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Differences in Weed Suppression between Two Modern and Two Old Wheat Cultivars at Different Sowing Densities

Yue Wu [1], Nianxun Xi [2,*], Jacob Weiner [3] and Da-Yong Zhang [1]

[1] MOE Key Laboratory for Biodiversity Science and Ecological Engineering, College of Life Sciences, Beijing Normal University, Beijing 100875, China; yuew@mail.bnu.edu.cn (Y.W.); zhangdy@bnu.edu.cn (D.-Y.Z.)
[2] School of Ecology, Sun Yat-sen University, Guangzhou 510275, China
[3] Department of Plant and Environmental Sciences, University of Copenhagen, DK-1871 Frederiksberg, Denmark; jw@plen.ku.dk
* Correspondence: xinianxun@mail.sysu.edu.cn; Tel.: +86-13759252962

Abstract: Crop losses to weeds can be exacerbated in modern agricultural systems because modern crop cultivars have high population yields but low individual competitiveness. High density cropping systems offer the possibility of effectively suppressing weeds by increasing the initial size-asymmetric advantage of crops over the weeds. We tested this hypothesis in an outdoor mesocosm experiment with two old (Cultivar Heshangtou (HST) and Jinbaoyin (JBY)) and two modern (Xihan2 (XH2) and Xihan3 (XH3)) cultivars of spring wheat (*Triticum aestivum* L.), grown in a uniform pattern at four sowing densities under high weed pressure. Two annuals (*Brassica napus* and *Linum usitatissimum*) were used as model weeds sown at the same density in all treatments. Weed growth decreased and wheat yield increased with increasing crop density for all the cultivars, although yield levelled off at the highest densities. The old cultivars suppressed weeds better than the new cultivars at low density, reflecting the decline in individual competitiveness in modern cultivars. At high crop density, however, the modern XH3 suppressed the weeds as well as the old cultivars, supporting the hypothesis that traits that promote weed suppression are different at low vs. high density. Increasing crop density can be an effective way to suppress weed growth in many agricultural systems, and there is great potential for developing genotypes that can do this and produce high yields much better than the cultivars currently available.

Keywords: evolutionary agroecology; individual competitiveness; population performance; sowing density

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1. Introduction

Weeds are the largest source of crop yield loss globally [1,2]. Chemical herbicides are extensively used to suppress weed growth, but they have adverse environmental impacts, such as water pollution, biodiversity loss in agricultural ecosystems, and increased carcinogenic risks for humans [3–6]. In addition, herbicide resistance is spreading rapidly in weeds. Alternative methods for weed control are needed. Increasing the competitive ability of crops relative to weeds is one potential approach to suppressing weed invasion [7,8]. One way to do this is to increase crop density [8].

Modern and old crop cultivars often differ in their competitive abilities [9]. Numerous studies have shown a trade-off between individual competitiveness and plot-level yield in crop plants [9–11]. In theory, active competition among crop individuals can cause redundant growth of resource-acquiring organs (such as leaves and roots) of individuals at the cost of population yields [12,13], leading to a so-called "tragedy of the commons" [14,15]. To achieve a high population yield, plant breeders select modern crop cultivars characterized by low competitive ability, such as short stems, small, erect leaves, and few tillers, resulting in a competitive disadvantage for light [16,17], and a small root system, resulting in a low competitive ability for soil resources [18,19]. Modern cultivars with low competitive ability produce high yields in a monoculture when weed abundance is limited. Under weedy conditions, however, the weak competitive ability means that modern crop cultivars may have a very limited capacity to suppress weeds and thereby resist weed invasion. Cultivars that are effective in suppressing weeds are usually old cultivars with high competitive ability [20,21].

Improving weed suppression through high-yielding crop cultivars is an urgent task in agroecology. Some researchers have argued that many crop seedlings (such as cereal crops) are larger than weed seedlings, and because of this larger seed size they can obtain a disproportionate competitive advantage over weeds in the early growth stage, a phenomenon called "size-asymmetric competition" [22]. However, weeds can avoid suppression by crops because weeds often have higher growth rates early in the growing season when competition between crops and weeds is not intense [23–25]. In theory, increasing crop density can increase the strength of competitive size-asymmetry, and thus benefit the crops at the cost of weeds [8,24]. Experimental research has shown that a crop's ability to suppress weeds increases with sowing density [24–26]. However, these studies did not explicitly compare the differences in weed suppression between modern and old cultivars at different densities. Modern cultivars require a high density to achieve their advantage as a group through efficient use of resources (light, soil nutrients, and space) and in suppressing weeds. Increasing sowing density may not improve the population yield of old cultivars, however, because strong within-cultivar competition decreases resource allocation to seed production at high density [10,18,19]. We hypothesize that some modern crop cultivars may have as much ability to suppress weeds as older crop cultivars at high sowing densities, but there is little experimental evidence for this.

Here, we report on an outdoor mesocosm experiment to test how sowing density influences both weed suppression and population yield of modern and old crop cultivars of spring wheat (*Triticum aestivum* L.). We selected four wheat cultivars that were released in two different periods in semi-arid areas of Northwest China. We tested the following hypotheses: (1) weed growth is lower at higher crop sowing density, and the old cultivars have a greater ability to suppress weeds than the modern cultivars at low density (Figure 1b); (2) grain yield increases with crop sowing density under high weed pressure, and the new cultivars produce a higher grain yield than old cultivars at high density (Figure 1b).

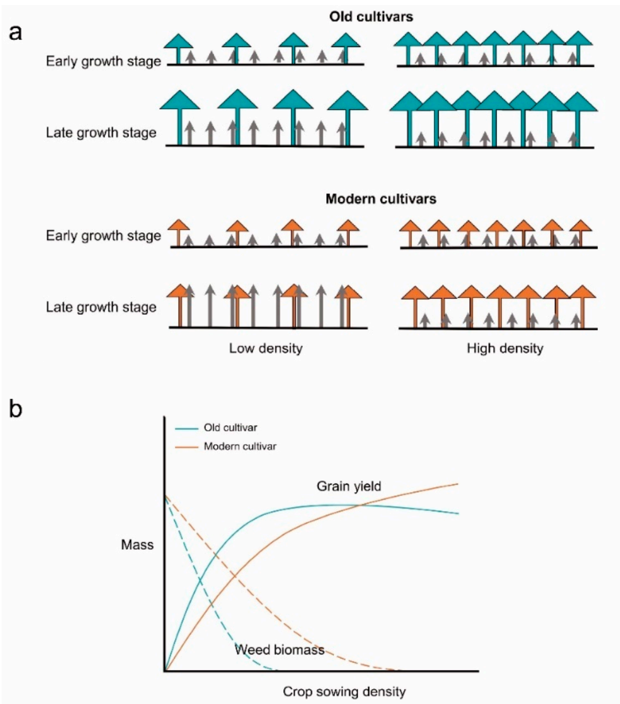

Figure 1. *Cont.*

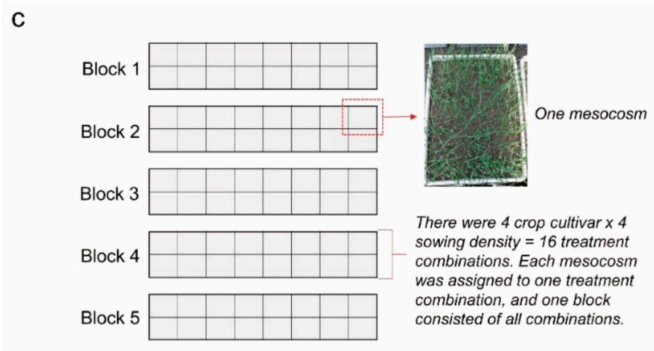

Figure 1. (**a**) Schematic diagram illustrating how crop sowing density influences size-asymmetric competition between crops and weeds at different growth stages of the crops. We assume that weed seeds and seedlings are smaller than crop seeds and seedlings, but they have a faster growth rate and as such weeds have the potential to grow as large as crops later in the growing season. The blue and orange figures represent the wheat, and the grey represent the weeds. (**b**) The curves for relationships between crop sowing density and weed biomass or grain yield (modified from Weiner et al., 2001 [24]). (**c**) All mesocosms were arranged with five blocks, with each block consisting of all treatment combinations.

2. Materials and Methods

2.1. Materials

Cultivar Heshangtou (HST) and Jinbaoyin (JBY) are old cultivars that were widely grown in the semi-arid region of Gansu province, China, in the early and mid-20th century, and the higher-yielding cultivars Xihan2 (XH2) and Xihan3 (XH3) were released in recent decades in the same region. Wheat grains were provided by the Arid Agroecology Experiment Station of Lanzhou University, the Seed Administrative Station of Huining, and the Wheat Breeding Farm, Yuzhong. We used *Brassica napus* and *Linum usitatissimum* as weedy species, because their growth season corresponds to that of spring wheat in the Gansu province, and they have characteristics of weeds such as small seed size and rapid growth.

2.2. Experimental Design

The outdoor mesocosm experiment was conducted at the botanic garden of Beijing Normal University, China (116°2′ E, 39°6′ N, ~54 m a.s.l.) in 2017. This site is representative of a warm temperate continental monsoon climate, with a mean annual precipitation of 538.9 mm and a mean annual temperature of 13.2 °C. We remolded plastic storage boxes (58 cm length, 40 cm width, 30 cm height) to use as growth mesocosms by drilling four holes (7 cm diameter) in the bottom. The soil was a mixture of peat, vermiculite, and perlite with a volume ratio of 4:2:1. Prior to sowing, irrigation with 0.2 g L^{-1} nutrient solution (Peter's Professional General Purpose Fertilizer, N-P-K: 20-20-20, J.R. Peters Inc., Allentown, PA, USA) was applied to each mesocosm.

Grains were sown at the depth of 4 cm on 19 March in a randomized block design with five replicates. There were four crop density treatments (48, 96, 140, and 186 grains per mesocosm, corresponding to 209, 417, 608, and 813 grains m^{-2}, and the normal seeding density in the area of spring wheat is about 200–400 grains m^{-2} according to weather condition) and four wheat cultivars in the experiment. The weeds were planted at a total density of 1000 seeds m^{-2} (500 seeds of each species). All mesocosms were arranged with five blocks, with each block including all treatment combinations (Figure 1c). Each block consisted of two columns and eight rows, and a 20 cm-wide alley between each two columns for later management. We also arranged 36 extra mesocosms around the experimental area to avoid edge effects. Prior to sowing, we germinated the wheat and selected those with a visible radicle to plant. We used a uniform sowing pattern to maximize effects of crop density on weed suppression, because the size-asymmetric advantage over weeds is greater when the crop is sown in a uniform pattern than in traditional rows [24]. Wire grids fastened to the top of the mesocosms were used to generate uniform planting-grid patterns. One germinated grain was dropped by hand within each grid square, and the grains were then covered with 4 cm of soil. Weed seeds were dropped on the soil surface and then harrowed gently. One week after germination, we selected half of the mesocosms randomly and counted the emergence of crop. The wheat emergence rate of the old cultivars was higher than the modern cultivars (HST: 95%, JBY: 91%, XH2: 76%, and XH3: 77%), probably due to freezing precipitation immediately after planting, so we used the observed density in the following analyses. Watering was performed every three to seven days depending on the weather. Insecticide (imidacloprid) was sprayed as needed to prevent aphid damage, and anti-bird netting (grid size: 2.5 cm × 2.5 cm) was placed above the mesocosms to exclude birds. In the middle of June, when they reached maximum biomass, we harvested the aboveground parts of the weeds. Wheat plants were harvested on 29 June to 2 July. Samples of each mesocosm were oven-dried at 70 °C for 48 h to determine dry biomass. We also calculated the harvest index of wheat at mesocosm level using the equation:

$$\text{Harvest Index} = (\text{grain biomass})/(\text{total aboveground biomass}) \quad (1)$$

2.3. Statistical Analyses

Linear mixed models were used to evaluate the effects of crop density and cultivar variety on wheat leaf + stem biomass and harvest index. Cultivar variety and crop density were treated as the fixed factors, and block was a random factor. We used emergence density rather than sowing density in the model and it was treated as a continuous variable. Relationships between density and weed biomass or wheat biomass were analysed using second-order polynomial regression ($y = ax^2 + bx + c + \varepsilon$), because previous research has shown that the realtionship between density and weed or wheat biomass is not linear [24,25]. Simple linear regressions were performed to analyze the relationships between the crop density and harvest index.

To test if wheat vegetative growth caused weed suppression, we conducted a linear mixed model using wheat variety, density, and leaf + stem biomass as fixed factors and block as a random factor. To test if weed growth contributed to grain yield loss, we conducted a linear model using wheat variety, density, and weed biomass as fixed factors and block as a random factor. Standardized major axis regressions were performed to test the relationships between weed biomass and wheat leaf + stem biomass or between grain yield and weed biomass using the "smatr" package in R. Linear, mixed models were performed using the "nlme" package in R. Mean, comparisons between treatments were performed using the "emmeans" package, and p values were adjusted with the Tukey method at 0.05 significance level. All data were analysed with R 3.5.1 [27].

3. Results

We observed significant differences in weed biomass among the wheat cultivars, with greater values in the modern XH2 than the other varieties (Figure 2a, Table 1). There was a negative relationship between weed biomass and wheat density (Figure 2a). The effects of crop density on weed biomass varied among the varieties (significant variety × density interaction, Table 1). The old cultivars HST and JBY reduced weed biomass more than the modern cultivars at low density, but there was no significant difference between the modern XH3 and the old cultivars at high density (Figure 2a, Table S1).

Grain yield increased with crop density for all cultivars (Table 2, Figure 2b). There was no significant difference in grain yield among varieties and no variety × density interaction (Table 2). Regression analyses showed that grain yield leveled off at high density (Figure 2b, Table S1).

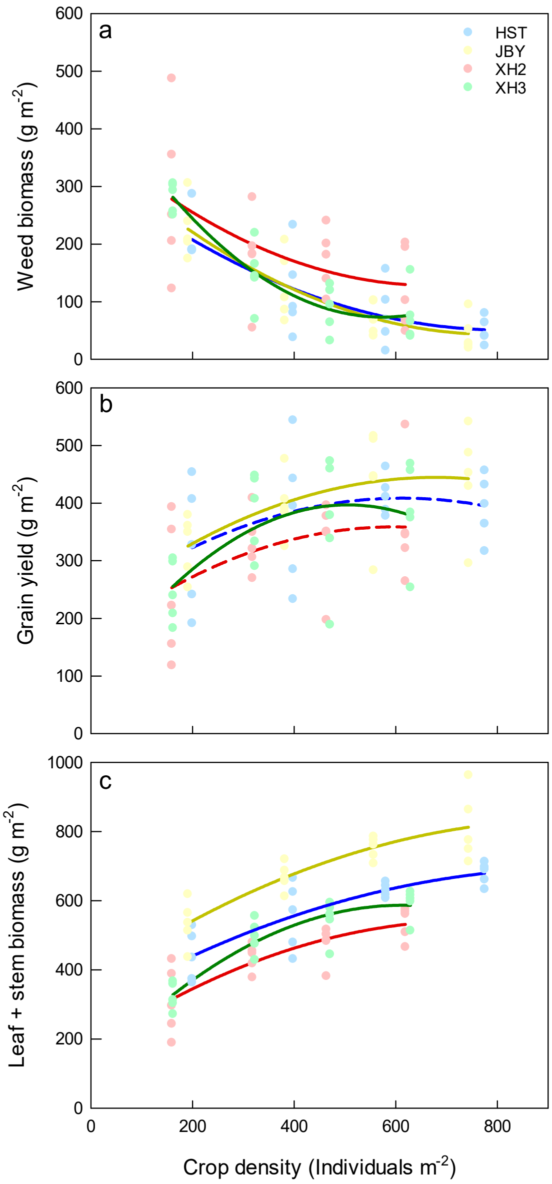

Figure 2. Relationships between crop density and (**a**) weed biomass, (**b**) grain yield, and (**c**) leaf + stem biomass, for two old cultivars Cultivar Heshangtou (HST) and Jinbaoyin (JBY) and two modern cultivars Xihan2 (XH2) and Xihan3 (XH3). Solid lines are the quadratic fits with $p < 0.05$, and the dashed lines indicate nonsignificant fits ($p > 0.05$).

Table 1. The effects of wheat density, wheat variety, leaf + stem biomass, and their interactions on weed biomass. *F* and *p* values with degree of freedom are shown based on mixed effect models. Bold type indicates significant effects ($p < 0.05$).

Effects	*df*	*F* Value	*p* Value
Density	1, 60	**279.42**	**<0.0001**
Variety	3, 60	**6.93**	**0.0004**
Leaf + stem biomass (LS biomass)	1, 60	**11.16**	**0.0014**
Density × variety	3, 60	**2.98**	**0.0384**
Density × LS biomass	1, 60	3.04	0.0862
Variety × LS biomass	3, 60	0.65	0.5838
Density × variety × LS biomass	3, 60	1.34	0.2683

Table 2. The effects of wheat density, wheat variety, weed biomass, and their interactions on grain yield. *F* and *p* values with degree of freedom are shown based on mixed effect models. Bold type indicates significant effects ($p < 0.05$).

Effects	*df*	*F* Value	*p* Value
Density	1, 60	**27.64**	**<0.0001**
Variety	3, 60	2.75	0.0506
Weed biomass	1, 60	**23.06**	**<0.0001**
Density × variety	3, 60	0.12	0.9485
Density × weed biomass	1, 60	2.55	0.1153
Variety × weed biomass	3, 60	0.71	0.5515
Density × variety × weed biomass	3, 60	1.39	0.2550

The modern XH2 and XH3 cultivars had lower vegetative biomass (i.e., leaf + stem biomass) than the old HST and JBY cultivars (Table 3, Figure 2c). For all cultivars, there were positive relationships between density and leaf + stem biomass, in which leaf + stem biomass tended to level off at high density (Figure 2c, Table S1). There was no significant interaction between variety and density for leaf + stem biomass (Table 3). The harvest index, which measures crop allocation to grains, decreased linearly with density (Table 3, Figure 3a, $R^2 = 0.13$, $p = 0.001$). Harvest index was lower in the old JBY than the modern XH2 and XH3, and there was no significant difference between the two old cultivars (Table 3, Figure 3b).

Table 3. The effects of wheat density, wheat variety, and their interactions on wheat leaf + stem biomass and harvest index. *F* and *p* values with degree of freedom are shown based on mixed effect models. Bold type indicates significant effects ($p < 0.05$).

Effects	*df*	*F* Value	*p* Value
(a) Leaf + stem biomass			
Density	1, 68	**235.10**	**<0.0001**
Variety	3, 68	**42.95**	**<0.0001**
Density × variety	3, 68	0.64	0.5900
(b) Harvest index			
Density	1, 68	**13.45**	**0.0005**
Variety	3, 68	**3.54**	**0.0192**
Density × variety	3, 68	0.13	0.9409

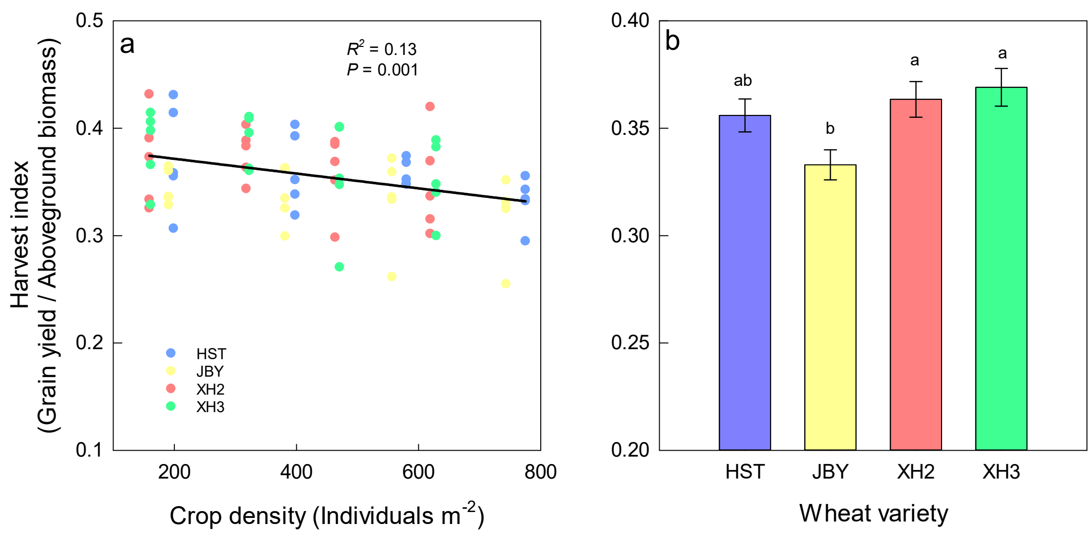

Figure 3. (**a**) The overall relationship between crop density and harvest index. The solid line is the simple linear fit. (**b**) The difference in harvest index among the 4 varieties. The old cultivars are Heshangtou (HST) and Jinbaoyin (JBY); the modern cultivars are Xihan2 (XH2) and Xihan3 (XH3). Data with different letters are significantly different ($p < 0.05$).

Weed biomass decreased linearly with increasing wheat vegetative biomass (i.e., leaf + stem biomass), with no significant differences among the cultivars (Table 1, Figure 4, Table S1). Grain yield decreased linearly with increasing weed biomass, with no significant differences among the cultivars (Table 2, Figure 5, Table S1).

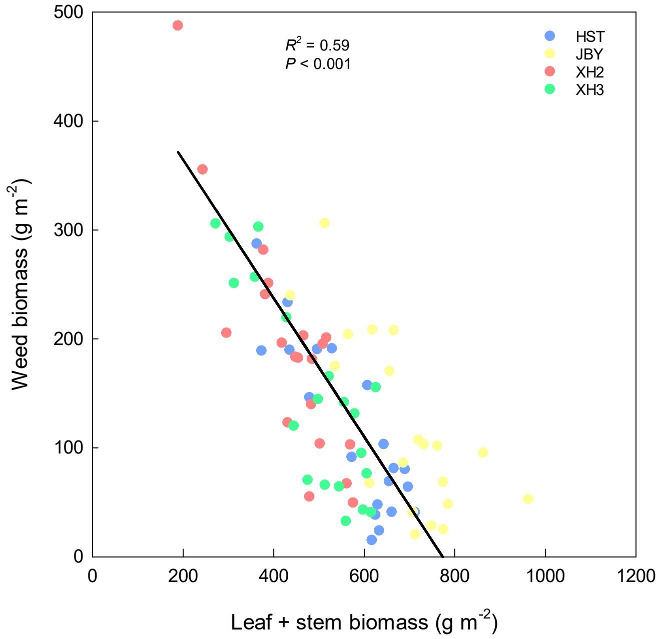

Figure 4. Relationships between wheat leaf + stem biomass and weed biomass. There were no significant differences among the cultivars. Solid lines are the fits of standardized major axis regressions.

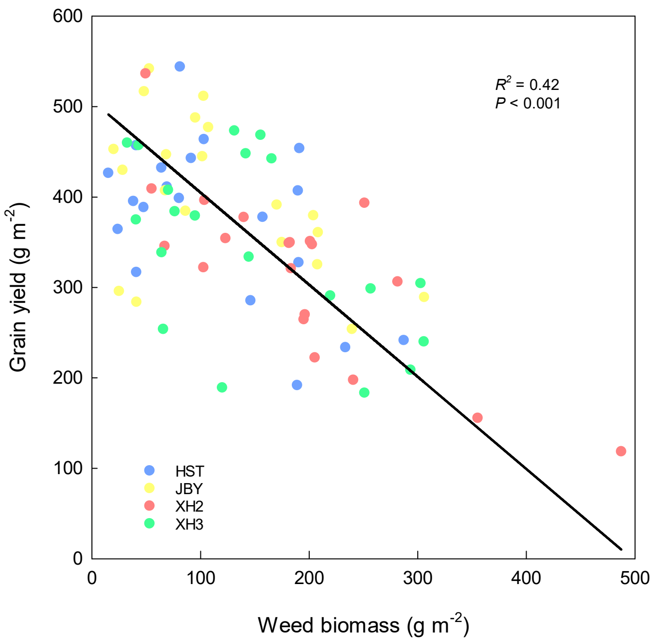

Figure 5. Relationships between weed biomass and grain yield. There were no significant differences among the cultivars. Solid lines are the fits of standardized major axis regressions.

4. Discussion

Evolutionary agroecology theory predicts that crop population performance can be improved by crop cultivars with low individual competitiveness [28,29]. Lower individual competitiveness can increase weed invasion and may lead to a greater yield loss in modern cultivars over old cultivars [20,21]. Increasing sowing density is one approach to suppressing weed growth by maximizing the size advantage of the crop at the early growth stage [8,23,24]. We compared weed suppression in two old and two modern cultivars and tested two interdependent hypotheses: (1) weed growth is lower at higher crop sowing density, and the old cultivars have a greater ability to suppress weeds than the modern cultivars at low crop density; (2) grain yield increases with crop sowing density in the presence of weeds, and the new cultivars have higher yields than old cultivars when grown at high density.

Our results support the first hypothesis and partially support the second hypothesis. Increasing sowing density significantly increased weed suppression. The old cultivars (HST and JBY) had a greater ability to suppress weeds than the modern cultivars (XH2 and XH3) at the lowest density. As the crop density increased, the grain yield increased for all cultivars, and there were no significant differences among cultivars. Grain yield tended to level off but not decline at the highest density. These findings confirmed the idea that weed growth can be suppressed by increasing crop density [24–26]. In our experiment, crop–weed competition was size-asymmetric, because (1) we added ample soil nutrients and water for crop growth, so light quickly became the limiting resource; (2) wheat had a significant initial size advantage; and (3) crop density increased the competitive advantage of the crop as there was a strong negative relationship between crop vegetative growth and weed growth. In practice, the sowing density of spring wheat is much lower than the 800 grains m^{-2} that we used for the highest density treatment, so increased wheat density is a practical way to increase weed suppression.

The lack of a consistent ability to suppress weeds of the modern cultivar XH2, in comparison with the old cultivars, is not surprising, since this cultivar has a lower height and fewer tillers, which decrease crop competitiveness for light (data not shown). However, the modern XH3 was able to suppress weeds as well as the old cultivars at high crop density. Our results support the hypothesis that crop attributes that promote weed suppression are different at low vs. high crop density [8], implying that the concept of "competitive ability" of a crop genotype is too crude and therefore can be misleading.

Contrary to our second hypothesis, the modern cultivars did not have a greater grain yield than the old cultivars, even at high density. This may be because modern crop breeding has not selected cultivars suitable for high yield at high density in the presence of weeds, because breeding has been performed with weed control. We hypothesize that the development of high density, weed-suppressing, high-yielding cultivars is achievable. High density cropping systems represent the next stage in the management of agricultural ecosystems to achieve high yield, low weed invasion, and increased sustainability [8]. Increasing crop density contributes to sustainability by increasing crop biomass and ground cover early in the growing season, reducing nutrient loss and erosion.

Our results provide some suggestions about attributes that could be tested in modern cultivars to achieve high weed suppression and high yields at high sowing densities. First, modern crops should be characterized by low individual competitiveness, high harvest index, and fast early-stage growth. Early growth of crops plays a critical role in the establishment of crop canopy architecture, which results in weed suppression [21,30]. In some cases, the most weed-suppressive cultivars are those that grow the fastest during the early growth stage, even though they may not be the tallest at maturity [31]. Second, plant breeders should select cultivars with high optimum sowing density. If harvestable yield decreases steeply above the optimum density, the densities required for weed suppression may give only low yields. If the density–yield curve is relatively flat, as it is for most cereals, these higher densities can be used for weed suppression [24]. Of course, environmental factors, such as precipitation and soil fertility, will determine if weed suppression at a high density is attainable in specific climate zones [32]. For example, in arid agricultural land, size-symmetric competition for soil resources can dominate plant interactions [18], and the increased sowing density may not result in effective weed suppression, because crops may not have the large size advantage to suppress weed growth. Future studies need to further test weed suppression by high crop density under low fertility and semi-arid cropping systems.

5. Conclusions

Our study provides the first test as to whether weed suppression through increased crop density is different for old and modern cultivars. We found that weed growth was effectively reduced at high crop density for both old and modern cultivars. The modern cultivars had lower weed suppression than the old cultivars at low density, reflecting a declining of individual competitiveness in modern cultivars. However, at high crop density, the modern cultivar XH3 was as effective in suppressing the weeds as the old cultivars. The modern cultivars did not have a higher optimum crop density compared to the old cultivars under high weed pressure. Our results suggest that modern crop breeding has not selected cultivars that are suitable for weed suppression and high yield at high density, and we provide hypotheses for traits that should be selected to achieve this. Further research is needed to test these hypotheses and obtain more information about the traits that are needed to increase weed suppression and produce high yields at high crop density.

Supplementary Materials: The following are available online at https://www.mdpi.com/2073-4395/11/2/253/s1, Table S1: Results of the regressions.

Author Contributions: Conceptualization, D.-Y.Z.; methodology, D.-Y.Z. and Y.W.; formal analysis, N.X. and Y.W.; investigation, Y.W.; writing—original draft preparation, Y.W. and N.X.; writing—review and editing, N.X. and J.W.; visualization, N.X. and Y.W.; funding acquisition, D.-Y.Z. All authors have read and agreed to the published version of the manuscript.

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Data Availability Statement: The data presented in this study are available on request from the corresponding author.

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