stands made to increase the WSC in older cultivars with newer neighbours and *vice-versa* at both nitrogen conditions ($0.0023<p<0.0073$, $7.1<s<8.8$).

Discussion

Here we reported a symmetric response of grain yield to neighbour providing new evidence in favour of Donald's communal plant. A high symmetry in the response to neighbour indicates a dominant role of reduced competitive ability as a driver of yield improvement. Symmetry of the response to neighbour was also apparent for yield components tiller fertility, grain number and shoot biomass. Under our experimental conditions, the effect of neighbour was not apparent for water and nitrogen status of plants at anthesis, irrespective of stand density and nitrogen supply. Competition for radiation, closely related to plant height, was therefore the main driver of neighbour effects. In two out of three conditions where yield responded to neighbour, carbohydrate reserves at anthesis also responded to neighbour, reinforcing the dominant role of competition for radiation and carbon assimilation. The superior yield of stands with shorter plants at the core of the Green Revolution was primarily attributed to higher allocation of biomass to grain and reduced lodging with high nitrogen fertiliser. A complementary explanation is that shorter plants are less competitive for radiation; shading during the critical period reduces grain set and yield. Indeed, plant height and canopy geometry are critical to competition for radiation. In our study, older, taller cultivars with more planophile canopies intercepted more radiation than their newer, shorter counterparts with more erect leaves. Higher radiation use efficiency in the newer cultivars compensated for their lower ability to intercept radiation.

Conclusion

Decades of selection for yield and agronomic adaptation shifted key traits from a low yielding, more competitive phenotype (left) to a high yielding, less competitive phenotype (right). The less competitive, higher yielding phenotype is shorter and intercepts less radiation. Higher radiation use efficiency compensates for the lower interception of radiation in the less competitive phenotype. Higher radiation use efficiency is independent of photosynthesis and respiration at leaf level, and relates to an erectophile canopy that favours more radiation and higher nitrogen concentration in leaves at the bottom of the canopy. The less competitive phenotype has a smaller root system with compensatory higher nitrogen uptake per unit root length.

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