# Effects of intra-variety root competition and soil fertility on resource allocation in a modern wheat variety and an old landrace

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## Abstract

Darwinian agriculture (also called Evolutionary agroecology) which focuses on the trade-off between individual fitness and community performance, can provide an efficient approach to enhance crop production. However, evolutionary or ecological processes, in particular the tragedy of the commons in crops, remain poorly understood. We used a pot experiment to examine whether wheat plants fell into this 'tragedy' when confronted with roots of an intra-variety neighbour and how the magnitude was influenced by soil fertility. Two varieties (old landrace Monkhead and modern variety 92-46) were selected for this study. Root competition scenarios were set by growing two plants of the same variety with a mesh or plastic partition. Soil fertility gradients were set by adding nutrient solutions with low or high application frequency. Biomass were tested and allometric relationship were analyzed to reveal resource allocation pattern. Old Monkhead had similar relative allocation to root biomass with modern 92-46, but had greater relative allocation to stem&leaf biomass and lower relative allocation to seed biomass. The presence of neighbour affected allometric relationships only in 4 out of 24 allometic comparisons, which all appeared in low fertility treatments. Fertilizer addition increased stem&leaf biomass allocation of Monkhead and decreased root and seed biomass allocation at the same time. By contrast, stem&leaf and seed allocation of 92-46 was not changed by fertilizer addition although root allocation was decreased. Our results demonstrated that there was a trade-off between non-reproductive and reproductive allocation for wheat varieties. There was not notable tragedy of the commons in wheat varieties, although a small degree was observed in Monkhead. Moreover, the occurrence and magnitude of the tragedy was dependent on resource availability and variety resource-use strategy. Our results underlie the importance of understanding the mechanisms behind the tragedy of the commons in crop varieties with different ecological strategies, and provide insights into the role of Darwinian agriculture in global food production.

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## Abstract

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**Keywords:** Root competition; Resource allocation; Growth redundancy; The tragedy of the commons; Trade-offs

## Introduction

In recent years, researchers or plant breeders have applied evolutionary or ecological theories to improve crop yields while maintaining or increasing agricultural sustainability, an approach called Darwinian agriculture (Denison et al. 2003; Denison 2012) or Evolutionary agroecology (Weiner et al. 2010; 2017). This approach can provide an efficient and correct solution to global crop risks through group selection for crop genotypes that have low individual fitness and high population yields (Zhang et al. 1999; Denison et al. 2003; Denison 2012; Weiner 2019).

In crop stands, genotypes of high competitiveness allocate more photosynthetic products to vegetative organs for capturing limiting resources, suppress weak competitors (e.g. Donald's ideotypes), and thus can be favoured by natural selection (Donald 1968). However, high individual competitive ability can have negative effects on other individuals and results in declines in population yield (Zhang et al. 1999; Weiner et al. 2017). It has been recognized that breeders should practice group selection to maximize the collective performance of crops (Weiner et al. 2010; Denison 2012). It has long been argued that high-yielding ideotypes should be weak competitors (Donald 1968). For example, the dwarf cereal varieties which contributed greatly to the green revolution (Borlaug 2007), are less competitive for light compared with taller varieties (Jennings and de Jesus 1968).

When competing for a common pool of resources crop plants increase growth of vegetative organs at the expense of reproductive growth (Zhang et al. 1999; Gersani et al. 2001; Maina et al. 2002; Padilla et al. 2013), resulting in a phenomenon called 'tragedy of the commons' (Hardin 1968). We expect that crop plants of higher competitiveness and growth redundancy have greater expression of the tragedy of the commons. However, direct empirical studies testing sensitivity to the tragedy of the commons in crop varieties remain rare.

The tragedy of the commons can arise if plants can detect and discriminate between their own roots and roots of their neighbours (i.e. self/non-self discrimination). The magnitude of the tragedy of the commons caused by root competition in crop plants may decline in fertile soil, because high soil fertility can decrease nutrient limitation for plant growth and alleviate competition below-ground between individual plants (O'Brien et al. 2005; Schenk 2006; de Kroon et al. 2012). On the global scale, plant species can be put along a continuum with exploitative and conservative growth strategies as two ends according to their resource environment they adapt to (Reich 2004; Wright et al. 2004). Exploitative species are characterized by traits related to resource-rich habitats including high resource acquisition and individual competitiveness, while conservative species have the opposite characteristic combination (Maire et al. 2009; Wooliver et al. 2016). We expect that crop varieties would possess different sensitivities to competition with neighbour plants if they are selected artificially under different resource (water and fertilization) conditions (Zhu and Zhang 2013; Weiner et al. 2017). However, little is known on how the magnitude of the tragedy of the commons varies in relation to resource availability.

Previous studies on the tragedy of the commons often involve treatments that provide a constant rooting space and amount of nutrients per plant (Gersani et al. 2001; Maina et al. 2002; O'Brien et al. 2005). However, this results in plants that share rooting space with a neighbour potentially having access to twice as much volume as plants grown alone (Schenk 2006; Semchenko et al. 2007; Semchenko et al. 2017). Thus, effects of detection of neighbours may be confounded with effects of size of rooting volume for each competitor (Hess and de Kroon 2007; Semchenko et al. 2007). Previous studies have shown that plant production increases in response to the increase in the volume to which a plant has access (McConnaughay and Bazzaz 1991; Hess and de Kroon 2007). To solve this problem, Semchenko et al. (2007) used a 'mesh partition' to separate two plants in a pot which halved the volume but allowed competition, in which each plant had access to the same volume as plants separated by a 'plastic partition'.

In this research, we adopted the method of Semchenko et al. to set up mesh partition and plastic partition (Semchenko et al. 2007), examining the responses of two varieties from different eras to the presence of intra-variety neighbours and changes in soil fertility. Old Monkhead was the local landrace and modern 92-46 was released in 2000. Both were widely grown in semi-arid areas in Gansu Province; modern 92-46 has a smaller root system but higher grain yield than old Monkhead (Zhu and Zhang 2013). We make the following predictions: (1) modern 92-46 has more reproductive allocation and less allocation to non-reproductive components than old Monkhead; (2) old Monkhead has a greater expression of the tragedy of the commons than modern 92-46; (3) the occurrence and magnitude of the tragedy of the commons is dependent on soil fertility.

## Materials and methods

### Materials

Spring wheat ( *Triticum aestivum* ) is the main grain crop in semi-arid areas of Northwest China. Monkhead, the local variety, was widely grown in 1940s. Modern 92-46 was released in 2000 and was widely grown at the beginning of 21 century. The two varieties have similar phenology, but Monkhead is awnless and highly tillering, thus can be easily distinguished from 92-46 when harvested (Zhu and Zhang 2013).

### Methods

We conducted a pot experiment in the greenhouse in Beijing Normal University from May until August in 2011. A randomized block design was used with three factors including root partition (two levels: plastic partition and mesh partition, Fig. 1), soil fertility (two levels: low fertility and high fertility) and varieties (two levels: Monkhead and 92-46). All experimental treatments were repeated 20 times with a total of 160 pots.

To set up partitions, we firstly put two nylon net bags (aperture size 20μ) filled with vermiculite into one pot (made by PVC pipes, 16cm diameter and 48cm long) which were equally separated by a plastic composite panel. Secondly, in mesh partition treatments, we removed the plastic composite panels, which permitted the movement of soil nutrients and root exudates from one side to the other while preventing direct contact between roots of the two individuals. In plastic partitions, the edges between the pots and the partitions were sealed with silicon (Fig. 1). In either plastic partition or mesh partition, all individuals have access to half volume of the pot, which enabled us to eliminate the effect of soil volume which might be confounded with effects of detection of neighbours (Semchenko et al. 2007). In low fertility treatments, pots were watered with nutrient solution (0.2 g L$^{-1}$ Peter's professional) until saturation every 14 days (1.6 L every 14 days), while in high fertility treatments, pots were watered every day (0.4 L every day).

All seeds were vernalized at 4 °C for one day, germinated at 25 °C. Two seedlings were transplanted into the pot with each in the centre of each half. Spike, stem&leaf and root were harvested at maturity for each individual plant. Roots were separated from the substrate and cleaned with tap water. All samples were dried at 65 °C to a constant weight and weighed. Seeds of each plant peeled out from ears were counted and weighed.

### Statistical analyses

We used a three-way ANOVA to test for the effects of partition treatments, wheat varieties and soil fertility on tiller number and plant biomass. Differences between treatments were determined by running SNK multiple comparisons. ANOVA was conducted with SPSS statistical software (version 17.0; SPSS Inc., Chicago, IL, USA).

We compared static allometric relationships between treatments using standardized major axis regression (SMA), in which whole-individual biomass was taken as the independent variable, and biomass of different parts (i.e. root, stem&leaf and seed biomass) as the dependent variables (Müller et al. 2000; Weiner 2004). Given that biomass variables are interdependent, the Model Type II regression was used to reduce measurement errors associated with allometric data (Henry and Aarssen 1999; Niklas 2006). The slopes of regression lines were compared by running multiple post-hoc multiple comparisons. SMA analyses were conducted using the Standardized Major Axis Tests and Routines (SMATR) 2.0 (Warton et al. 2006). Biomass data were log-transformed before analysis when necessary to improve normality of residuals and homogeneity of variances.

## Results

### Tiller number and plant biomass

Tiller number was significantly greater in Monkhead compared with 92-46, but tiller number generally increased in high fertility irrespective of variety (Table 1, Fig. 2a). Increase of tiller number in response to fertilizer addition was more in Monkhead compared with 92-46 (significant Variety × Fertility interaction, Table 1, Fig. 2a). Root biomass and stem&leaf biomass were greater in Monkhead (Table 1, Fig. 2b-c), but there was no significant difference in seed biomass between the two wheat varieties (Table 1, Fig. 2d). Fertilizer addition increased plant biomass in all plant components (Table 1, Fig. 2). Root and stem&leaf biomass responses to fertility differed between the two varieties (significant Variety × Fertility interaction, Table 1), with Monkhead showing more pronounced responses to high fertility compared with 92-46 (Fig. 2b-c). We did not detect significant interactions between variety and fertility for seed biomass (Table 1, Fig. 2d). There were no significant effects of partition treatments on tiller number or biomass, and we did not detect significant Variety × Partition interactions, Fertility × Partition interactions or Variety × Fertility × Partition interactions (Table 1).

### Allometric relationships

We found significant linear relationships between whole plant biomass and reproductive or non-reproductive components across treatments (Table 2). In root-total relationships, the slope and intercept were similar between Monkhead and 92-46 at either fertility level (Table 2, Fig. 3a-b). Fertilizer addition did not affect the slope but lower the intercept for both varieties (Table 2, Fig. 3a-b). In (stem+leaf)-total relationships, the slope was similar between the two varieties whilst the intercept for Monkhead was greater than that of 92-46 at either fertility level (Table 2, Fig. 3c-d). Fertilizer addition did not affect the slope for both varieties and the intercept for 92-46, but increased the intercept for Monkhead (Table 2, Fig. 3c-d). In seed-total relationships, the slope for Monkhead was greater than that of 92-46 whilst the intercept was lower at either fertility level (Table 2, Fig. 3e-f). Fertilizer addition did not affect the slope for both varieties and the intercept for 92-46, but decreased the intercept for Monkhead (Table 2, Fig. 3e-f).

In all 24 allometic comparisons (both slopes and intercepts) between mesh partition and plastic partition, only 4 showed small differences in slope or intercepts, and all of them were in low fertility treatments (Table 3, Appendix 1 and 2 ). For Monkhead in low fertility treatments, the intercept in seed-total biomass regression was lower in mesh partition than in plastic partition, whilst in (stem+leaf)-total biomass regression was greater (Table 3, Appendix 1c and e). For 92-46 in low fertility treatments, the slope in root-total biomass regression was greater in mesh partition whilst the intercept was lower (Table 3, Appendix 1b).

## Discussion

### Modern 92-46 had greater relative seed production by reducing stem&leaf allocation

Previous studies suggest that modern crop varieties have higher population yields, but lower competitive ability and individual fitness (Zhang et al. 1999; Zhai et al. 2016; Weiner et al. 2017). Our first prediction was based on these findings and was supported by our results in this research, which showed that old Monkhead had significantly greater stem&leaf and root biomass than modern 92-46, but the two wheat varieties had similar seed production per individual plant (Fig. 2). Static allometric analysis suggested that there were no significant differences in root-total allometric relationship between Monkhead and 92-46 regardless of fertility levels (Table 2, Fig. 3a-b). However, Monkhead had greater relative allocation to stem&leaf biomass than modern 92-46 (i.e. greater intercepts of the stem&leaf biomass – total biomass regression, Table 2, Fig. 3c-d), and lower relative allocation to seed biomass (i.e. lower intercepts of the seed biomass – total biomass regression, Table 2, Fig. 3e-f). This is to say, modern 92-46 consumed less resources / biomass to produce the same amount of seeds compared to old Monkhead, reflecting more efficient conversion of vegetative biomass to reproductive biomass (Weiner 2004).

Our results provided evidence that there was a trade-off between non-reproductive and reproductive allocation for these wheat varieties (Zhang et al. 1999). However, our findings were not in line with previous studies that found root redundancy in old grain plant varieties (Siddique et al. 1990; Semchenko et al. 2007), and did not confirm our previous experimental finding that old Monkhead had more root redundancy than modern 92-46 (Zhu and Zhang 2013). To be caution, however, these previous studies tested root redundancy or allocation patterns using absolute root biomass or biomass ratio perspectives, and indeed these analysis approaches have been criticized that they confound effects of plant size on resource allocations because plant growth is allometric (Weiner et al. 2009; Qin et al. 2012; Du et al. 2020). It is possible that the magnitude of root redundancy of old Monkhead was over-estimated in our previous study (Zhu and Zhang 2013). The presence of stem&leaf redundancy in old Monkhead in the present study may simply reflect greater tiller number in individual plants (Fig. 2a), and an increased cost of stem&leaf biomass in producing unit seed biomass. Moreover, light competition is likely to be more intense than nutrient competition in our system because plants tend to allocate more resources to stems and leaves to obtain size-asymmetric advantages over neighbouring plants (Schwinning and Weiner 1998; Zhang et al. 1999), resulting in a greater risk of stem&leaf redundancy.

### No notable tragedy of the commons was found in Monkhead or in 92-46

Pot partitioning treatments allowed us to exclude confounding effects of rooting space when testing plant responses to neighbours (Semchenko et al. 2007). We predicted that old Monkhead would have a greater expression of the tragedy of the commons than modern 92-46. However, our results showed that most allometric relationships were not affected by the presence of roots from an intra-variety neighbour (Table 3, Appendix 1, 2), which suggested stable allometric relationships in wheat crop when confronted with root competition. However, in low fertility treatments, old Monkhead did show some tragedy of the commons, with slightly increased allocation to stem&leaf biomass whilst reduced seed allocation in mesh partition compared with plastic partition (Table 3, Appendix 1c and e). This slightly allometric plasticity due to competition was also found in a research in *Senecio vulgaris*(Weiner, 2009). Anyway, as the magnitude of 'the tragedy of the commons' was small, they might not have ecological and agricultural significance. However, in a recently research, both Monkhead and another modern variety showed significant root proliferation in the presence of neighbour's roots and the response was much higher in Monkhead (Zhu et al., 2019). More researches using more varieties were needed to examine the universality of this tragedy of the commons. Moreover, old Monkhead increased relative stem&leaf allocation in the presence of root competition, indicating the capacity of neighbour-identity recognition via the phytochrome system (Smith 2000) or root exudates (Dudley and File 2007; Chen et al. 2012; Fang et al. 2013; Kong et al. 2018).

### The occurrence and magnitude of the tragedy of the commons were affected by soil fertility

In low fertility, old Monkhead showed some tragedy of the commons and modern 92-46 changed the slope of root-total allometic relationships when confronted with an intra-variety neighbour, whilst in high fertility all these patterns disappeared and both varieties showed consistent allocation trajectories between two partition treatments (Table 3). Therefore, our results provided support for the third hypothesis that the occurrence and magnitude of the tragedy of the commons were affected by soil fertility. Different fertilization effects on the old and modern varieties were likely to be driven by different resource strategies and sensitivity to competitive environments (Semchenko and Zobel 2005; Guo et al. 2012; Wang et al. 2014).

Modern varieties which were subjected to human domestication to improve seed yield often possess a smaller root system, shorter root length and smaller diameter of the metaxylem vessels of the seminal roots (Li and Zhang 1999). These characteristics in modern 92-46 make cooperation between individuals possible when confronted with neighbour's roots. Landraces and old varieties were subjected to long-term natural selection under high-input nutrient conditions (Roucou et al. 2018), and thus resulted in exploitative resource strategies represented by higher growth rates, larger root systems, larger fine-root proportion, and these landraces are likely limited more by light than soil nutrients.

Different resource strategies may result in between-species differences in plant – plant interactions, with resource-exploitative old landraces being more plastic in response to light competition compared with resource-conservative modern varieties. Our results were consistent with this idea; old Monkhead showed significant changes in relative allocation to stems and leaves across fertilization rates, whereas no change was recorded for modern 92-46 (Table 2, Fig. 3c-d). We deduced that under low fertility rates, plant communications were likely mediated by root recognition (Dudley and File 2007; Chen et al. 2012), because of higher relative allocation to root biomass and lower tiller numbers in wheat varieties which minimized extensive between-individual communications at the level of above-ground organs. Under high fertility rates, the lack of differences in allometric relationships between plants in two partition treatments potentially reflected that above-ground sensing had dominated plant communications via the photochrome system (Smith 2000), and that individual plants could develop extensive communications even in the plastic partition treatments due to higher relative allocation to stem&leaf biomass and greater tiller numbers. However, future work is needed to examine whether the occurrence and magnitude of the tragedy of the commons varies with soil fertility by experimentally separating plant communications between above-ground and below-ground components.

## Conclusions

In conclusion, our results suggested that modern wheat allocated more resource to reproduction than to vegetative growth. Old Monkhead can fall into a small degree of the tragedy of the commons when confronting with intra-variety root competition, and the occurrence and magnitude of the tragedy of the commons were dependent on resource availability and variety resource-use strategy. Modern 92-46 has shown a conservative strategy related to efficiency in seed production, while old Monkhead has adopted an exploitative resource strategy related to greater individual competitiveness. Based on our findings, we suggest that crop breeding can increase population yield by consciously selecting varieties which reduce individual competitiveness.

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## Conflict of Interest

The authors declare that they have no conflict of interest.

## Data Availability Statement

The data that supports the findings of this study are available from Dryad: https://doi.org/10.5061/dryad.3bk3j9kkg

## References

Borlaug NE (2007) Sixty-two years of fighting hunger: personal recollections. Euphytica 157: 287-297. https://doi.org/10.1007/s10681-007-9480-9

Callaway R, Brooker R, Choler P, Choler P, Kikvidze Z, Lortie CJ, Michalet R, Paolini L, Pugnaire FI, Newingham B, Aschehoug ET, Armas C, Kikodze D, Cook BJ (2002) Positive interactions among alpine plants increase with stress. Nature 417: 844-848. https://doi.org/10.1038/nature00812.

Chen BJW, During HJ, Anten NPR (2012) Detect thy neighbor: identity recognition at the root level in plants. Plant Sci 195: 157-167. https://doi.org/10.1016/j.plantsci.2012.07.006.

de Kroon H, Hendriks M, van Ruijven J, Ravenek J, Padilla FM, Jongejans E, Visser E, Mommer L (2012) Root responses to nutrients and soil biota: drivers of species coexistence and ecosystem productivity. J Ecol 100: 6-15. https://doi.org/10.1111/j.1365-2745.2011.01906.x.

Denison RF (2012) Darwinian Agriculture: How understanding evolution can improve agriculture. Princeton University Press, Princeton.

Denison RF, Kiers ET, West SA (2003) Darwinian agriculture: when can humans find solutions beyond the reach of natural selection? Q Rev Biol 78: 145-168. https://doi.org/10.1086/374951.

Donald CM (1968) The breeding of crop ideotypes. Euphytica 17: 385-403. https://doi.org/10.1007/BF00056241.

Dudley SA, File AL (2007) Kin recognition in an annual plant. Biol Lett 3: 435-438. https://doi.org/10.1098/rsbl.2007.0232.

Du YL, Xi Y, Cui T, Anten NPR, Weiner J, Li XM, Turner NC, Zhao YM, Li FM (2020) Yield components, reproductive allometry and the tradeoff between grain yield and yield stability in dryland spring wheat. Field Crops Res. 257: 107930.

Fang SQ, Clark RT, Zheng Y, Iyer-Pascuzzi AS, Weitz JS, Kochian LV, Edelsbrunner H, Liao H, Benfey PN (2013) Genotypic recognition and spatial responses by rice roots. Proc Natl Acad Sci USA 110: 2670-2675. https://doi.org/10.1073/pnas.1222821110/-/DCSupplemental.

Gersani M, Brown JS, O'Brien EE, Maina GM, Abramsky Z (2001) Tragedy of the commons as a result of root competition. J Ecol 89: 660-669. https://doi.org/10.1046/j.0022-0477.2001.00609.x.

Guo H, Weiner J, Mazer S, Zhao Z, Du G, Li B (2012) Reproductive allometry in Pedicularis species changes with elevation. J Ecol 100: 452-458. https://doi.org/10.1111/j.1365-2745.2011.01884.x.

Hardin G (1968) The tragedy of the commons. Science 162: 1243-1248.

Henry HAL, Aarssen LW (1999) The interpretation of stem diameter-height allometry in trees: biomechanical constraints, neighbor effects, or biased regressions? Ecol Lett 2: 89-97. https://doi.org/doi: 10.1046/j.1461-0248.1999.22054.x.

Hess L, de Kroon H (2007) Effects of rooting volume and nutrient availability as an alternative explanation for root self/non-self discrimination. J Ecol 95: 241-251. https://doi.org/10.1111/j.1365-2745.2006.01204.x.

Jennings PR, de Jesus J (1968) Studies on competition in rice. I. Competition in mixtures of varieties. Evolution 22: 119-124.

*https://doi.org/10.1111/j.1558-5646.1968.tb03455.x.*

Kong CH, Zhang SZ, Li YH, Xia ZC, Yang XF, Meiners SJ, Wang P (2018) Plant neighbor detection and allelochemical response are driven by root-secreted signaling chemicals. Nature communications 9:3867. https://doi.org/10.1038/s41467-018-06429-1.

Li H, Zhang DY (1999) Morphological characteristics and growth redundancy of spring wheat root system in semi-arid regions. Chinese Journal of Applied Ecology 10: 26-30 (in Chinese with English abstract).

Müller I, Schmid B, Weiner J (2000) The effect of nutrient availability on biomass allocation patterns in 27 species of herbaceous plants. Perspect Plant Ecol Evol Syst 3: 115-127. https://doi.org/10.1078/1433-8319-00007.

Maina GG, Brown JS, Gersani M (2002) Intra-plant versus inter-plant root competition in beans: avoidance, resource matching or tragedy of the commons. Plant Ecol 160: 235-247. https://doi.org/10.1023/A:1015822003011.

Maire V, Gross N, da Silveira Pontes L, Picon-Cochard C, Soussana J-F (2009) Trade-off between root nitrogen acquisition and shoot nitrogen utilization across 13 co-occurring pasture grass species. Funct Ecol 23: 668-679. https://doi.org/10.1111/j.1365-2435.2009.01557.x.

McConnaughay KDM, Bazzaz FA (1991) Is physical space a soil resource? Ecology 72: 94-103. https://doi.org/10.2307/1938905.

Niklas KJ (2006) Plant allometry, leaf nitrogen and phosphorus stoichiometry, and interspecific trends in annual growth rates. Ann Bot 97: 155-163. https://doi.org/10.1093/aob/mcj021.

O'Brien EE, Gersani M, Brown JS (2005) Root proliferation and seed yield in response to spatial heterogeneity of below-ground competition. New Phytol 168: 401-412. https://doi.org/10.1111/j.1469-8137.2005.01520.x.

Padilla FM, Mommer L, de Caluwe H, Smit-Tiekstra A, Wagemaker CHM, Ouborg NJ, de Kroon H (2013) Early root overproduction not triggered by nutrients decisive for competitive success belowground. PLos One 8: e55805. https://doi.org/10.1371/journal.pone.0055805.

Qin X, Niklas KJ, Qin L, Xiong Y, Li F (2012) The effects of domestication on the scaling of below- vs. aboveground biomass in four selected wheat (Triticum; Poaceae) genotypes. Am J Bot 99: 1112-1117. https://doi.org/10.3732/ajb.1100366.

Reich PB (2004) The world-wide 'fast–slow' plant economics spectrum: a traits manifesto. J Ecol 102: 275-301. https://doi.org/10.1111/1365-2745.12211.

Roucou A, Violle C, Fort F, Roumet P, Ecarnot M, Vile D (2018) Shifts in plant functional strategies over the course of wheat domestication. J Appl Ecol 55: 1-13. https://doi.org/10.1111/1365-2664.13029.

Schenk HJ (2006) Root competition: beyond resource depletion. J Ecol 94: 725-739. https://doi.org/10.1111/j.1365-2745.2006.01124.x.

Schwinning M, Weiner J (1998) Mechanisms determining the degree of size asymmetry in competition among plants. Oecologia 113: 447-455. https://doi.org/doi: 10.1007/s004420050397.

Semchenko M, Hutchings MJ, John EA (2007) Challenging the tragedy of the commons in root competition: confounding effects of neighbour presence and substrate volume. J Ecol 95: 252-260. https://doi.org/10.1111/j.1365-2745.2007.01210.x.

Semchenko M, Saar S, Lepik A (2017) Intraspecific genetic diversity modulates plant–soil feedback and nutrient cycling. New Phytol 216: 90-98. https://doi.org/10.1111/nph.14653.

Semchenko M, Zobel K (2005) The effect of breeding on allometry and phenotypic plasticity in four varieties of oat ( *Avena sativa L.* ). Field Crops Res 93: 151-168. https://doi.org/10.1016/j.fcr.2004.09.019.

Siddique KHM, Belford RK, Tennant D (1990) Root:shoot ratios of old and modern, tall and semi-dwarf wheats in a Mediterranean environment. Plant Soil 121: 89-98. https://doi.org/10.1007/BF00013101.

Smith H (2000) Phytochromes and light signal perception by plants—an emerging synthesis. Nature 407: 585-591.

Tilman D, Balzer C, Hill J, Befort BL (2011) Global food demand and the sustainable intensification of agriculture. Proc Natl Acad Sci USA 108: 20260-20264. https://doi.org/10.1073/pnas.1116437108.

Wang P, Weiner J, Cahill JF, Zhou DW, Bian HF, Song YT, Sheng LX (2014) Shoot competition, root competition and reproductive allocation in*Chenopodium acuminatum* . J Ecol 102: 1688-1696. https://doi.org/10.1111/1365-2745.12313.

Warton DI, Wright IJ, Falster DS, Westoby M (2006) Bivariate line-fitting methods for allometry. Biological Reviews 81: 259-291. https://doi.org/10.1017/S1464793106007007.

Weiner J (2004) Allocation, plasticity and allometry in plants. Perspect Plant Ecol Evol Syst 6: 207-215. https://doi.org/10.1078/1433-8319-00083.

Weiner J (2019) Looking in the wrong direction for higher-yielding crop genotypes. Trends Plant Sci 24: 927-933. https://doi.org/10.1016/j.tplants.2019.07.001.

Weiner J, Andersen SB, Wille WKM, Griepentrog HW, Olsen JM (2010) Evolutionary agroecology: the potential for cooperative, high density, weed-suppressing cereals. Evolutionary Applications 3: 473-479. https://doi.org/10.1111/j.1752-4571.2010.00144.x.

Weiner J, Du Y, Zhang C, Qin X, Li F (2017) Evolutionary agroecology: individual fitness and population yield in wheat (*Triticum aestivum* ). Ecology 98: 2261-2266. https://doi.org/10.1002/ecy.1934.

Weiner J, Rosenmeier L, Massoni ES, Vera JN, Plaza EH, Sebastia MT (2009) Is reproductive allocation in *Senecio vulgaris* plastic? Botany-botanique 87: 475-481. https://doi.org/10.1139/B09-012.

Wooliver R, Pfennigwerth AA, Bailey JK, Schweitzer JA (2016) Plant functional constraints guide macroevolutionary trade-offs in competitive and conservative growth responses to nitrogen. Funct Ecol 30: 1099-1108. https://doi.org/10.1111/1365-2435.12648.

Wright IJ, Reich PB, Westoby M, Ackerly DD, Baruch Z, Bongers F, Cavender-Bares J, Chapin T, Cornelissen JHC, Diemer M, Flexas J, Garnier E, Groom PK, Gulias J, Hikosaka K, Lamont BB, Lee T, Lee W, Lusk C, Midgley JJ, Navas M-L, Niinemets U, Oleksyn J, Osada N, Poorter H, Poot P, Prior L, Pyankov VI, Roumet C, Thomas SC, Tjoelker MG, Veneklaas EJ, Villar R (2004) The worldwide leaf economics spectrum. Nature 428: 821-827. https://doi.org/10.1038/nature02403.

Zhai L, Xie R, Wang P, Liu G, Fan P, Li S (2016) Impact of recent breeding history on the competitiveness of Chinese maize hybrids. Field Crops Res 191: 75-82. https://doi.org/10.1016/j.fcr.2016.02.017.

Zhang DY, Sun GJ, Jiang XH (1999) Donald's ideotype and growth redundancy: a game theoretical analysis. Field Crops Res 61: 179-187. https://doi.org/10.1016/S0378-4290(98)00156-7.

Zhu L, Zhang DY (2013) Donald's ideotype and growth redundancy: a pot experimental test using an old and a modern spring wheat cultivar. Plos One 8: e70006. https://doi.org/10.1371/journal.pone.0070006.

Zhu YH, Weiner J, Li FM (2019) Root proliferation in response to neighbouring roots in wheat (*Triticum aestivum* ). Basic Appl Ecol 39: 10-14.

**Table 1** Effects of variety, soil fertility and partition on tiller number and biomass. $F$ and $P$ values are shown.

| Factors | *df* | Tiller number<br>*F* | Tiller number<br>*P* | Root biomass<br>*F* | Root biomass<br>*P* | stem&leaf biomass<br>*F* | stem&leaf bioma<br>*P* |
|---|---|---|---|---|---|---|---|
| Cultivar (C) | | 1061.185 | **<0.001** | 501.757 | **<0.001** | 948.540 | **<0.001** |
| Fertility (F) | | 658.706 | **<0.001** | 277.922 | **<0.001** | 1156.570 | **<0.001** |
| Partition (P) | | 0.456 | 0.500 | 0.044 | 0.834 | 2.130 | 0.146 |
| C × F | | 188.419 | **<0.001** | 151.220 | **<0.001** | 375.146 | **<0.001** |
| C × P | | 0.290 | 0.591 | 0.489 | 0.485 | 0.038 | 0.846 |
| F × P | | 0.023 | 0.879 | 1.439 | 0.232 | 0.061 | 0.805 |
| C × F × P | | 1.599 | 0.208 | 1.602 | 0.208 | 0.510 | 0.476 |

**Table 2** Standardized major axis regressions for log-transformed data of root, seed, stem&leaf biomass and whole plant biomass of Monkhead and 92-46 varieties. L = low fertility; H = high fertility. Slopes and intercepts with different letters are significantly different among treatments.

| Regressions | Treatments | Treatments | Slopes (95% CI) | Intercept (95% CI) | $R^2$ | *P* |
|---|---|---|---|---|---|---|
| Root ˜ whole plant | L | Monkhead | 1.69a (1.30,2.19) | -1.50**a** (-1.80,-1.20) | 0.37 | <0.001 |
| | | 92-46 | 1.49a (1.26,1.76) | -1.40**a** (-1.49,-1.32) | 0.74 | <0.001 |
| | H | Monkhead | 1.47a (1.14,1.89) | -1.64**b** (-2.10,-1.18) | 0.38 | <0.001 |
| | | 92-46 | 1.75a (1.54,1.99) | -1.97**b** (-2.14,-1.79) | 0.85 | <0.001 |
| stem&leaf ˜ whole plant | L | Monkhead | 0.95a (0.84,1.08) | -0.23**b** (-0.32,-0.15) | 0.85 | <0.001 |
| | | 92-46 | 0.96a (0.86,1.08) | -0.32**c** (-0.36,-0.28) | 0.88 | <0.001 |
| | H | Monkhead | 0.87a (0.75,1.00) | -0.04**a** (-0.19,0.10) | 0.81 | <0.001 |
| | | 92-46 | 1.08a (0.95,1.23) | -0.37**c** (-0.48,-0.26) | 0.84 | <0.001 |
| Seed ˜ whole plant | L | Monkhead | 2.31**a** (1.89,2.83) | -1.69**b** (-2.01,-1.37) | 0.61 | <0.001 |
| | | 92-46 | 1.31**b** (1.14,1.52) | -0.67**a** (-0.74,-0.60) | 0.81 | <0.001 |
| | H | Monkhead | 2.89**a** (2.28,3.67) | -3.30**c** (-4.14,-2.47) | 0.47 | <0.001 |
| | | 92-46 | 1.29**b** (1.05,1.59) | -0.82**a** (-1.04,-0.61) | 0.60 | <0.001 |

**Table 3** Standardized major axis regression for log-transformed data of root, stem&leaf, seed and whole plant biomass across root partition treatments in the two fertility treatments. L = low fertility; H = high fertility; MP = mesh partition; PP = plastic partition. Slopes or intercepts with different letters are different between partition treatments.

| Treatments | Treatments | Treatments | Monkhead variety<br>Slopes (95% CI) | Monkhead variety<br>Intercept (95% CI) | Monkhead variety<br>$R^2$ | Monk<br>*P* |
|---|---|---|---|---|---|---|
| Root ˜ whole plant | L | MP | 1.65a (1.16, 2.35) | -1.49a (-1.91, -1.07) | 0.47 | 0.001 |
| | | PP | 2.00a (1.29, 3.10) | -1.69a (-2.28, -1.09) | 0.16 | 0.082 |
| | H | MP | 1.36a (0.97, 1.91) | -1.52a (-2.08, -0.96) | 0.52 | <0.00 |
| | | PP | 1.66a (1.07, 2.58) | -1.86a (-2.77, -0.94) | 0.15 | 0.088 |
| stem&leaf ˜ whole plant | L | MP | 0.82a (0.67, 1.01) | -0.13**a**(-0.25, -0.01) | 0.83 | <0.00 |
| | | PP | 1.04a (0.88, 1.22) | -0.29**b**(-0.41, -0.18) | 0.89 | <0.00 |
| | H | MP | 0.82a (0.69, 0.98) | 0.01a (-0.16, 0.19) | 0.87 | <0.00 |
| | | PP | 0.97a (0.75, 1.26) | -0.18a (-0.49, 0.13) | 0.72 | <0.00 |
| Seed ˜ whole plant | L | MP | 2.49a (1.95, 3.18) | -1.86**b**(-2.29, -1.42) | 0.75 | <0.00 |
| | | PP | 2.35a (1.62, 3.39) | -1.68**a**(-2.26, -1.10) | 0.42 | 0.002 |
| | H | MP | 4.31a (3.12, 5.94) | -5.06a (-6.75, -3.38) | 0.57 | <0.00 |
| | | PP | 3.63a (2.72, 4.85) | -4.21a (-5.50, -2.93) | 0.65 | <0.00 |

## Figure legends

**Figure 1** Schematic representation of mesh partition and plastic partition treatments.

**Figure 2** Effects of partition type, soil fertility and variety on tiller number (a), root biomass (b), stem&leaf biomass (c) and seed biomass (d). Low = low fertility; High = high fertility. Mean ±SE are shown (n = 20).

**Figure 3** Regressions between whole plant biomass and root biomass (a-b), stem&leaf biomass (c-d) and seed biomass (e-f) of Monkhead and 92-46. Regression lines are shown.

**Fig. 1**

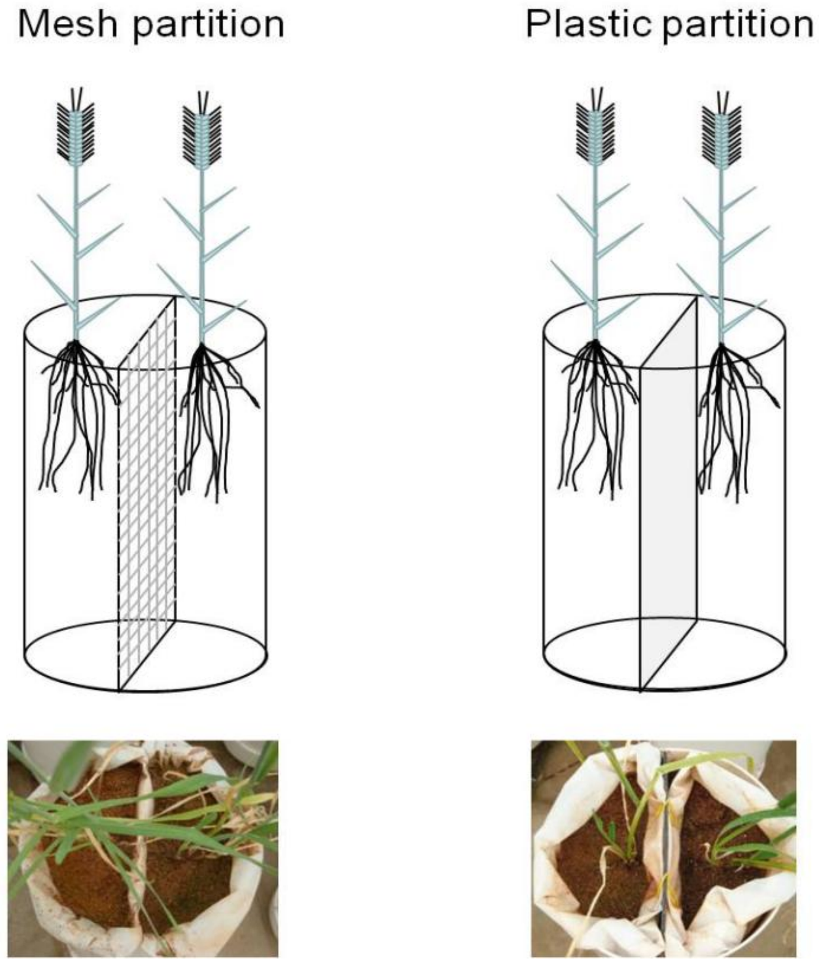

**Fig. 2**

**Fig. 3**