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The growth behaviour of winter wheat (*Triticum aestivum* L.) in the presence of inter- and intraspecific neighbours

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Abstract

Competition is an important factor shaping plant communities. We studied the interaction of winter wheat (*Triticum aestivum* L. “AP503cl2”) with neighbouring plant species under controlled greenhouse conditions. We observed that winter wheat leaves growing toward other winter wheat cultivars were shorter when compared with leaves growing toward non-wheat neighbours. The angle between the lateral tillers of neighbours varied as follows: 63° where the neighbours were winter wheat of the same cultivar (“AP503cl2”), 92° where no neighbours exist, and 94°–134° with all other neighbours. Generally, roots were longer compared with the shoots, but more biomass was allocated to the shoots compared with roots.

Key words: *Triticum aestivum* L. “AP503cl2”, intraspecific competition, interspecific competition, angles

Résumé

La concurrence joue un rôle important dans la formation des peuplements végétaux. Les auteurs ont étudié les interactions du blé d’hiver (*Triticum aestivum* L., cultivar AP503cl2) avec les plantes voisines, en serre, dans des conditions contrôlées. Les feuilles du blé d’hiver poussant vers d’autres variétés de blé d’hiver sont plus courtes que celles qui poussent vers les plantes d’une autre espèce. L’angle entre les talles latérales des plants voisins varie comme suit : 63 degrés quand il s’agit de plants de blé d’hiver de la même variété (AP503cl2), 92 degrés en l’absence de voisin et de 94 à 134 degrés au voisinage d’autres plantes. Les racines sont généralement plus longues que les pousses, mais la biomasse des secondes dépasse la biomasse des premières. [Traduit par la Rédaction]

Mots-clés : *Triticum aestivum* L. AP503cl2, concurrence intraspécifique, concurrence interspécifique, angles

Introduction

The presence of neighbours drives plant competition and causes individuals to alter growth to avoid, tolerate, or aggressively confront their neighbours (Novoplansky 2009). Kin selection, or the “recognition of kin” (Hamilton 1964), suggests that a plant’s fitness can be increased by reducing competition potential between related individuals. In the interaction among related individuals, a plant and its relative may “cooperate” and reduce the competition against each other to maintain fitness (Axelrod and Hamilton 1981). The proportion of relatives compared with strangers may be important in shaping plant communities (Mommer et al. 2016), but the impact of relatedness is still not well understood in highly selected crop cultivars and their interactions with other species such as weeds (Yang et al. 2018).

Plants can respond to neighbouring vegetation by altering root allocation, architecture, exudates, and biomass (Biedrzycki and Bais 2010). Many studies have shown that plant root allocations increase when plants grow with dif-

ferent plant species (e.g., Dudley and File 2007; Biedrzycki and Bais 2010). Other studies have shown the opposite: that root allocations decrease when a plant grows with other species (e.g., Callaway and Mahall 2007). Above-ground growth can also be affected by neighbours; *Arabidopsis thaliana* (L.) Heynh. seedlings can re-orient to rotate away and avoid shading their relative neighbours (Crepy and Casal 2014).

The presence of neighbouring species influences the availability of water and nutrients and promotes interaction (competition) among those species. The resource availability within any competitive interaction such as shade avoidance is responsible for the substantial yield loss in major agronomic crops, but the mechanistic understanding of these interspecific interactions is still poorly understood. The objective of this research was to evaluate whether a winter wheat cultivar “AP503cl2” responded differently in the presence of intra- and interspecific neighbours by measuring its above- and below-ground growth.

Materials and methods

Selected species of study

To evaluate intra- and interspecific interactions, we selected winter wheat (*Triticum aestivum* L.) cultivar “AP503cl2” as our focal plant, and included two additional wheat cultivars “Avery” and “Denali”. Other species included three crop species: barley (*Hordeum vulgare* L.), oat (*Avena sativa* L.), and rye (*Secale cereale* L.); and three common weed species: downy brome (*Bromus tectorum* L.), jointed goatgrass (*Aegilops cylindrica* Host.), and foxtail barley (*Hordeum jubatum* L.). These species represent a range of “relatedness” to winter wheat from within the *Poaceae* family.

Experimental procedures and study design

Seeds were germinated in 96-cell germinating trays for 1 week using potting media (bark mix BM7 from Berger®). Focal wheat seedlings were then transplanted into round 0.75 L pots either with or without a neighbour seedling, for a total of up to two plants per pot. Pots were distributed on the same bench within the greenhouse in a completely randomized design. Plants were grown for 8 weeks at a set temperature of 24 °C day/15 °C night without supplemental lighting. Pots were watered once daily without adding any fertilizers.

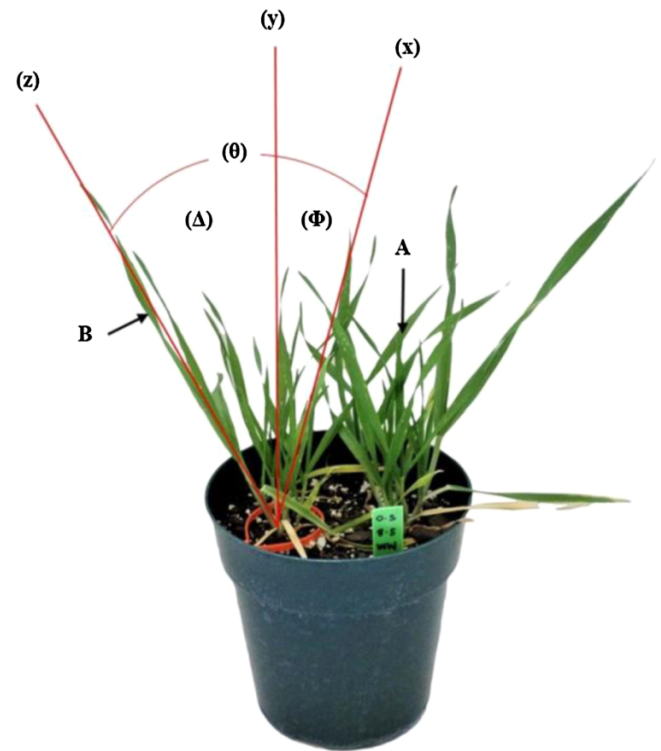
Measurements and statistical analysis

Four weeks after transplanting, leaf angles of the focal plant were measured by taking the angle between the lateral tillers in degrees using a protractor (Fig. 1). The main (original) wheat stem (y) was typically erect at 90° to the horizon. The lateral tiller nearest the neighbouring plant (x) formed an angle Δ with wheat's main stem, $\Delta = 90 - \Delta_0$ ($\Delta_0 < 90^\circ$), while the lateral tiller furthest from the neighbouring plant (z) formed an angle $\Phi = \Phi_0 - 90$ ($\Phi_0 > 90^\circ$). The total plant leaf angle was $\theta = \Delta + \Phi$ ($0^\circ < \theta < 180^\circ$).

At the end of the 8-week experiment, we measured the lengths of outer (away from the neighbour) and inner (toward the neighbour) leaves. Plants were removed from the pots and the total shoot and root lengths were measured. Roots were then washed thoroughly and whole plants were dried at 60 °C for 48 h and then weighed. All measurements were collected on the focal plant only, and not the neighbours.

A mixed-effects ANOVA was conducted using the lme4 package (v1.1-23) and convenience functions from the lmer Test package (v3.1-2) in the R statistical language (R Development Core Team 2015) to determine whether neighbour presence affected growth parameters. For each growth parameter, we first analysed whether winter wheat “AP503cl2” responded differently when grown next to other wheat plants compared with other grass species, assuming that experimental run was a random effect to account for the time of year, wheat cultivar was a random effect within the wheat group, and grass species was a random effect within the non-wheat group. Estimated marginal means were obtained from the model using the emmeans package (v1.4.6) and separated using Tukey-adjusted pairwise comparisons with the mult-

Fig. 1. Winter wheat *Triticum aestivum* L. “AP503cl2” with a neighbour (“AP503cl2”); the focal plant was labelled with an orange stripe. A is the inner leaf (toward the neighbour), B is the outer leaf (out of the pot), x is the right lateral tiller, y is wheat's main stem, z is the left lateral tiller, Δ is the angle between the right lateral tiller (x) and the wheat's main stem (y), Φ is the angle between the left lateral tiller (z) and the wheat's main stem (y), and θ is total plant leaf angle and is equal to $\Delta + \Phi$.



comp package (v1.4-13). We then analysed the response of “AP503cl2” in response to each species separately as a fixed effect, keeping the experiment run as a random effect. The second analysis allowed for better observations of changes compared with no neighbour and also to determine whether there were outliers among the wheat or non-wheat groups in the response they elicited.

Results and discussion

Wheat leaf angles varied by neighbouring species, but the distinction of wheat compared with non-wheat was not a strong predictor of total leaf angle ($P = 0.1037$, Table 1). When the focal wheat was grown without a neighbour, the leaf angle was 92° on average (Table 2). The presence of neighbour of the same cultivar resulted in the most upright growth (62°). All other neighbours resulted in leaf angles between 94° and 134°.

The outer/inner leaf length ratio was greater when “AP503cl2” was grown near other wheat neighbours compared with when it was grown next to non-wheat grass species ($P < 0.001$, Table 1). When the focal plant was grown with another wheat plant, the ratio was > 1 indicating

Table 1. Estimated marginal means for winter wheat “AP503cl2” growth parameters when it was grown with wheat vs. other grass species as a random effect.

Neighbour	Angle	Outer/inner leaf length	Root/shoot length	Root/shoot biomass
Wheat	87	1.2	1.09	0.59
Other grass species	111	0.87	1.26	0.49
P value	0.1037	0.0004	0.1121	0.0872

Table 2. Estimated marginal means for winter wheat “AP503cl2” growth parameters when it was grown with wheat and other grass species as a fixed effect.

Neighbour	Angle	Outer/inner leaf length	Root/shoot length	Root/shoot biomass
AP503cl2*	92ab	1abc	1.98b	0.72c
AP503cl2	62a	1.15bc	1.33a	0.7bc
Avery	104bc	1.21c	0.94a	0.55abc
Denali	96ab	1.24c	1.01a	0.52abc
Barley	102bc	0.98abc	1.34a	0.47a
Oat	101bc	0.94abc	1.26a	0.49abc
Rye	126bc	0.84ab	1.32a	0.48ab
Jointed goatgrass	94ab	0.84a	1.15a	0.48ab
Downy brome	109bc	0.88ab	1.17a	0.59abc
Foxtail barley	134c	0.74a	1.32a	0.41a
P	<0.0001	<0.0001	<0.0001	0.0003

Note: Within column, the values followed by the same letter(s) are not significantly different according to Tukey’s honestly significant different test, $\alpha = 0.05$. * The focal plant was grown without neighbours.

longer leaves away from the kin neighbour (Table 2). Conversely, when grown with non-wheat plants, the focal plant outer/inner leaf length ratio was <1 indicating longer leaves toward the non-kin neighbour. Wheat plants allocated relatively less leaf length toward wheat neighbours and more leaf length toward non-wheat neighbours, suggesting that wheat was reducing light competition toward “kin”. Similar results were reported from studying the wheat/maize intercropping effect (Zhu et al. 2016; Wang et al. 2017), where the inner wheat leaves toward maize in intercropping were longer compared with those in the margins or in the monoculture.

The root/shoot length ratio was reduced by all neighbours compared with when the focal plant was grown alone (Table 2, $P < 0.001$); however, there were no differences in the root:shoot length ratio among neighbouring species. Focal plants consistently allocated more biomass to shoots compared with roots (Table 2), but appeared to allocate slightly more to shoots (e.g., lower root/shoot ratio) when grown near non-wheat neighbours (Table 1; $P = 0.087$), especially if the neighbour was the same cultivar (Table 2). This finding is similar to other works demonstrating that neighbours generally cause a reduction in root/shoot biomass allocation due to shade avoidance responses. Here, it appears that kin plants may result in a less pronounced shade avoidance response.

identity. In response to an intraspecific neighbour, winter wheat “AP503cl2” reduced leaf length in the direction of winter wheat cultivars but increased leaf length in the direction of non-wheat neighbours. Winter wheat “AP503cl2” also decreased root/shoot biomass allocation more in response to non-wheat neighbours. Although the findings from this greenhouse study are relatively limited in scope, they suggest that wheat has the ability to respond differently to its neighbours compared with other species. This has implications for the future of plant breeding and weed management, if further research can elucidate a mechanistic understanding of these altered growth patterns. In unmanaged plant communities, kin selection can increase fitness of a species by ensuring that more individuals survive under limited resources. However, in a wheat crop where many resources are not limited because of irrigation, fertilization, and seeding rate, the altered growth of the wheat plants in an effort to be “altruistic” may be maladaptive to total yield potential. Conversely, the response we observed here may be a result of breeding under resource-rich, high-density conditions, and the observed traits may actually be maladaptive under natural conditions. A better understanding of intra- and interspecies plant competitive interactions can only improve crop production efficiency over the long term by increasing yield potential under different environments, or identifying traits that allow crops to tolerate, avoid, or compete aggressively with other species.

Conclusions

The growth and architecture of winter wheat “AP503cl2” in the presence of neighbours depend on the neighbour’s

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