Euphytica (2021) 217:202
https://doi.org/10.1007/s10681-021-02930-9

Breeding wheat for weed-competitive ability: I. Correlated traits

L. Kissing Kucek · E. B. Mallory · H. M. Darby · J. C. Dawson · M. E. Sorrells

Received: 5 January 2021 / Accepted: 20 September 2021 / Published online: 25 October 2021

Abstract Competition from weeds often reduces wheat yields, especially in organic management systems or when herbicide-resistant weeds are present. Breeding wheat for increased competitive ability is an important aspect of integrated weed control. Selecting directly for weed-competitive ability (WCA), however, is challenged by difficult field measurements, genotype by environment interactions, and low heritability. To improve selection efficiency, breeding programs can utilize secondary selection traits that are easier to measure, have higher heritability and are highly correlated with WCA. To identify potential secondary selection traits for WCA, we conducted a meta-analysis of the published literature, and contributed new data from the northeastern United States. Among studies worldwide, early vigor was easy to measure and consistently correlated with WCA. Early plant height also showed promise as a correlated secondary selection trait for WCA, and had high heritability. Tillering, maturity timing, and growth habit were inconsistently correlated with WCA among environments and weed species studied. WCA and the correlated trait of early vigor were influenced by genotype by environment interactions. As a result, decentralized breeding would maximize gain from selection for WCA.

Keywords Wheat · Weed competition · Indirect selection · Trait correlations

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10681-021-02930-9.

L. Kissing Kucek (✉)
U.S. Dairy Forage Research Center, USDA-ARS, 1925 Linden Dr., Madison, WI 53706, USA
e-mail: lisakissing@gmail.com

E. B. Mallory
School of Food and Agriculture, University of Maine, 495 College Avenue, Orono, ME 04473, USA

H. M. Darby
Department of Plant and Soil Science, University of Vermont, 278 S. Main Street, St. Albans, VT 05478, USA

J. C. Dawson
Department of Horticulture, University of Wisconsin-Madison, 1575 Linden Dr, Madison, WI 53706, USA

M. E. Sorrells
School of Integrated Plant Science, Cornell University, 306 Tower Rd, Ithaca, NY 14850, USA

Introduction

Weeds can lower wheat (*Triticum aestivum* L.) yields by reducing productive tillers per unit area, kernel numbers per plant, and grain size per kernel (Mason et al. 2007b). Weed competition is particularly damaging when herbicide-resistant weeds are present (Heap 2014) or there are herbicide limitations (Teasdale et al. 2007; Cavigelli et al. 2008). However, some wheat genotypes are less impacted by the presence of weeds. Selecting such genotypes can be an important component of weed management in agricultural systems. Competitive wheat genotypes can buffer chemical, mechanical, and cultural weed management practices, which occasionally fail to control weeds (Rasmussen 2004; Kolb et al. 2010; Norsworthy et al. 2012). Competitive crop genotypes can also reduce farm labor requirements and decrease the complexity of in-field weed management (Bastiaans et al. 2008). Despite the trait's importance, wheat breeding programs have exhibited a 70-year decline in competitive ability (Sadras and Lawson 2011). Although the reason for this decline is unclear, some suggest that modern wheat breeding has selected for a "communal" ideotype, optimizing grain yield by allocating resources efficiently among wheat plants (Donald 1968; Denison 2015). This process may have inadvertently selected against individual plant competitiveness (Lemerle et al. 2001a; Weiner et al. 2017).

Weed-competitive ability

The WCA of a genotype is typically described by two metrics: weed suppression and crop tolerance. *Weed suppression*, also known as "crop interference," describes a crop's ability to reduce weed growth and reproduction (Jordan 1993). Wheat plants deprive weeds of light via plant height, tillering, leaf angle, canopy structure, seedling ground cover, leaf area index (LAI), early leaf area expansion rate. Additionally, wheat plants compete for nutrients and water through early root and shoot growth, high nutrient uptake rates, maturity timed to seasonal water availability, resource use efficiency, and locating roots near nutrient and water supplies (Wicks et al. 1986; Huel and Hucl 1996; Lemerle et al. 2001a; Mason et al. 2007b). Secretion of allelopathic compounds can further reduce weed emergence and growth. Weed suppression is generally measured as weed biomass and/or weed seed production in competition with wheat—two measures that are highly correlated (Mason et al. 2007b; Worthington et al. 2013). When compared to highly suppressive lines, poorly suppressive wheat genotypes allowed 79% more *Aegilops cylindrica* Host (jointed goatgrass) seed weight (Ogg and Seefeldt 1999), 29% more *Avena sativa* L. (oat) biomass (Huel and Hucl 1996), double the *Bromus tectorum* L. (downy brome) biomass (Blackshaw 1994), seven times the *Lolium rigidum* biomass (Lemerle et al. 1996), and up to 5.7 times the resident weed biomass (Wicks et al. 1986; Murphy et al. 2008).

Crop tolerance is focused on crop yield in the presence of weeds. In addition to direct competition with weeds (measured through weed suppression), crop tolerance is influenced by the avoidance strategies employed by the crop. Crops may have high tolerance if their peak resource demands occur at times when weed demand for light, nutrients, or water use is low. Crop tolerance is reported as either (1) the absolute yield of a variety under weedy conditions, or (2) the percent yield loss under weedy conditions as compared with weed-free conditions. In previous studies, absolute yield showed stronger correlations with weed seed or weed biomass production than with percent yield loss (Coleman et al. 2001; Worthington et al. 2013). Nevertheless, percent yield loss is a factor that influences farm profitability during years with variable weed densities. In years of low weed pressure, a farmer could lose revenue if using a weed-suppressive variety that has low yield potential in weed-free conditions (Jordan 1993; Lemerle et al. 2001a). Documented percent yield loss from weed competition varied from 23 to 60% (Huel and Hucl, 1996; Blackshaw, 1994; Mason et al., 2007b; Balyan et al. 1991).

An ideal wheat plant for WCA would express both high weed suppression and crop tolerance (Lemerle et al. 2001a). Genotypes with high weed suppression would limit weed growth and reduce the soil weed seedbank. Genotypes with high crop tolerance would ensure good wheat yields regardless of varying weed seedbank conditions among farms and year-to-year variability within one farm. As few genotypes excel in weed suppression and crop tolerance (Challaiah et al. 1986; Lemerle et al. 1996, 2001a; Zerner et al. 2016), selecting superior genotypes requires measuring both components of WCA.

Gains in selection for weed-competitive genotypes

The Breeder's Equation (Eq. 1; Falconer 1981) outlines how wheat can be genetically improved for WCA. With high heritability traits (h^2), large phenotypic variance in the parental population (σ_P^2), and strong selection intensity (i), breeders can maximize gains in selection (R).

$$R = \sigma_P i h^2 \quad (1)$$

Previous studies indicate that weed suppression and crop tolerance are complex and quantitative traits exhibiting low heritability (Coleman et al. 2001). Additive genetic variance (σ_a^2) and genetic variance (σ_g^2) for WCA tend to be lower than environmental variance (σ_e^2) and genotype by environment interaction variance (σ_{ge}^2; Eq. 2).

$$h^2 = \frac{\sigma_a^2}{\left(\sigma_g^2 + \sigma_e^2 + \sigma_{ge}^2\right)} \quad (2)$$

Heritability can be improved with robust experimental design, which reduces environmental variance. To accurately measure WCA, trials should establish weed pressure at a density that differentiates competitive ability among wheat genotypes. Covariates for stand counts of both weeds and wheat, and calculating crop tolerance based on adjacent weed-free controls reduce within-trial error variance (Mokhtari et al. 2002; Mason et al. 2007b). Large plot sizes and numbers of replicates are often necessary to distinguish genetic signal from noise (Cousens and Mokhtari 1998; Le Campion et al. 2014). However, such aspects of robust experimental design increase the land, seed, and labor required per genotype evaluated. Direct measurement of WCA is impractical for early stages of breeding, when available seed quantities are low and many genotypes are screened.

Large genotype by environment (G*E) interactions also lower heritability when calculated across environments. Rankings for WCA correlated among some site-years, but not for others (Lemerle et al. 1996, 2001b; Cousens and Mokhtari 1998; Worthington et al. 2015a, b; Kissing Kucek 2017). Measuring crop tolerance is important for managing G*E interactions, as there is often no correlation between wheat yields without weeds and wheat yields when weed competition is present (Lemerle et al. 1996), although exceptions do exist (Challaiah et al. 1986).

Indirect selection

Due to low heritability and difficulty directly measuring WCA, direct selection for WCA is not efficient for breeding programs. The cost to screen genotypes for weed suppression and crop tolerance also makes direct selection very expensive. Indirect selection seeks to identify a secondary trait (x) that is strongly correlated (ρ) with the primary trait of competitive ability (y), yet has higher heritability and is easier to evaluate (Eq. 3; Acquaah 2012). When two traits are highly correlated in their response to selection (CRy), these traits are likely functionally related in physiological processes, or genetically linked through pleiotropism or linkage disequilibrium.

$$CR_y = i \rho h_x \sigma_{gy} \quad (3)$$

Identifying the secondary selection traits with highest correlation to weed suppression and crop tolerance could improve gains from selection for WCA. Linear regression demonstrated that many traits are correlated with WCA in wheat (Challaiah et al. 1986; Lemerle et al. 1996; Bertholdsson 2005; Murphy et al. 2008). However, each published study included few environments from a relatively small region. As correlations between WCA and some traits change depending on the environment and weed community evaluated (Ogg and Seefeldt 1999; Coleman et al. 2001; Bertholdsson 2005), an analysis among studies is necessary to identify whether certain secondary selection traits are globally or only regionally appropriate (Worthington and Reberg-Horton 2013).

We conducted a meta-analysis of the literature to find traits correlated with WCA, and assessed how trait correlations change among studied global environments. The analysis includes a new spring wheat dataset from the northeastern United States, which was evaluated for WCA trait correlations.

Table 1 Studies included in the meta-analysis that measured traits correlated to weed- competitive ability in wheat

Reference	Wheat habit	Sites studied	Genotypes evaluated	Broad diversity of lineage and trait phenotypes included?	Years studied	Plot replications	Weeds seeded?	Model weed species planted	Weed stand counts?[b]	Wheat stand counts? [b]	Weed-free control? [b]	Plot size for biomass sampling (m^2)
Andrew (2016)	Winter	1	8	Y	3	3	Y	*Alopecurus myosuroides*	N	N	N	0.06
Bertholdsson (2011)	Winter	1	12	Y	2	3	Y	*Brassica napus, Apera spica- venti*	U	U	N	0.5
Bertholdsson (2005)	Spring	1	20	Y	2	3	N	resident	U	U	N	0.25
Challaiah et al. (1986)	Winter	2	10	N (all tall)	2	6	Y	*Bromus tectorum*	U	U	U	1.44
Coleman et al. (2001)	Spring	1	161	N (one cross)	2	2	Y	*Lolium rigidum*	N	N	Y	0.5
Feledyn-Szewczyk and Jończyk (2015)	Spring	1	6	Y	3	4	N	resident	Y	Y	N	0.5
Huel and Hucl (1996)	Spring	2	16	N (two crosses)	3	4	Y	*Avena sativa, Brassica juncea*	Y	Y	Y	1.23
Lemerle et al. (1996)	Spring, Durum	1	250[a]	Y	2	1	Y	*Lolium rigidum*	Y	Y	Y	0.75
Mason et al. (2007a)	Spring	2–4	27	Y	3	4	N	resident	U	U	N	0.13
Mason et al. (2007b)	Spring	2	9	Y	2	3	Y	*Avena sativa*	Y		N	0.13
Murphy et al. (2008)	Spring	1	63	Y	3	3	N	resident	U	U	N	3.13
Ogg and Seefeldt (1999)	Winter	1	7	moderate	2	4	Y	*Aegilops cylindrica*	U	Y	Y	0.75
Wicks et al. (1986)	Winter	1	20[a]	moderate	3	3–10	N	resident	U	Y	Y	visual estimate
Worthington et al. (2015a)	Winter	4	9	Y	2	4	Y	*Lolium perenne*	Y	U	Y	weed heads in 1 m^2

Table 1 continued

Reference	Wheat habit	Sites studied	Genotypes evaluated	Broad diversity of lineage and trait phenotypes included?	Years studied	Plot replications	Weeds seeded?	Model weed species planted	Weed stand counts?[b]	Wheat stand counts? [b]	Weed-free control? [b]	Plot size for biomass sampling (m^2)
Worthington et al. (2015b)	Winter	4	53	Y	2	3	Y	*Lolium perenne*	U	U	N	weed heads in 0.5 m^2
Zerner et al. (2016)	Spring	2	86	Y	2	Y	Y	*Avena sativa*	Y	Y	Y	wheat seed vs. weed seed in 7.5 m^2
Present study, data from Mallory et al. (2014)	Spring	3	33[a]	Y	1	4	N	resident	N	Y	N	0.3–0.4
Present study, 2016 data	Spring	1	30	Y	1	3	Y	*Sinapsis alba*	N	N	N	0.5

[a]Indicates that varieties changed among site-years

[b]U indicates that this aspect of experimental design was unspecified for this study

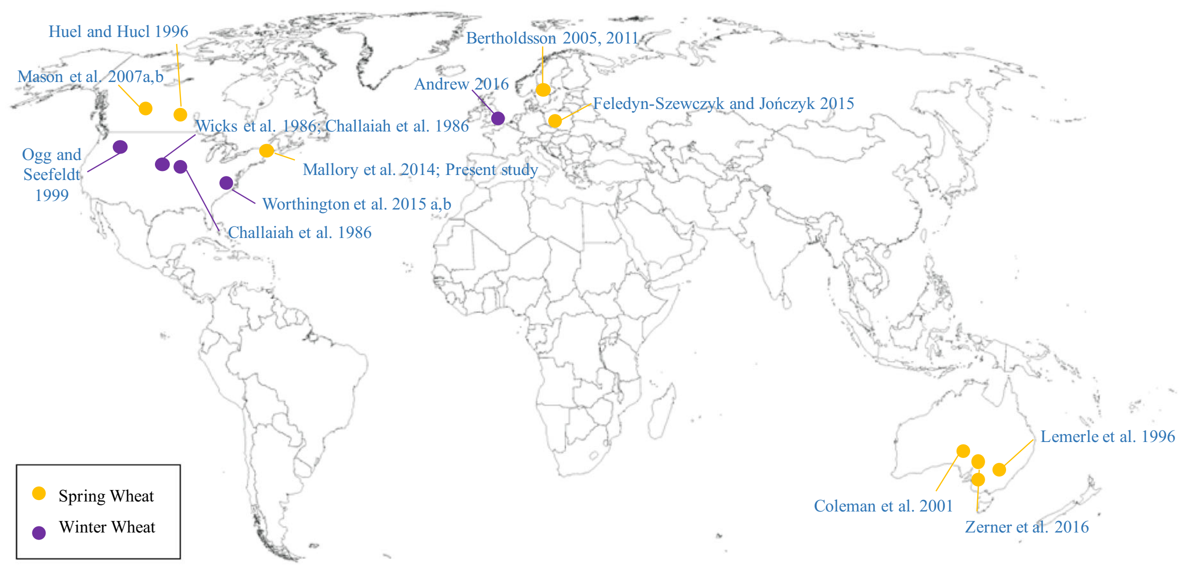

Fig. 1 Locations of studies included in the meta-analysis. Background map provided by Wikimedia Commons (2016)

Methods

Meta-analysis of secondary traits for selection of WCA

A meta-analysis of the literature sought traits that were correlated with WCA, highly heritable, and easy to evaluate. On Google Scholar and Web of Science, search terms included "wheat" combined with "weeds," "competition," or "traits." Eighteen studies (Table 1) from diverse global environments (Fig. 1) met the minimum inclusion criteria of more than five genotypes with broad phenotypic diversity screened for WCA, weed pressure applied to obtain variability in competition phenotypes, weed competition sampled through biomass or visual means, and correlations reported. Two of the 18 studies are novel to this publication (see *Correlated traits for WCA in the northeastern United States).*

We evaluated secondary selection traits for their relationship to weed suppression and crop tolerance. The response of weed biomass, weed seed weight, or the number of weeds counted was analyzed as weed suppression. When reported, the response of grain yield loss due to weed competition was considered crop tolerance. When not reported, grain yield was used as crop tolerance. Traits were labeled as "early" if measured before or during jointing stage, and "mature" if measured after anthesis.

The quality of studies varied widely (Table 1). Each study evaluated from six to 250 wheat genotypes during one to six site-years. Twelve of 18 studies seeded weeds into study plots, while another six studies evaluated resident weeds. Six of 18 studies reported correcting WCA values based on weed stand counts, and seven of 18 reported correcting WCA values based on wheat stand counts. Seventy-eight percent of crop tolerance observations were calculated as the grain yield difference between weed-free and weedy plots (Online Resource 1), while 22% reported grain yield without a weed-free control. The size of quadrats sampled for weed and wheat biomass varied from 0.06 to 3.13 m^2 per plot. Experimental replicates varied from one to ten per study. To visually emphasize more robust results that included more site-years and number of genotypes studied in Fig. 2, a quality index was calculated for each study (Eq. 4). The quality index determined the size of each correlation data point presented from the literature in Fig. 2, but did not influence any quantitative analyses from the dataset. As the number of genotypes studied were much larger than the number of site-years, which is typical for studies of plant genetics, the number of site-years were multiplied by 20 to more evenly weigh the contribution of genotype and environmental diversity on each presented data point. Data were plotted using R (R Core Team 2019). The complete dataset from the meta-analysis is available in Online Resource 1.

$$\text{Quality index} = \text{Number of environments} * 20 + \text{Number of genotypes studied} \quad (4)$$

Correlated traits for WCA in the northeastern United States

We contributed two additional datasets for correlated traits with weed competition from the northeastern United States. We analyzed one dataset previously published by Mallory et al. (2014) that assessed diverse wheat varieties for weed biomass, wheat grain yield, the ratio of wheat biomass to weed biomass, mature height, and early vigor in the northeastern United States. Twenty-five varieties of spring wheat were grown in four replicates at five site-years: Alburgh, VT in 2010 and 2011; Old Town and Sidney, ME in 2010; and Willsboro, NY in 2010. An additional nine varieties were included in some, but not all site-years. Vigor was visually rated on a "one" to "five" scale between second leaf stage and early tillering, with "five" being the most vigorous. Weed and wheat biomass were each determined by collecting biomass from three to four 0.1 m^2 quadrats per plot (total of 0.3–0.4 m^2), separating out wheat from weed biomass, drying at 55 °C, and weighing. Due to low weed presence, two site-years (Alburgh 2011 and Willsboro 2010) were removed from the analysis. Weed biomass and the ratio of wheat-to-weed biomass were logarithmically-transformed due to a right-skewed distribution for weed biomass (Online Resource 2).

A second dataset from the northeastern United States evaluated diverse wheat breeding populations for weed biomass, wheat grain yield, the ratio of wheat biomass to weed biomass, mature height, and early vigor. At Old Town, ME in 2016, thirty-five F_7 or F_4:F_7 breeding populations from eight diverse wheat crosses, along with four check lines and four parental lines were grown in three replicates. Details of the breeding populations are reported in Part 2 of this series. Briefly, at four organic farms in the northeastern United States, bi-parental breeding populations were individual plant selected for high early vigor, or bulk selected under resident weed pressure. Plot size was 7.3 m^2. Plots were overseeded with a surrogate weed, *Sinapsis alba* cv. 'Idagold,' using a Brillion seeder at a rate of 75 viable seeds per m^2. A weed-only plot was included in each replicate, and demonstrated low variability among replicates for surrogate weed biomass (3864 +/− 268.5 kg/ha). Vigor was visually rated on a "one" to "nine" scale between fourth and fifth leaf stage, with "nine" being the most vigorous. Weed and wheat biomass were each determined by collecting biomass from three to four 0.1 m^2 quadrats per plot (total of 0.3–0.4 m^2), separating out wheat from weed biomass, drying at 55 °C, and weighing. Wheat yield was standardized based on moisture content.

The same breeding populations tested at Old Town, ME in 2016 were also evaluated for consistency of early vigor rankings at Varna, NY in 2016. A calibration trial was conducted to assess the consistency of visual early vigor genotype rankings among evaluators. Six graduate student evaluators were trained on visual rating of early vigor for five minutes, and then asked to rate 20 spring wheat genotypes for early vigor over three replicates. Through the package 'lme4' [version1.1-10] (Bates et al. 2015), the random effects of genotype, replicate, evaluator, and the interaction between genotype and evaluator were tested for variance in early vigor scores.

Using Pearson's Correlation Coefficient, we evaluated whether crop tolerance (measured as grain yield and wheat biomass) and weed suppression (measured as weed biomass and the ratio of wheat to weed biomass) were linearly related to height and early vigor.

All data were analyzed and plotted in R [version 3.6.0] (R Core Team 2019). Correlations were determined significant at a threshold of $\alpha<0.05$.

Results and discussion

Meta-analysis of secondary selection traits for WCA

The studies included in the meta-analysis assessed 18 potential secondary selection traits for WCA: allelopathic activity; thousand-kernel weight; early biomass; early and mature height; early and mature LAI; early spectral vegetation indices, including the normalized difference vegetation index (NDVI) and ratio vegetation index (RVI); early and mature photosynthetically active radiation (PAR); early and mature vigor; length and width of early leaves and the flag leaf; tillering; and growth habit. Six traits (allelopathic activity, early NDVI/RVI, early PAR, width of early leaves, growth habit, and tillering) demonstrated both positive and negative significant correlations with weed suppression and/or crop tolerance among studies (Fig. 2). For nine traits (allelopathic activity, thousand-kernel weight, early biomass, length of early leaves, width of early leaves, width of flag leaf, length of flag leaf, mature LAI, mature vigor), at least half of measured correlations with WCA were nonsignificant. Early vigor, early height, and early LAI showed promise as secondary selection traits, as the majority of correlations with WCA were positive and significant.

Early vigor

The meta-analysis revealed early vigor to be the most promising secondary selection trait for WCA. Although encompassing many complex processes, such as emergence, growth rate, and resource use efficiency, early vigor is a simple visual rating of seedling size. Early wheat growth is essential for successful competition with weeds. If a wheat plant fails to establish an effective early cover to shade weeds, it struggles to compete with weeds later in the season (Jordan 1993). Among all reviewed studies, early vigor was positively correlated with WCA. Moreover, early vigor was significantly correlated with weed suppression and crop tolerance in 78 and 69% of trials, respectively. However, the strength of

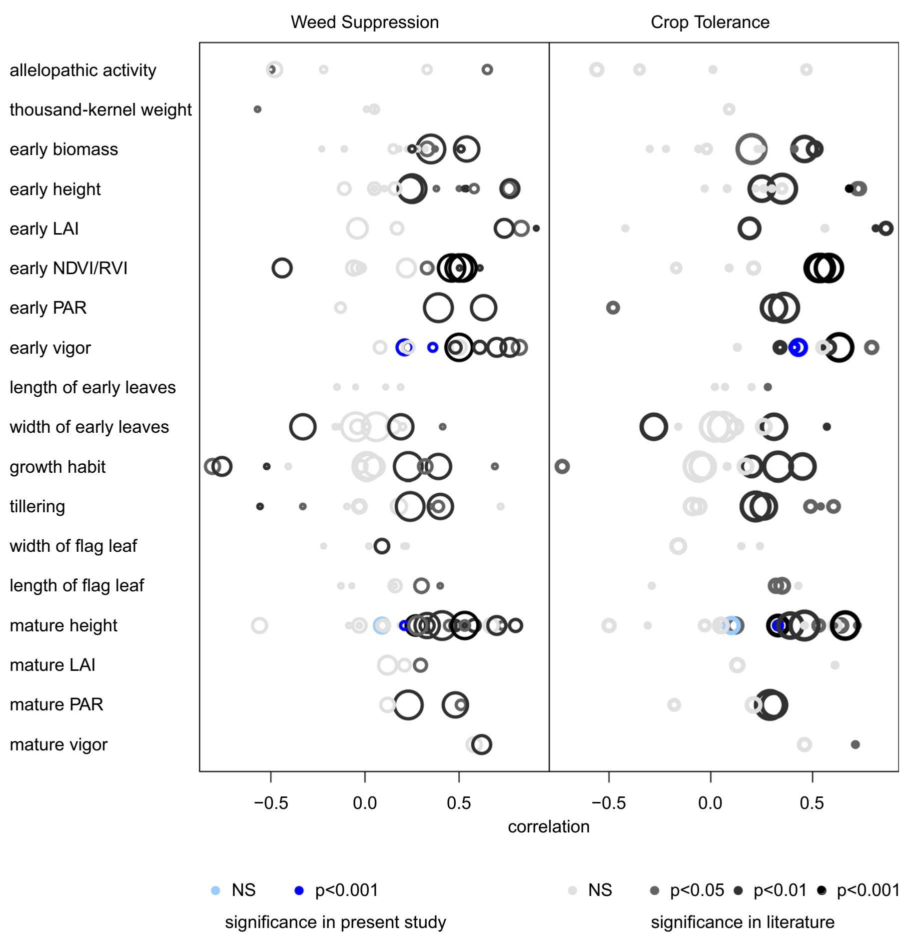

Fig. 2 Meta-analysis of secondary traits correlated with weed suppression and crop tolerance. Each circle represents one value presented in the literature. Larger circles denote studies that included more site-years and diversity of genotypes, based on the index of (site-years*20) + number of genotypes studied. Darker circles indicate more significance of the correlation. Blue circles show the correlations for the new data presented in this paper from the northeastern United States

correlations varied broadly among studies, from r = 0.13 to r = 0.79 (Worthington et al. 2015a).

Seed size can be a strong contributor to early vigor (Evans and Bhatt 1977; Lafond and Baker 1986; Rebetzke and Richards 1999). As seed size is influenced by environmental conditions during grain fill (Jannink et al. 2001), seed of tested genotypes screened for early vigor should be ideally sourced from the same environment. Larger seed sorted from one spring wheat variety showed improved weed suppression (Xue and Stougaard 2002). Thousand-kernel weight was not significantly correlated to weed suppression or crop tolerance in the meta-analysis (Fig. 2). However, the literature lacks robust studies that included multiple genotypes of wheat grown in multiple site-years.

One disadvantage of using early vigor as a secondary selection trait is the effect of G*E (Kissing Kucek 2017), which can reduce heritability across environments (Coleman et al. 2001). While studies have evaluated components of early vigor that have higher heritability, most are not ideal secondary selection traits. Although the length and width of early leaves are highly heritable (h^2 = 0.67 and 0.76, respectively; Rebetzke and Richards 1999), the meta-analysis indicates that these traits are not consistently correlated with WCA (Fig. 2). Early biomass and leaf area are good surrogates for early vigor, but only have moderate heritability at h^2 = 0.35 and 0.30, respectively, and are more laborious to measure (Rebetzke and Richards 1999).

Height

Early and mature wheat height are also promising secondary selection traits. Taller plants exponentially decrease the amount of PAR available in the canopy (Ford 1980). Therefore, tall genotypes reduce available light for weeds (weed suppression), while simultaneously avoiding shade cast by tall weeds (crop tolerance). Height has the added benefit of being highly heritable (h^2 = 0.9; Coleman et al. 2001). However, height of mature wheat was not always positively correlated with WCA. Sixteen percent of trials in the meta-analysis found negative correlations between mature height and WCA (Fig. 2). Ogg and Seefeldt (1999) reported that the rate of height gain, particularly early in the season, was more related to weed competition and crop tolerance than the mature height of the variety. The advantage of early height may help a wheat plant acquire more resources to fuel size-asymmetric competition later in the season (Andrew et al. 2015). The meta-analysis confirmed a more consistent positive relationship between early height and WCA, with 92% of trials reporting correlations above zero (Fig. 2). However, early height was significantly correlated with WCA in fewer studies than early vigor. Early height was significantly correlated with weed competition in 69% of studies, and with crop tolerance in 45% of studies, respectively. Similar to early vigor, the strength of correlations between early height and WCA varied broadly, from r = − 0.11 to 0.77.

Tall varieties typically come at the cost of lower harvest index, reduced grain yield, and frequent lodging. Consequently, selecting varieties that perform well in weedy and weed-free field conditions can be a challenge (Challaiah et al. 1986; Wicks et al. 1986; Seefeldt and Ogg 1999; Coleman et al. 2001). Selecting genotypes with tall height early in the season, but intermediate height at maturity, may improve both WCA and grain yield. Although many dwarfing alleles (Rht1 and Rht2) reduce gibberellin sensitivity and seedling growth (Rebetzke and Richards 1999; Seefeldt and Ogg 1999; Murphy et al. 2008; Addisu et al. 2009), one semi-dwarf gene (*Rht8c*) maintained the early vigor needed for weed competition (Addisu et al. 2009). For all dwarf and semi-dwarf alleles, the study showed that early growth could be partially recovered when paired with the photoperiod insensitivity allele, *Ppd-D1a*. Selection for early height and grain yield in weedy and weed-free conditions may identify genotypes that excel in diverse field conditions.

Canopy density

Although little data have been published, measures of wheat canopy density showed promise as secondary selection traits for WCA. Leaf Area Index (LAI) estimates the crop area per unit area of ground, accounting for multiple layers of leaves. Higher LAI can starve weeds of light and reduce weed seed germination by lowering red to far red ratios. Early LAI was positively correlated with WCA in 80% of studies, and significant in 60% of studies. Correlations between weed suppression and early LAI tended to be stronger than early vigor or height, with a mean of r = 0.52 (range − 0.04 to 0.91) reported in six trials (Coleman et al. 2001; Murphy et al. 2008; Worthington et al. 2015a,nnb). Measures of vegetation cover, such as normalized difference vegetation index (NDVI) or ratio vegetation index (RVI) were less consistently correlated with WCA than LAI. Only half of trials showed significant correlations between vegetation indices and WCA. In a study by Reiss et al. (2018), LAI and NDVI tended to group together in variance decomposition when explaining the response of weed biomass. However, LAI explained more variance than NDVI. LAI provides higher resolution measurements of leaf architecture and canopy structure that influence competition, when compared to presence/absence vegetation measurements provided by NDVI and RVI. Photosynthetically Active Radiation (PAR) captured by the wheat canopy showed inconsistent correlation with tolerance and/or suppression among two studies (Wicks et al. 1986; Lemerle et al. 1996), but few observations limit the confidence of this conclusion.

Further studies are needed to explore the potential of LAI as a secondary selection trait for weed competition and crop tolerance. Time-series studies would be most useful, as the critical periods of competition between weeds and wheat depend on a region's weather and common weed species. Time-series studies could identify the growth stage(s) of wheat that are most relevant to weed competition in a target region, and therefore, identify optimum timing to measure LAI for selection. LAI is confounded with planting density (Andrew 2016). Consequently, studies need to carefully control for density effects when measuring LAI. As visual measures of canopy density can be difficult in the presence of weeds, screening would need to take place in weed-free conditions. Future studies would need to confirm a consistently strong correlation between LAI and WCA to merit its use as secondary selection traits, since LAI is a more involved measurement than height and vigor. Evidence exists that LAI and height explain different aspects of weed competition (Reiss et al. 2018).

Correlated traits for WCA in the northeastern United States

Among four site-years studied in the northeastern United States, early vigor had a moderately low correlation with weed biomass (r = − 0.24, $p < 0.0001$ in 2016 and − 0.21, $p < 0.0001$ in 2010; Table 2) and the ratio of wheat to weed biomass (r = 0.36, $p < 0.0001$ in 2016 and r = 0.25, $p < 0.0001$ in 2010; Table 2). Grain yield under weed pressure was moderately correlated with early vigor (r = 0.41, $p < 0.0001$ in 2016 and r = 0.43, $p < 0.0001$ in 2010). However, the strength and significance of these correlations depended on location in 2010 (Table 2).

Varietal ratings for early vigor were consistent among different evaluators. After six evaluators visually rated early vigor of 20 spring wheat genotypes over three replicates, 70% of the variance in early vigor was explained by genotype. Although evaluators did have slightly different rating scales, with 11% of the variance in early vigor explained by the evaluator, evaluators did not differ in their ranking of varieties for early vigor. Only 0.09% of variance in early vigor was explained by the interaction between evaluator and genotype. Consequently, visual estimation seems to be a reliable measure of early vigor among genotypes, even if different evaluators complete field measurements after receiving similar training instructions.

Mature height was moderately or weakly correlated to the ratio of wheat to weed biomass across all sites (r = 0.4, $p < 0.0001$ in 2016 and r = 0.22, $p < 0.0001$ in 2010). However, weed biomass was not correlated with mature height in two of four site-years (r = − 0.35, $p < 0.0001$ in 2016 and r = − 0.09 p = 0.3808 at Sidney 2010; r = 0.04, p = 0.6825 at Old Town 2010; r = − 0.25, p = 0.0053 at Alburgh 2010; Table 2). Mature height had a negative correlation with grain yield in one of four site-years (r = 0.33, $p < 0.0001$ in 2016; r = 0.27, p = 0.0065 at Sidney 2010; r = − 0.31, p = 0.001 at Old Town 2010; r = 0.55, $p < 0.0001$ in Alburgh 2010; Table 2). Similar to the global meta-analysis results, mature height does not appear to be a reliable secondary selection trait for weed suppression in the northeastern United States.

Grain yield was the most consistently correlated trait with weed suppression among site-years (Table 2). Grain yield was moderately to highly correlated with the ratio of wheat to weed biomass (r = 0.56, $p < 0.0001$ in 2016 and r = 0.7, $p < 0.0001$ in 2010), and the relationship was significant at every site-year (Table 2). Grain yield was significantly negatively correlated with weed biomass

Table 2 Correlations between wheat traits and measures of weed-competitive ability from four site-years in the northeastern United States

	Grain yield	Mature height	Early vigor	Ratio of wheat to weeds	Wheat biomass	Weed biomass
Old Town 2010						
Grain yield		− 0.32***	0.32***	0.47***	0.33***	− 0.42***
Mature height			− 0.27**	0.03	0.27**	0.04
Early vigor				0.12	0.33***	− 0.05
Ratio of wheat to weeds					0.51***	− 0.97***
Wheat biomass						− 0.3**
Weed biomass						
Sidney 2010						
Grain yield		0.27**	0.36***	0.34***	0.66***	− 0.12
Mature height			0.01	0.29**	0.62***	− 0.09
Early vigor				0.02	0.14	0.04
Ratio of wheat to weeds					0.53***	− 0.84***
Wheat biomass						− 0.21*
Weed biomass						
Alburgh 2010						
Grain yield		0.55***	0.34***	0.4***	0.57***	− 0.24**
Mature height			0.13	0.42***	0.61***	− 0.25**
Early vigor				0.13	0.18	− 0.06
Ratio of wheat to weeds					0.73***	− 0.94***
Wheat biomass						− 0.48***
Weed biomass						
Old Town 2016[a]						
Grain yield		0.33***	0.41***	0.56***	0.7***	− 0.38**
Mature height			0.49**	0.4**	0.47**	− 0.35***
Early vigor				0.36***	0.62***	− 0.24**
Ratio of wheat to weeds					0.76***	− 0.89***
Wheat biomass						− 0.54***
Weed biomass						

[a]Indicates that a different population of wheat genotypes was included in this evaluation

'*', '**', and '***' indicate significance of a correlation at $p < 0.05$, $p < 0.01$, and $p < 0.001$, respectively

($r = -0.38$, $p < 0.0001$ in 2016 and $r = -0.58$, $p < 0.0001$ in 2010), and the directionality of the correlation did not change among site-years (Table 2). Our results show that under organic growing conditions with substantial weed pressure (which is typical for spring wheat in the northeastern United States), grain yield may be a more reliable trait to select for WCA than early vigor or mature height. As grain yield is already measured in advanced breeding trials, it may also be the most cost-effective measure of WCA screening in later stages of a breeding program. To accurately distinguish differences in WCA among advanced lines, trials should seek conditions with uniform weed competition or overseed trials with a surrogate weed. For early-stage breeding, however, when lack of seed makes grain yield measurement impractical or unreliable, early vigor, early height, or LAI can be used as secondary selection traits for WCA.

Environment and weed species influence on competitive ability

Genotype performance for WCA may differ among environments and weed species present. In the global meta-analysis, correlations between traits and competitive ability were highly variable by year and location (Ogg and Seefeldt 1999; Bertholdsson 2005; Feledyn-Szewczyk and Jończyk 2015; Andrew 2016). Correlations for some traits were opposite in different years (e.g. Coleman et al., 2001). Traits such as maturity timing, early vigor (Coleman et al. 2001; Kissing Kucek 2017), leaf area (Rebetzke and Richards 1999), tillering and canopy diameter (Challaiah et al. 1986) were not consistently correlated with weed competition in different environments.

A trait commonly confounded with weather conditions in many studies was maturity timing (Challaiah et al. 1986; Lemerle et al. 1996; Bertholdsson 2005; Murphy et al. 2008). Later flowering genotypes are effective at competing with weeds in climates with high nutrient and water availability late in the season. However, early maturity is important for drier climates in which wheat varieties must compete for limited early rainfall (Mason et al. 2007a).

In different fields and years, farmers experience a wide range in weed competition. An ideal wheat genotype would yield well relative to other genotypes under both heavy and light weed pressure (Lemerle et al. 2001a). Weed suppression and crop tolerance do not directly assess such plasticity. As observed by Challaiah et al. (1986), a wheat variety with little percent yield loss under weedy conditions (i.e. high crop tolerance) could have relatively low yield under weed-free conditions. To improve grain yield under weed-free conditions, secondary selection traits for WCA should reduce intraspecific competition with wheat while imposing interspecific competition with weeds (Weiner et al. 2010, 2017; Denison 2015). The promising secondary selection traits of early vigor or early height were positively correlated or unrelated to weed-free grain yield (Coleman et al. 2001; Botwright et al. 2002), with the significance of the relationship varying by environment. These studies validate the proposal by Denison (2015) that traits conferring early season weed competition can prevent negative trade-offs with grain yield in pure stands (Denison 2015). Mature height, tillering, and growth habit (e.g. leaf angle) were negatively correlated with grain yield under weed-free conditions (Challaiah et al. 1986; Sadras and Lawson 2011; Coleman et al. 2001). Such traits can deprive nearby weeds of light, but also compete with nearby wheat plants when weed pressure is low (Lemerle et al. 2001a). After using secondary selection traits such as early vigor, early height, or early canopy density, advanced stages of a breeding program could test lines for yield under both weed-free and weedy conditions to identify genotypes with desired plasticity.

Weed species exert unique competition patterns with wheat in time and space. A robust secondary selection trait would effectively compete with weed species using diverse resource acquisition strategies. Maturity timing, tillering, growth habit, and allelopathy do not consistently compete with different weed species. Maturity was significantly correlated with yield reduction in competition with *A. sativa*, but not with *B. juncea* (Huel and Hucl, 1996). Early maturity may have allowed wheat to escape periods of peak competition with oat, yet aligned with periods of resource use for mustard. Tillering and/or growth habit was negatively correlated with WCA in *Alopecurus mysuroides* and *L. perenne*, but positively correlated in *Bromus tectorum*, *L. rigidum*, *A. sativa* and *Brassica juncea* (Online Resource 3). Allelopathic activity was only a useful selection trait if the regional weed species of concern are susceptible to the allelopathic chemicals excreted by wheat. Bertholdsson (2011) reported that allelopathy was significantly and positively correlated with the control of *S. alba*, but not that of *L. perenne*.

The meta-anlaysis cannot distinguish which traits are most correlated with WCA for specific weed species. Out of 18 studies, ten evaluated one weed species, two evaluated two weed species, and six used resident weed populations without identifying species. Each weed species was not studied among diverse environments (Table 1), confounding the effects of weed species with location and year effects. Boxplots of WCA trait correlations provide rough indications of differences among species of weeds (Online Resource 3). Two promising secondary selection traits identified in the meta-analysis, early vigor and early height, were positively correlated with WCA for all studied weed species (Online Resource 3). Growers often encounter multiple weed species in their fields, and weed species change with weather and field conditions of each season. Consequently, the aggregate data presented in this metanalysis, which includes observations from many weed species, may be more useful for choosing correlated traits with WCA that are relevant to diverse environments. Selection for multiple traits correlated with WCA may improve the estimate of a wheat genotype's competitive ability with multiple weed species. Reiss et al. (2018) reported that height explained more variance in biomass of two weed species (*Avena fatua*, *Sinapsis alba*), while LAI explained more variance in the biomass of *Chenopodium album*.

Interactions between genotype by environment and genotype by weed species may inhibit the selection of broadly adapted varieties for WCA. Breeding programs would benefit from testing and using regionally appropriate secondary selection traits (Worthington and Reberg-Horton 2013). Decentralizing selection into mega-environments with similar climatic variables and predominant weed species could reduce the impact of G*E, thereby increasing heritability and gains in selection for WCA (Eqs. 1 and 2).

Conclusions

Breeding directly for WCA is costly, laborious, and challenged by differential genotype performance across environments. Global datasets indicate that early vigor and early height are two promising secondary selection traits to improve WCA among diverse weed species. Early LAI shows promise as a secondary selection trait, but more studies are needed to confirm the correlation between LAI and WCA. Early vigor is an easy-to-measure trait that is correlated with WCA, and presents no known negative tradeoffs with harvest index and grain yield. However, early vigor has low heritability due to high G*E interactions. As the most consistently correlated trait with high heritability, early height may be the most globally useful method to select for WCA in wheat. However, breeding programs may struggle to identify alleles that promote early season height gain, yet maintain high harvest index for adequate grain yield. Due to high G*E interactions for competitive ability and correlated traits, breeding programs should develop regression models to identify what traits are highly correlated with WCA in regions of interest, and select for that trait using a decentralized approach.

Acknowledgements We thank Tom Molloy and Erica Cummings for data collection, and Profs. Matt Ryan and Jean-Luc Jannink for valuable feedback on the manuscript and experimental design. Funding was provided by United States Department of Agriculture, Organic Research and Extension Grant 2011-51300-30697; United States Department of Agriculture, Sustainable Agriculture Research and Education Grants LNE12-318; Hatch Project 149-430, 149-449; and by United States Department of Agriculture, National Institute for Food and Agriculture, Agriculture and Food Research Initiative Grants 2009-65300-05661 and 2011-68002-30029.

Funding Funding was provided by United States Department of Agriculture, Organic Research and Extension Grant 2011-51300-30697; United States Department of Agriculture, Sustainable Agriculture Research and Education Grant LNE12-318; Hatch Project 149-430, 149-449; and by United States Department of Agriculture, National Institute for Food and Agriculture, Agriculture and Food Research Initiative Grants 2009-65300-05661 and 2011-68002-30029.

Availability of data and material Through Online Resource 1.

Data availability The datasets generated and analyzed during the current study are included in Online Resource 1.

Declarations

Conflict of interest The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest. Mention of trade names or commercial products in this publication is solely for the purpose of providing specific information and does not imply recommendation or endorsement by the U.S. Department of Agriculture. The funders had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript, or in the decision to publish the results.

References

Acquaah G (2012) Principles of plant genetics and breeding, 2nd edn. Wiley-Blackwell, West Sussex

Addisu M, Snape JW, Simmonds JR, Gooding MJ (2009) Reduced height (Rht) and photoperiod insensitivity (Ppd) allele associations with establishment and early growth of wheat in contrasting production systems. Euphytica 166:249–267. https://doi.org/10.1007/s10681-008-9838-7

Andrew IK (2016) Identifying and evaluating competitive traits in wheat for sustainable weed management. University of Nottingham

Andrew IKS, Storkey J, Sparkes DL (2015) A review of the potential for competitive cereal cultivars as a tool in integrated weed management. Weed Res 55:239–248. https://doi.org/10.1111/wre.12137

Balyan RS, Malik RK, Panwar RS, Singh S (1991) Competitive ability of winter wheat cultivars with wild oat (*Avena ludoviciana*). Weed Sci 39:154–158

Bastiaans L, Paolini R, Baumann DT (2008) Focus on ecological weed management: what is hindering adoption? Weed Res 48:481–491

Bates D, Maechler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. J Stat Softw 67:1–48

Bertholdsson N-O (2005) Early vigour and allelopathy - two useful traits for enhanced barley and wheat competitiveness against weeds. Weed Res 45:94–102. https://doi.org/10.1111/j.1365-3180.2004.00442.x

Bertholdsson NO (2011) Use of multivariate statistics to separate allelopathic and competitive factors influencing weed suppression ability in winter wheat. Weed Res 51:273–283. https://doi.org/10.1111/j.1365-3180.2011.00844.x

Blackshaw RE (1994) Differential competitive ability of winter wheat cultivars against downy brome. Agron J 86:649–654. https://doi.org/10.2134/agronj1994.00021962008600040012x

Botwright TL, Condon AAG, Rebetzke GJ, Richards RA (2002) Field evaluation of early vigour for genetic improvement of grain yield in wheat. Aust J Agric Res 16:1137–1145

Cavigelli MA, Teasdale JR, Conklin AE (2008) Long-term agronomic performance of organic and conventional field crops in the Mid-Atlantic region. Agron J 100:785. https://doi.org/10.2134/agronj2006.0373

Challaiah BOC, Wicks GA, Johnson VA (1986) Competition between winter wheat (*Triticum aestivum*) cultivars and downy brome (*Bromus tectorum*). Weed Sci 34:689–693

Coleman RK, Gill GS, Rebetzke GJ (2001) Identification of quantitative triat loci for traits conferring weed competitiveness in wheat (*Triticum aestivum* L.). Aust J Agric Res 52:1235–1246

Cousens RD, Mokhtari S (1998) Seasonal and site variability in the tolerance of wheat cultivars to interference from *Lolium rigidum*. Weed Res 38:301–307

Denison RF (2015) Evolutionary tradeoffs as opportunities to improve yield potential. Field Crop Res 182:3–8. https://doi.org/10.1016/j.fcr.2015.04.004

Donald CM (1968) The breeding of crop ideotypes. Euphytica 17:385–403

Evans LE, Bhatt GM (1977) Influence of seed size, protein content and cultivar on early seedling vigor in wheat. Can J Plant Sci 57:929–935

Falconer DS (1981) Introduction to quantitative genetics, 2nd edn. Longmann Group, London

Feledyn-Szewczyk B, Jończyk K (2015) Differences between organically grown varieties of spring wheat, in response to weed competition and yield. J Plant Prot Res 55:254–259. https://doi.org/10.1515/jppr-2015-0036

Ford E (1980) Competition for light in a plant monoculture modelled as a spatial stochastic process. Diggle, PJ 48:481–500

Heap I (2014) Herbicide resistant weeds. Integrated pest management. Springer Netherlands, Dordrecht, pp 281–301

Huel DG, Hucl P (1996) Genotypic variation for competitive ability in spring wheat. Plant Breed 115:325–329

Jannink J-L, Jordan NR, Orf JH (2001) Feasibility of selection for high weed suppressive ability in soybean: absence of tradeoffs between rapid initial growth and sustained later growth. Euphytica 120:291–300

Jordan N (1993) Prospects for weed control through crop interference. Ecol Appl 3:84–91

Kissing Kucek L (2017) Participatory breeding of wheat for organic production. Cornell University

Kolb LN, Gallandt ER, Molloy T (2010) Improving weed management in organic spring barley: physical weed control vs. interspecific competition. Weed Res 50:597–605. https://doi.org/10.1111/j.1365-3180.2010.00818.x

Lafond GP, Baker RJ (1986) Effects of genotype and seed size on speed of emergence and seedling vigor in nine spring wheat cultivars 1. Crop Sci 26:341–346. https://doi.org/10.2135/cropsci1986.0011183x002600020027x

Le Campion A, Oury F-X, Morlais J-Y et al (2014) Is low-input management system a good selection environment to screen winter wheat genotypes adapted to organic farming? Euphytica 199:41–56. https://doi.org/10.1007/s10681-014-1172-7

Lemerle D, Gill GS, Murphy CE et al (2001a) Genetic improvement and agronomy for enhanced wheat competitiveness with weeds. Aust J Agric Res 52:527–548

Lemerle D, Verbeek B, Cousens RD, Coombes NE (1996) The potential for selecting wheat varieties strongly competitive against weeds. Aust J Agric Res 36:505–513

Lemerle D, Verbeek B, Orchard B (2001b) Ranking the ability of wheat varieties to compete with *Lolium rigidum*. Weed Res 41:197–209. https://doi.org/10.1046/j.1365-3180.2001.00232.x

Mallory E, Darby H, Molloy T, Cummings E (2014) maine and vermont organic spring wheat variety trial results 2010–2013

Mason H, Navabi A, Frick B et al (2007a) The weed-competitive ability of Canada western red spring wheat cultivars grown under organic management. Crop Sci 47:1167. https://doi.org/10.2135/cropsci2006.09.0566

Mason H, Navabi A, Frick B et al (2007b) Cultivar and seeding rate effects on the competitive ability of spring cereals grown under organic production in Northern Canada. Agron J 99:1199. https://doi.org/10.2134/agronj2006.0262

Mokhtari S, Galwey NW, Cousens RD, Thurling N (2002) The genetic basis of variation among wheat F3 lines in tolerance to competition by ryegrass (*Lolium rigidum*). Euphytica 124:355–364

Murphy KM, Dawson JC, Jones SS (2008) Relationship among phenotypic growth traits, yield and weed suppression in spring wheat landraces and modern cultivars. Field Crop Res 105:107–115. https://doi.org/10.1016/j.fcr.2007.08.004

Norsworthy JK, Ward SM, Shaw DR et al (2012) Reducing the risks of herbicide resistance: best management practices and recommendations. Weed Sci. https://doi.org/10.1614/WS-D-11-00155.1

Ogg AG, Seefeldt SS (1999) Characterizing traits that enhance the competitiveness of winter wheat (*Triticum aestivum*) against jointed goatgrass (*Aegilops cylindrica*). Weed Sci 47:74–80

R Core Team (2019) R: a language and environment for statistical computing organization

Rasmussen IA (2004) The effect of sowing date, stale seedbed, row width and mechanical weed control on weeds and

yields of organic winter wheat. Weed Res 44:12–20. https://doi.org/10.1046/j.1365-3180.2003.00367.x
Rebetzke GJ, Richards RA (1999) Genetic improvement of early vigour in wheat. Aust J Agric Res 50:291–301
Reiss A, Fomsgaard IS, Mathiassen SK et al (2018) Weed suppression by Canadian spring cereals: relative contribution of competition for resources and allelopathy. Chemoecology 28:183–187. https://doi.org/10.1007/s00049-018-0267-3
Sadras VO, Lawson C (2011) Genetic gain in yield and associated changes in phenotype, trait plasticity and competitive ability of South Australian wheat varieties released between 1958 and 2007. Crop Pasture Sci 62:533–549. https://doi.org/10.1071/CP11060
Seefeldt SS, Ogg AG (1999) Near-isogenic lines for *Triticum aestivum* height and crop competitiveness. Weed Sci 47:316–320
Teasdale JR, Coffman CB, Mangum RW (2007) Potential long-term benefits of no-tillage and organic cropping systems for grain production and soil improvement. Agron J 99:1297–1305. https://doi.org/10.2134/agronj2006.0362
Wicks GA, Ramsel RE, Nordquist PT, Schmidt JW (1986) Impact of wheat cultivars on establishment and suppression of summer annual weeds. Agron J 62:59–62
Weiner J, Andersen SB, Wille WKM et al (2010) Evolutionary agroecology: the potential for cooperative, high density, weed-suppressing cereals. Evol Appl 3:473–479. https://doi.org/10.1111/j.1752-4571.2010.00144.x
Weiner J, Du YL, Zhang C et al (2017) Evolutionary agroecology: individual fitness and population yield in wheat (Triticum aestivum). Ecology 98:2261–2266. https://doi.org/10.1002/ecy.1934
Wikimedia Commons (2016) World map blank black lines 4500px monochrome
Worthington M, Reberg-Horton C (2013) Breeding cereal crops for enhanced weed suppression: optimizing allelopathy and competitive ability. J Chem Ecol 39:213–231. https://doi.org/10.1007/s10886-013-0247-6
Worthington M, Reberg-Horton SC, Brown-Guedira G et al (2015a) Relative contributions of allelopathy and competitive traits to the weed suppressive ability of winter wheat lines against Italian Ryegrass. Crop Sci 55:57. https://doi.org/10.2135/cropsci2014.02.0150
Worthington M, Reberg-Horton SC, Brown-Guedira G et al (2015b) Morphological traits associated with weed-suppressive ability of winter wheat against Italian ryegrass. Crop Sci 55:50. https://doi.org/10.2135/cropsci2014.02.0149
Worthington M, Reberg-Horton SC, Jordan D, Murphy JP (2013) A comparison of methods for evaluating the suppressive ability of winter wheat cultivars against Italian ryegrass (*Lolium perenne*). Weed Sci 61:491–499. https://doi.org/10.1614/WS-D-12-00167.1
Xue Q, Stougaard RN (2002) Spring wheat seed size and seeding rate affect wild oat demographics. Weed Sci 50:312–320. https://doi.org/10.1614/0043-1745(2002)050[0312:swssas]2.0.co;2
Zerner MC, Rebetzke GJ, Gill GS (2016) Genotypic stability of weed competitive ability for bread wheat (*Triticum aestivum*) genotypes in multiple environments. Crop Pasture Sci 67:695–702. https://doi.org/10.1071/CP15198