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Morphological Traits Associated with Weed-Suppressive Ability of Winter Wheat against Italian Ryegrass

Margaret Worthington,* S. Chris Reberg-Horton, Gina Brown-Guedira, David Jordan, Randy Weisz, and J. Paul Murphy

ABSTRACT

Weed-suppressive wheat (*Triticum aestivum* L.) cultivars have been suggested as a complement to chemical and cultural methods of weed control. The objectives of this study were to assess the range of weed-suppressive ability against Italian ryegrass [*Lolium perenne* L. ssp. *multiflorum* (Lam.) Husnot] existing in winter wheat lines adapted to North Carolina and to identify wheat morphological traits that could facilitate indirect selection for weed suppression in the southeastern United States. Fifty-three commercially available cultivars and advanced experimental lines were overseeded with a uniform, high rate of Italian ryegrass, evaluated for various morphological traits throughout the growing season, and investigated for weed-suppressive ability at a total of four field sites. Genotypic differences in Italian ryegrass seed head density ($P \leq 0.05$) were detected among the wheat lines. Reduced Italian ryegrass seed head density was correlated ($P \leq 0.05$) with high vigor during tillering and heading (Zadoks growth stage [GS] 25, 29, 55), erect growth habit (GS 29), low normalized difference vegetation index (NDVI) (GS 29), high leaf area index (LAI) at stem extension (GS 31), early heading date, and tall height throughout the growing season (GS 29, 31, 55, 70 to 80) in three of four sites. Multiple regression models show that 71% of variation in weed-suppressive ability was accounted for by final height (GS 70 to 80) and either height or plant vigor at late tillering (GS 29). Thus, breeders could improve weed-suppressive ability using weighted index selection for genotypes that are tall or vigorous during tillering with tall final height.

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Abbreviations: AUHPC, area under height progress curve; DOY, day of year; GS, Zadoks growth stage; LAI, leaf area index; LS, least square; NC OVT, North Carolina official variety test; NDVI, normalized difference vegetation index; RCBD, randomized complete block design.

The development of wheat cultivars with improved weed-suppressive ability has been suggested as a complement to chemical and cultural means of weed control (Hoad et al., 2012; Wolfe et al., 2008; Worthington and Reberg-Horton, 2013). However, despite the body of literature describing variation in weed-suppressive ability within small grain crops, no breeding programs have released cultivars with documented weed-suppressive ability. The identification of gross morphological traits strongly associated with competitive ability could enable breeders to indirectly select for weed-suppressive lines in weed-free nurseries, ensuring that continual progress is made in selection for improved weed suppression.

Competitive ability is conferred by a combination of morphological traits that allow the crop to utilize a greater portion of limited resources than neighboring weeds. Wheat morphological traits, including end of season cultivar height (Coleman et al., 2001; Huel and Hucl, 1996; Lemerle et al., 1996; Mason

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et al., 2007; Murphy et al., 2008; Vandeleur and Gill, 2004), tillering capacity (Coleman et al., 2001; Korres and Froud-Williams, 2002; Lemerle et al., 1996; Mason et al., 2007; Wicks et al., 2004), leaf angle and canopy structure (Drews et al., 2009; Huel and Hucl, 1996; Korres and Froud-Williams, 2002; Lemerle et al., 1996), early vigor (Bertholdsson, 2005; Huel and Hucl, 1996; Lemerle et al., 1996; Mason et al., 2007), and time to maturity (Huel and Hucl, 1996; Mason et al., 2007), have all been associated with weed-suppressive ability.

Most studies on weed-suppressive ability were either conducted in spring wheat (Bertholdsson, 2005; Lemerle et al., 1996; Mason et al., 2007; Murphy et al., 2008) or winter wheat grown in harsh winter environments including Germany (Drews et al., 2009), Sweden (Bertholdsson, 2011), and Nebraska (Wicks et al., 2004). It is not clear if substantial variation in weed-suppressive ability exists within germplasm adapted to the southeastern United States and whether the same morphological traits confer an advantage to winter wheat lines competing against Italian ryegrass in mild climates. Therefore, the objectives of this study were to assess the range of weed-suppressive ability existing in commercially available winter wheat cultivars and advanced lines adapted to North Carolina growing conditions and to identify wheat morphological traits that could facilitate indirect selection for weed suppression in the southeastern United States.

MATERIALS AND METHODS

Experimental Design and Plant Material

Fifty-one entries from the 2012 North Carolina Official Variety Test (NC OVT) and two hard winter wheat cultivars developed by the USDA-ARS at North Carolina State University (Appalachian White and Nu East) were evaluated for weed-suppressive ability in 2012 and 2013 at a total of four field sites (Table 1). In the first year of testing, the experiment was planted on 24 Oct. 2011 at Piedmont Research Station in Salisbury, NC and on 25 Oct. 2011 at Caswell Research Station in Kinston, NC. The following year, the experiment was planted on 25 Oct. 2012 at Caswell Research Station and on 15 Nov. 2012 at the Tidewater Research Station in Plymouth, NC (Table 2). The test was organized as a randomized complete block design (RCBD) with three replications per site. Wheat was planted in 3-m-long plots using a calibrated cone drill with seven rows at 17.1-cm spacing with depth set at 2.5 cm. Gulf Italian ryegrass, a commercial turf cultivar, was then sown in a 1-m wide swath across the center of each plot using the same planter driving perpendicular to the direction in which wheat was planted with depth set at 1 to 5 mm. This experiment was planted alongside a parallel study focused on assessing the relative contributions of allelopathy and competitive traits to the weed-suppressive ability of winter wheat lines (Worthington et al., 2015). Further information on the study sites, field preparation, seeding rates, nutrient management, and control of broadleaf weeds can be found in Worthington et al. (2015).

Table 1. Italian ryegrass head density for the 53 released cultivars and advanced experimental lines included in the experiment.

Line†	Accession number‡	Italian ryegrass seed heads m^{-2}	
		Pooled sites§	Tidewater 2013
AgriMAXX 413	NA	390	499
AgriMAXX 415	NA	413	422
AGS 2026	PI 658065	314	531
AGS 2035	PI 658066	298	527
AGS 2056	NA	432	620
AGS 2060	PI 655074	275	544
Appalachian White	PI 657998	428	634
ARS 08–0047	NA	289	528
Coker 9553	PI 643092	327	482
DG 9012	NA	384	589
DG 9053	PI 657988	392	505
DG 9171	PI 657988	381	600
DG Baldwin	PI 657988	281	497
DG Dominion	PI 642937	386	381
DG Shirley	PI 656753	395	483
Featherstone VA258	PI 664272	269	450
Jamestown	PI 653731	344	512
Merl	PI 658598	390	529
NC08–23089	NA	364	609
NC08–23324	NA	328	575
NC-Cape Fear	PI 659089	322	477
NC-Neuse	PI 633037	344	449
NC-Yadkin	PI 663206	322	539
Nu East	PI 657997	320	543
Oakes	PI 658040	369	537
Pioneer 25R32	PI 658151	451	601
Pioneer 26R10	PI 664270	373	497
Pioneer 26R12	PI 631475	327	577
Pioneer 26R20	PI 658150	390	499
Pioneer 26R22	PI 638717	404	497
Progeny 117	NA	327	576
Progeny 125	NA	351	557
Progeny 185	NA	362	476
Progeny 357	NA	348	534
Progeny 870	NA	411	546
SS 520	NA	300	553
SS 5205	NA	384	587
SS 8308	NA	357	438
SS 8340	NA	364	448
SS 8641	PI 652450	331	540
SS 8700	NA	434	577
SY 9978	PI 659818	320	423
TV 8525	NA	386	521
TV 8535	NA	418	465
TV 8848	NA	390	389
TV 8861	PI 659787	369	435
USG 3120	NA	298	444
USG 3201	NA	386	473
USG 3209	PI 617055	351	596
USG 3409	NA	333	568

(cont'd)

Table 1. Continued.

Line†	Accession number‡	Italian ryegrass seed heads m^{-2} Pooled sites§	Tidewater 2013
USG 3438	NA	483	601
USG 3555	PI 654454	354	551
USG 3665	NA	367	511
Mean		361	520
LSD (0.05)		57	131
F genotype		5.41	1.94
P		<0.01	0.01

† AGS, AgSouth Genetics; DG, DynaGro; SS, Southern States; SY, Syngenta; TV, Terral; USG, UniSouth Genetics.

‡ Accession number from the USDA-ARS National Small Grains Collection. 'NA' indicates that no USDA-ARS accession number for the line is available.

§ Pooled sites are Caswell 2012, Piedmont 2012, and Caswell 2013.

Table 2. Dates when sites were planted and wheat morphological traits were measured at each experimental site when Pioneer 26R12 reached early tillering (Zadoks growth stage [GS] 25), late tillering (GS 29), stem extension (GS 31), heading (GS 55), and grain ripening (GS 70 to 80).

	2012		2013	
	Caswell	Piedmont	Caswell	Tidewater
Planting	25 Oct.	24 Oct.	25 Oct.	15 Nov.
Zadoks GS 25	31 Dec.	26 Dec.	14 Jan.	10 Jan.
Zadoks GS 29	7 Feb.	11 Feb.	4 Mar.	11 Apr.
Zadoks GS 31	18 Mar.	17 Mar.	28 Mar.	23 Apr.
Zadoks GS 55	16 Apr.	6 Apr.	19 Apr.	8 May
Zadoks GS 70 to 80	8 May	24 Apr.	5 May	17 May

Growing Conditions

Precipitation was below average in both years with 500 and 620 mm of rainfall falling between November and May in the Caswell and Piedmont locations in 2012 and 520 and 470 mm in the Caswell and Tidewater locations in 2013. Thirty-year climatic norms for the period between November and May were 650, 650, and 690 mm for the Caswell, Piedmont, and Tidewater sites. Cool spring conditions and late planting date contributed to suppressed tiller development and delayed stem extension at the Tidewater 2013 site (Table 2). While 2298, 1930, and 1918 growing degree days (0°C minimum base temperature) were accumulated in the Caswell 2012, Piedmont 2012, and Caswell 2013 sites between the date of planting and 1 May, only 1554 growing degree days were accumulated in Tidewater 2013 during the same period.

Morphological Traits Measured

Data on wheat morphological traits potentially correlated with weed-suppressive ability were collected in the 1-m long weed-free area at the edges of each plot when Pioneer 26R12, a cultivar with intermediate heading date, reached early tillering (GS 25), advanced tillering (GS 29), stem extension (GS 31), heading (GS 55), and grain fill (GS 70 to 80) (Zadoks et al., 1974). The dates when measurements were made varied widely due to differences in growing conditions across sites (Table 2). The range of heading dates for the tested wheat lines was 21 d (day of year [DOY] 86 –107) in 2012 and 19 d (DOY 102–121) in 2013. Consequently, not all genotypes had attained the exact same growth stage when measurements were collected. Such "snapshot" comparisons of wheat lines at specific instances throughout the growing season were considered appropriate given that the primary objective of this experiment was to identify measurements or traits that breeders could use to indirectly select for lines with high weed-suppressive ability in their weed-free nurseries.

Measurements of NDVI and visual ratings of early vigor were made during early and late tillering (GS 25 and 29). Readings of NDVI were taken using a Crop Circle ACS-210 Plant Canopy Reflectance Sensor (Holland Scientific, Inc., Lincoln, NE). Visual ratings of early vigor, based on a combination of percent ground cover and height, were made on a 1 to 9 scale with the most vigorous genotypes rated as 1 following Zhao et al. (2006). Growth habit was also rated on a 1 to 9 scale during late tillering (GS 29) with the most erect genotypes rated as 1 and the most prostrate genotypes rated as 9. The LAI was estimated during stem extension (GS 31) and heading (GS 55) using an LAI-2000 sensor (LI-COR Environmental, Lincoln, NE) in overcast conditions. Plant vigor was also visually estimated on a 1 to 9 scale during heading (GS 55), with the fullest canopies rated as 1 and the sparsest canopies rated as 9. The heading date of each experimental entry was measured in single 1.2-m row plots at Lake Wheeler Road Field Laboratory in Raleigh, NC during 2012 and 2013 as described by Worthington et al. (2015).

Plant height was estimated as the distance from ground level to the top of the canopy before heading (GS 29, 31). During and after heading, plant height was estimated as the distance from ground level to the tip of the average head, excluding awns (GS 55, 70 to 80). An area under height progress curve (AUHPC) index was created to describe height accumulation during the course of the growing season modeled after the area under disease progress curve developed by Shaner and Finney (1977):

$$\text{AUHPC} = \sum_{i=1}^{n} \left[(H_{i+1} + H_i)/2 \right] \left[X_{i+1} - X_i \right]$$

where H_i is height at the *ith* observation, X_i is time (days) at the *ith* observation, and n is the total number of observations. All genotypes were assumed to have equal height on 1 January (DOY 0) in each site. The date of the final height score for all sites was set to 17 May (DOY 138), the date when all genotypes had reached final height in Tidewater 2013.

Weed-suppressive ability was measured by counts of Italian ryegrass seed heads in a 0.5 m^2 quadrat placed in the center of the weedy area in each plot during grain fill (GS 70–80) as described by Worthington et al. (2013). Italian ryegrass seed head density was previously correlated with Italian ryegrass to wheat biomass ratio and visual ratings of Italian ryegrass biomass in North Carolina (Worthington et al., 2013).

Statistical Analyses

Statistical analyses were conducted using ASREML (VSN International LTD., Hemel Hempstead, UK) and SAS 9.2 (SAS Institute Inc., Cary, NC). Individual locations were first analyzed in ASREML with genotype treated as a fixed effect and block treated as a random effect. Plots of model-predicted values versus residual errors showed that Italian ryegrass heads m^{-2} and all wheat morphological traits met the assumption of normal error distribution. Spatial variation across the field was not captured by blocking structure in several cases. Therefore, spatially correlated errors were addressed in post-hoc analysis. A first order autoregressive model in two dimensions (AR1 × AR1) was compared with the RCBD base model for Italian ryegrass heads m^{-2} and all wheat morphological traits in each individual location. Because the spatially adjusted model was nested relative to the base model, they were compared with a likelihood ratio test with two degrees of freedom. In instances where the spatially adjusted model was deemed optimum but the variance component for row effect was notably small, a reduced model was tested with residuals correlated based solely on their distance in the column direction and compared with the full model (AR1 × AR1) using a log likelihood test with one degree of freedom.

When the optimum level of spatial adjustment was chosen for each trait–location combination, the combined experiment was evaluated in ASREML with genotype treated as a fixed effect; site, block nested within site, and the interaction of genotype and site treated as random effects; and spatially correlated error structure included for each location as determined in the preliminary analysis. The average pairwise Pearson correlations between genotype rankings for weed-suppressive ability between Tidewater 2013 and other sites was nonsignificant ($r = 0.15$), whereas the average pairwise Pearson correlation between the genotypic rankings of all other sites was much higher ($r = 0.41$, $P \leq 0.01$). When Tidewater 2013 was removed from the combined model, the variance component for genotype × site interaction decreased from 475 to 405. Thus, the results from Tidewater 2013 are presented separately from the pooled analysis of Caswell 2012, Piedmont 2013, and Caswell 2013 in this manuscript.

Genotype least square (LS) means were generated in ASREML for Italian ryegrass heads m^{-2} and all wheat morphological traits using the optimal spatially adjusted model for the pooled sites and Tidewater 2013. Mean separation was performed using Fisher's protected LSD ($P \leq 0.05$). Pearson's correlation coefficient was used to test the significance of correlations between LS means of wheat morphological traits potentially affecting weed suppression and Italian ryegrass heads m^{-2} in SAS 9.2. Stepwise multiple linear regression was conducted to identify wheat morphological traits that strongly influenced weed suppression. Model information criteria methods including Schwarz Bayesian Criteria, Bayesian Information Criteria, and Akaike's Information Criteria were utilized to choose the optimal models for predicting the weed-suppressive ability of wheat genotypes. Model information criteria were dependent on all parameters being significant at $P \leq 0.10$. Estimated condition indices and variance inflation factors showed that collinearity was not problematic in either optimal model.

Lines that did not differ from the genotype with the lowest LS mean for Italian ryegrass head density according to Fisher's protected LSD ($P \leq 0.05$) were considered the most weed-suppressive group. Likewise, lines that did not differ from the genotype with the highest LS mean for Italian ryegrass head density were considered the least weed-suppressive group. Chi square tests were performed for each molecular marker to determine whether the most and least weed-suppressive groups deviated from expected allelic ratios on the basis of allele frequency found in all 39 genotypes tested. Deviation from expected allelic ratios ($P \leq 0.05$) was considered evidence of possible association between molecular markers and weed-suppressive ability.

RESULTS AND DISCUSSION

A large amount of variation in weed-suppressive ability was observed among elite adapted germplasm from the southeastern United States. Differences in end of season Italian ryegrass seed heads m^{-2} ($P \leq 0.05$) were detected among the wheat genotypes tested in both the pooled sites and Tidewater 2013 (Table 1). Least square means of Italian ryegrass seed heads m^{-2} ranged from 269 to 483 in the pooled analysis and 381 to 634 in Tidewater 2013 (Table 1). Despite a nonsignificant Pearson correlation between the weed-suppressive ability rankings of genotypes in the pooled sites and Tidewater 2013 ($r = 0.09$), several lines performed consistently in all environments. Five lines (Dyna-Gro Baldwin, NC-Cape Fear, Featherstone VA258, SY 9978, and USG 3120) performed as well as the most weed-suppressive line in both analyses. All four lines that performed as poorly as the least suppressive line in the pooled analysis (AGS 2056, Appalachian White, SS 8700, and USG 3438) were also among the least weed-suppressive groups in Tidewater 2013 (Table 1).

The precision of genotypic weed-suppressive ability estimates was greater in the pooled sites than Tidewater 2013, as evidenced by a smaller genotype LSD and higher F statistic for genotype (Table 1). The late planting date and cool early spring conditions at Tidewater 2013 influenced wheat development and delayed the onset of stem extension (GS 31) by 36 d compared with the next latest site (Table 2). While these growing conditions set Tidewater 2013 apart from other study sites, growers in the Tidewater region of North Carolina often plant wheat in mid-November if wet conditions postpone the harvest of spring-sown crops and delay field preparation. These findings suggest that selection for weed-suppressive ability may not be equally efficient in all environments and that weed-suppressive genotypes may be affected by planting date and other environmental conditions.

Morphological Traits Associated with Weed-Suppressive Ability

Reduced Italian ryegrass seed head density was correlated ($P \leq 0.05$) with high vigor during tillering (GS 25, 29) and heading (GS 55), erect growth habit (GS 29), low NDVI (GS 29), high LAI at stem extension (GS 31), early heading date, tall height throughout the growing season (GS 29, 31, 55, 70 to 80), and high AUHPC in the pooled analysis of Caswell 2012, Piedmont 2012, and Caswell 2013 (Table 3). In contrast, only early vigor and high NDVI during tillering (GS 25) were correlated ($P \leq 0.05$) with weed-suppressive ability in Tidewater 2013 (Table 3).

Table 3. Correlations between Italian ryegrass seed heads m^{-2} and wheat morphological traits measured throughout the growing season.

Trait†	Pooled sites‡	Tidewater 2013
Zadoks GS§ 25		
Vigor	0.70**	0.48**
NDVI	−0.22	−0.33*
Zadoks GS 29		
Growth habit	0.76**	0.02
Height	−0.77**	−0.05
Vigor	0.77**	0.08
NDVI	0.44**	0.04
Zadoks GS 31		
LAI	−0.74**	−0.17
Height	−0.77**	0.11
Zadoks GS 55		
LAI	−0.12	−0.21
Height	−0.70**	−0.16
Vigor	0.62**	0.23
Zadoks GS 70 to 80		
Height	−0.28*	−0.1
Not GS specific		
Heading date	0.61**	0.08
AUHPC	−0.84**	−0.05

* Significant at the 0.05 probability level.

** Significant at the 0.01 probability level.

† NDVI, normalized difference vegetation index; LAI, leaf area index; AUHPC, area under height progress curve.

‡ Pooled sites are Caswell 2012, Piedmont 2012, and Caswell 2013.

§ GS, growth stage.

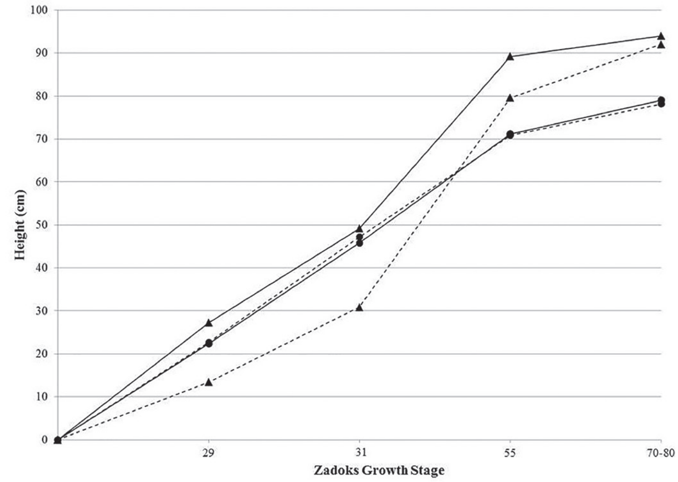

Figure 1. Mean height of lines in the most and least weedsuppressive groups in the pooled sites (Caswell 2012, Piedmont 2012, and Caswell 2013) and Tidewater 2013 according to Fisher's protected LSD ($P < 0.05$) measured at Zadoks Growth Stage 29, 31, 55, and 70 to 80. Triangle, pooled sites; circle, Tidewater 2013. The most suppressive groups are plotted with solid lines while the least suppressive groups are plotted with dashed lines.

End of season height was associated with competitive ability of wheat lines in many studies (Coleman et al., 2001; Huel and Hucl, 1996; Lemerle et al., 1996; Mason et al., 2007; Murphy et al., 2008; Vandeleur and Gill, 2004). However, while final height was correlated with weed-suppressive ability in the pooled sites, correlations between height and weed-suppressive ability were much stronger earlier in the growing season (Table 3). The competitive advantage gained by rapid early growth and the accumulation of height throughout the season was far more important than final cultivar height in determining weed suppression (Ogg and Seefeldt, 1999). A plot of AUPHC constructed with the mean height of the genotypes that performed as well as the most weed-suppressive line or as poorly as the least weed-suppressive line shows that height accumulated during the course of the growing season influenced competitive ability against weeds in the pooled sites (Fig. 1).

A recent review of breeding for improved weed suppression in organically grown cereals stated that crop ground cover was the most influential characteristic affecting weed-suppressive ability (Hoad et al., 2012). Prostrate growth habit was correlated with high weed-suppressive ability of spring wheat in at least two studies (Huel and Hucl, 1996; Lemerle et al., 1996). However, erect growth habit at tillering (GS 29) was strongly associated with weed-suppressive ability in the pooled sites in this study (Table 3). Erect growth habit during tillering was also correlated with improved weed suppression in a study of winter wheat in the UK (Korres and Froud-Williams, 2002).

Early vigor ratings during tillering (GS 25, 29) were also correlated with improved weed-suppressive ability (Table 3). Many other studies have also found that early vigor was correlated with weed-suppressive ability in wheat (Huel and Hucl, 1996; Lemerle et al., 1996; Mason et al., 2007). Interestingly, high NDVI during early tillering (GS 25) was associated with reduced Italian ryegrass seed head density in Tidewater 2013, while high NDVI during late tillering (GS 29) was associated with increased Italian ryegrass seed head density in the pooled analysis of other sites. The NDVI was correlated ($P \leq 0.05$, data not shown) with prostrate growth habit at GS 29 in the pooled sites, possibly confounding results.

Early heading (Huel and Hucl, 1996) and maturing (Mason et al., 2007) lines were associated with high weed-suppressive ability in wheat in some studies, while other studies found no significant association between maturity and competitive ability (Bertholdsson, 2005) or found that later maturing lines were better weed suppressors (Coleman et al., 2001; Wicks et al., 2004). Early heading date was correlated with reduced Italian ryegrass seed head density in the analysis of pooled sites (Table 3). However, early heading date is associated with increased susceptibility to late spring freeze (Worland, 1996) and is not considered a desirable breeding trait. Competitive traits such as tall height, erect growth habit, and vigor during tillering (GS 29) were correlated ($P \leq 0.05$) with early heading date in the pooled sites (data not shown). However,

Table 4. Multiple regression models for wheat morphological traits influencing Italian ryegrass seed heads m^{-2}. Model criteria include Akaike's Information Criteria (AIC), Schwarz's Bayesian Criteria (SBC), and Sawa's Bayesian Information Criteria (BIC).

Model variable	Zadoks GS†	Partial R^2	Model R^2	Variable *P*
Pooled sites‡				
Vigor	29	0.59	0.59	<0.0001
Height	55	0.12	0.71	<0.0001
NDVI§	29	0.06	0.77	0.0007
Y¶ = 43.84 + 25.06 (vigor, GS 29) − 3.78 (height, GS 55) + 678.21 (NDVI, GS 29)				
SBC = 344.0 (lowest value), AIC = 391.1 (lowest value), BIC = 338.8 (lowest value)				
Tidewater 2013				
Vigor	25	0.23	0.23	0.0003
Y¶ = 373.46 + 33.92 (vigor, GS 25)				
SBC = 428.7 (lowest value), AIC = 479.73 (lowest value), BIC = 426.3 (lowest value)				

† GS, growth stage.

‡ Pooled sites are Caswell 2012, Piedmont 2012, and Caswell 2013.

§ NDVI, normalized difference vegetation index.

¶ Y, predicted influencing Italian ryegrass seed heads m^{-2}.

several vigorous, erect lines (DG 9053, DG Baldwin, and SY 9978) had later than average heading dates. Thus, it should be possible to breed for improved early vigor and erect growth habit without impacting local adaptation and increasing susceptibility to late spring freeze.

Multiple Regression

The wheat morphological traits measured in this study were included in multiple regression models to determine which characteristics most influenced weed suppression (Table 4). Early vigor (GS 25) was the only variable chosen as influential in weed suppression in Tidewater 2013, explaining just 23% of variation in weed-suppressive ability (Table 4). Vigor during tillering (GS 29), height at heading (GS 55), and NDVI during tillering (GS 29) were selected as the most influential traits affecting Italian ryegrass seed head density in the pooled sites, together accounting for 77% of observed variation in the weed-suppressive ability of genotypes (Table 4). Many of the morphological traits associated with competitive ability were also correlated with one another, so some model terms could be substituted without losing much of goodness of fit. Six models involving combinations of vigor, growth habit, or height at tillering (GS 29) with either height at heading (GS 55) or final height (GS 70 to 80) explained at least 70% of the observed variation in the weed-suppressive ability of genotypes in the pooled sites (data not shown).

CONCLUSIONS

Researchers have suggested that weed-suppressive ability may be negatively correlated with grain yield under weed-free conditions (Donald and Hamblin, 1976; Olofsdotter et al., 2002). However, many of the weed-suppressive lines identified in this experiment yielded competitively in separate trials conducted in conventional and organic conditions in North Carolina. Featherstone VA258 and USG 3120 were both ranked in the top 10% of lines screened in the NC OVT in 2012 and 2013 (North Carolina Official Variety Test, 2012) and Featherstone VA258 had the highest two-year rank of 20 lines screened in the 2011 to 2013 Organic Wheat Official Variety Trials (RAFI-USA, 2013). Breeding for improved weed-suppressive ability in North Carolina is, therefore, not expected to negatively impact grain yield.

The lack of correlation between the weed-suppressive ability of genotypes in Tidewater 2013 and the other study sites and the weak association between morphological traits and weed suppression ability in Tidewater 2013 suggest that selection for weed-suppressive ability may not be equally efficient in all environments. Furthermore, highly weed-suppressive genotypes may not perform reliably if planting date is delayed or cool spring conditions inhibit plant development. Still, correlations between the weed-suppressive ability of adapted genotypes and many wheat morphological traits in the pooled sites suggest that indirect selection for weed-suppressive ability in weed-free environments is likely to be generally effective.

Multiple regression models in the pooled sites indicated that 59% of variation in the weed-suppressive ability of tested genotypes was explained by either visual ratings of plant vigor or measurements of canopy height during tillering (GS 29), while 71% of variation in weed-suppressive ability was accounted for when final genotype height (GS 70 to 80) was added to either model. Thus, breeders should select weed-suppressive winter wheat lines in weed-free breeding nurseries by imposing a weighted selection index for genotypes that are either tall or vigorous during late tillering (GS 29) and tall at the end of the growing season (GS 70 to 80). Given their stronger correlation with weed-suppressive ability, genotype height or vigor rating at tillering (GS 29) should be given more weight than final height in the selection index. Breeders should also discard lines that reach heading (GS 55) before early checks in their breeding nurseries to ensure that selected lines are well adapted and not susceptible to late spring freeze. Final genotype height and heading date are routinely measured in winter wheat breeding programs (North Carolina Official Variety Test, 2012). Thus, the proposed selection index would require only one additional phenotyping step (either a visual rating of plant vigor or measurement of canopy height) by the breeder when average-heading lines have reached late tillering (GS 29) in the early spring.

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