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Article

Analysis of Traits Related to Weed Competitiveness in Sweet Corn (*Zea mays* L.)

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Abstract: Weed management in sweet corn can be costly; genetic improvements in sweet corn competitiveness may reduce this expense. Competitive ability can exist as weed suppressive ability (WSA), or crop tolerance (CT). Previous studies in corn have found year of hybrid release, maturity, plant height, leaf angle and leafiness may affect WSA, while hybrid era, maturity, and plant height may affect CT. However, many of these studies were limited to very few genotypes. The objective of this study was to assess the effects of phenomorphological traits on sweet corn competitiveness and the inheritance of these traits. An incomplete half-diallel from seven historic sweet corn inbred lines of varying morphologies was evaluated in a split-block randomized complete block design in three environments. Forage sorghum was interplanted in half of the blocks to act as a model weed. Significant differences among hybrids were generally found for both phenomorphological traits and traits measuring WSA and CT, such as sorghum biomass and yield stability, respectively. Crop plant height was most predictive of WSA and CT. In this set of genotypes, competitive ability may be passed with reasonable fidelity from parent to offspring, suggesting that sweet corn could be bred for competitive ability.

Keywords: *Zea mays*; sweet corn; weed competition; crop tolerance; weed suppressive ability

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1. Introduction

Among fresh vegetables sweet corn is the eighth most valuable out of the 25 tracked by the USDA, and in the processing market, it is second out of eight [1]. In 2007, Wisconsin grew over 38,000 hectares of fresh market and processing sweet corn with a farm gate value of $64.5 million [2].

Weeds represent an economically important challenge for crop production. In the United States, average crop yields are depressed by 12% due to weeds [3]. Also, in the US, over $6 billion were spent overall on herbicides in 2001, with $17 million spent on herbicides for sweet corn production [4,5].

Weeds compete with crops when they remove a portion of a resource from a shared resource pool, leaving the crop with less of the resource than is needed for optimum growth [6]. Competition may occur for water, creating or exacerbating water stress. It may occur for nutrients such as nitrogen, leading to chlorosis, leaf senescence and reduced yields [7,8]. Competition may also occur for light, which may alter plant growth by reducing the quantity or quality of light received [9,10].

Crop competitive ability consists of two mechanisms: weed suppressive ability (WSA), and crop tolerance (CT). WSA is the ability of a crop to inhibit weed germination, growth, or reproduction. CT is the increased ability to produce stable crop yields in environments of high and low weed stress [11]. Improved WSA can provide a reduction of weed pressure and a reduction in weed seed bank levels. However, a crop with good CT may still allow the weed seed bank to increase [12,13]. The competitive ability of a crop is also influenced by a number of cultural factors, including the planting density and the planting date [14].

Many traits have been hypothesized to affect competitive ability, including those that improve competitiveness of the crop for water, nutrients, and light. Traits related to competitiveness for water and nutrients include: root density, root length, water uptake rate, and root surface area. Traits related to light competitiveness include: plant height, leaf area, canopy, and leaf orientation. [15].

Callaway [16] reviewed research conducted on crop competitive ability in many crop species. A few traits were found to be important for competitive ability across many trials, including greater plant height, early canopy closure, and greater leaf area. As weed density increases or crop density decreases, competition theory predicts greater yields of weeds up to an asymptote. If weed density is constant, increasing crop density will increase crop yield and decrease weed yield [14]. Planting date can also influence CT. Corn planted in May yielded better under weedy conditions than when it was planted three weeks earlier [17]. Williams [18] found that, to avoid significant yield losses, early planted sweet corn needed to be kept weed-free for a longer period than late planted sweet corn.

In corn, a number of factors have been examined in relation to crop competitive ability, both in terms of WSA and CT. Studies have found inconsistent results for many of these factors. The era in which the corn was developed has been shown to affect WSA, with inconsistent results. Lindquist and Mortensen [19] found that older hybrids had better WSA than newer hybrids. However, corn densities varied between the modern hybrids and the old hybrids, and may have confounded the comparison between hybrid eras.

Roggenkamp *et al.* [20] found that hybrids with erect leaves had better WSA than those with horizontal leaves. Makus [21] found in two sweet corn cultivars that the taller, later hybrid better suppressed weeds. Williams *et al.* [12,13] found that in three sweet corn hybrids, mid-season, leafy and taller hybrids suppressed weeds better than the early, short, less leafy hybrid. However, Begna [22] studied three field corn hybrids, and found that weed mass was lower in two early hybrids than in the late hybrid. Woolley and Smith [23] found that leafy field corn had greater WSA than less leafy cultivars.

Many studies have assessed the differences in CT between corn varieties. Lindquist and Mortensen [19] found that older hybrids had greater CT than newer hybrids. On the other hand, Tollenaar *et al.* [8,24] found that, when comparing an old and a new field corn hybrid, the new hybrid had greater CT relative to the older hybrid. Like WSA, the comparison of old and new hybrids for CT may be confounded by planting density. Maturity may also relate to CT. Staniforth [25] found that grain yield was least reduced in the earliest hybrid and most reduced in the latest hybrid. Other morphological traits, including plant height, have been examined for their effect on CT. Makus [21] found that yield was reduced more in a taller cultivar than a shorter cultivar.

Many of the above mentioned studies examined few genotypes, making it impossible to separate the general effects of particular traits on CT and WSA from the performance of a particular cultivar. In addition, there is a need to determine the genetics and inheritance of those traits which confer competitiveness.

The objectives of this study were to strengthen the body of knowledge by identifying phenomorphological traits (traits measuring either plant phenology or plant morphology) that can be used in selection to increase crop competitive ability. This experiment compares 19 hybrids for phenomorphological differences and differences in suppression and tolerance of interplanted sorghum. The 19 hybrids in the study were created from an incomplete half diallel mating design. The hybrids in this design were made from all but two of the possible crosses between seven inbred parents. Using these defined genetic relationships, this study determined the general (GCA) and specific combining abilities (SCA) of the seven inbred parents for these traits. With this information, future breeding efforts will have additional direction on ways to select sweet corn for competitive ability.

2. Results and Discussion

2.1. Hybrid Evaluation

Results demonstrated that there were differences between hybrids for many phenomorphological traits and competitive factors, that some phenomorphological traits accounted for differences in competitive ability in the hybrids, and that, for some of these traits, hybrid performance can be predicted based on parentage.

Consistent differences between hybrids existed for most phenomorphological traits and competitive factors. Hybrid effects existed for all traits except ear length, ear length stability, and ear width stability (Tables 1,2). Hybrid-by-environment (H × E) effects existed for 100 kernel mass, ears per plant, early leaf area, late leaf area, average leaf height, early height, mid-season height, and yield stability. However, Spearman rank-change H × E effects existed only for ears per plant and average leaf height. In all traits that had hybrid effects, GCA effects also existed, except for 100 kernel mass stability. In all traits that had hybrid effects, SCA effects also existed, except for 100 kernel mass stability, average leaf height, average number of tillers, mid-season height, ear number stability, and early sorghum biomass.

Table 1. Significance of mean squares from analysis of variance for phenological and morphological traits of 19 hybrids from a seven line diallel and Jubilee, a check, measured in Arlington, WI 2007, and West Madison, WI 2008.

Source	**Hybrid**	**Environment**	**Hybrid × Environment**	**Environment × Treatment**	**GCA**	**SCA**	**Treatment**	**Hybrid × Treatment**
Yield	**	**			**	**	**	
100 kernel mass	**		**	*	**			*
Ear length		*			**		*	
Ear Width	**				**	*	**	
Ears per plant	**		**	*	**	*	**	*
GDD to anthesis	**	**			**	**		
Early-season leaf area	**	**	**		**	*		
Late-season leaf area	**	**	**	**	**	**	**	
Average leaf height	**	**	**		**			
Early-season plant height	**	**	**		**	*		
Mid-season plant height	**	**	**		**	**		
Late-season plant height	**				**	**		
Tiller number	**				**		**	*
Above-ear leaf angle	**	*			**	*	**	
Yield stability	**	*	*	**	**	**	**	**
Ear length stability		*		**	*		**	**
Ear width stability				**	*		**	**
100 kernel mass stability	*	*		**			**	**
Ear number stability	*	*		**	**		**	**
Early sorghum biomass	*	**		**	**		**	**
Late sorghum biomass	**			**	**		**	**

*, ** Significant at 0.05 and 0.01 probability levels, respectively.

Table 2. Means for phenological and morphological traits for 19 hybrids from a seven line diallel and Jubilee, a check, averaged across one or more of the following locations: Arlington WI, 2007, and West Madison, WI, 2008.

Hybrid	Yield	100 kernel mass	Ear length	Ear width	Ear number		GDD to anthesis	Early-season leaf area	Late-season leaf area
	All (kg ha^{-1})	All (g)	All (cm)	All (cm)	A07	WM08	All	All (cm)	All (cm)
Ia5125 × C68	4842	18.4	14.7	4.4	0.96	0.93	975	4842	18.4
Ia5125 × P39	3605	14.6	14.0	4.1	0.92	0.98	972	3605	14.6
Ia5125 × P51	4179	16.6	13.4	3.9	1.03	1.03	936	4179	16.6
Ia5125 × We10	2833	18.3	12.8	4.0	0.78	0.65	759	2833	18.3
Ia5125 × IL101t	4162	19.0	14.6	3.9	0.97	0.98	947	4162	19.0
Ia5125 × C40	4685	23.4	15.0	4.2	0.91	1.02	907	4685	23.4
C68 × P39	4059	17.3	14.3	3.8	0.95	0.95	1045	4059	17.3
C68 × P51	4394	19.3	13.6	3.8	1.10	0.96	1150	4394	19.3
C68 × We10	4089	21.4	13.9	4.0	0.92	0.93	1022	4089	21.4
C68 × IL101t	4681	21.1	14.9	3.9	0.98	0.98	1138	4681	21.1
C68 × C40	4742	24.4	14.6	4.1	0.88	0.95	1162	4742	24.4
P39 × P51	2553	14.2	12.6	3.3	0.92	1.05	967	2553	14.2
P39 × We10	2663	15.8	12.9	3.6	0.78	0.88	1033	2663	15.8
P39 × IL101t	3389	16.5	13.8	3.4	1.04	1.03	970	3389	16.5
P39 × C40	3834	18.7	14.3	3.6	0.95	1.03	1264	3834	18.7
P51 × We10	3549	20.0	13.8	3.6	0.98	0.97	1055	3549	20.0
P51 × IL101t	3770	21.0	13.2	3.4	1.17	1.07	1108	3770	21.0
C40 × P51	3448	21.8	14.4	3.5	0.92	0.95	1122	3448	21.8
C40 × We10	4134	24.6	15.3	4.0	0.93	0.92	1165	4134	24.6
Jubilee	3659	14.1	14.5	3.9	0.97	1.10	731	3659	14.1
CV	0.15	0.10	0.16	0.06	0.19	0.13	0.18	0.15	0.10
LSD (0.05)	482	1.7	1.9	0.2	0.15	0.17	152	482	1.7

Table 2. *Cont.*

Hybrid	**Early-season plant height**	**Mid-season plant height**	**Late-season plant height**	**Upper leaf angle**	**100 kernel mass stability**	**Ears per plant stability**	**Early-season sorg. mass**	**Late-season sorg. mass**
	All (cm)	All (cm)	All (cm)	All (°)	All (%)	All (%)	All (g)	All (g)
Ia5125 × C68	14.7	4.4	4.4	58	125	112	13	53
Ia5125 × P39	14.0	4.1	4.1	76	91	86	16	72
Ia5125 × P51	13.4	3.9	3.9	64	95	90	14	71
Ia5125 × We10	12.8	4.0	4.0	58	102	63	18	68
Ia5125 × IL101t	14.6	3.9	3.9	56	96	99	14	71
Ia5125 × C40	15.0	4.2	4.2	56	97	97	15	66
C68 × P39	14.3	3.8	3.8	62	92	79	15	74
C68 × P51	13.6	3.8	3.8	53	94	83	13	67
C68 × We10	13.9	4.0	4.0	46	98	87	14	68
C68 × IL101t	14.9	3.9	3.9	46	106	94	12	65
C68 × C40	14.6	4.1	4.1	44	99	69	14	50
P39 × P51	12.6	3.3	3.3	69	73	64	17	74
P39 × We10	12.9	3.6	3.6	60	97	67	16	77
P39 × IL101t	13.8	3.4	3.4	61	98	78	17	78
P39 × C40	14.3	3.6	3.6	65	108	83	15	65
P51 × We10	13.8	3.6	3.6	57	122	77	16	75
P51 × IL101t	13.2	3.4	3.4	52	96	83	15	70
C40 × P51	14.4	3.5	3.5	54	100	84	15	74
C40 × We10	15.3	4.0	4.0	54	102	93	14	58
Jubilee	14.5	3.9	3.9	57	84	74	18	82
CV	0.16	0.06	0.06	0.10	0.21	0.23	0.20	0.17
LSD (0.05)	1.9	0.2	0.2	4.6	27	26	3.4	13

All = all environments; A07 = Arlington 2007; WM08 = West Madison 2008; NS = Entry effects were non-significant; NA = No value exists for mean.

Correlations were seen between the sorghum-free plot means of many of the phenomorphological traits and the three factors used to assess competitive ability: early sorghum biomass, late sorghum biomass, and yield stability (Table 3). The three traits most correlated with reduced early-season sorghum mass were mid-season plant height ($r = -0.62$) (Figure 1), early-season leaf area ($r = -0.61$) (Figure 2), and yield ($r = -0.60$) (Table 3). Stepwise regression found that early-season plant height and early-season leaf area combined accounted for 67% of the variation present in early-season sorghum mass ($p < 0.01$), and additional traits did not significantly improve the model (data not shown). Early-season plant height ($r = -0.78$) (Figure 3), 100 kernel mass ($r = -0.62$), and yield ($r = -0.61$) were most correlated with reduced late-season sorghum biomass. Early-season plant height accounted for 61% of variation in late-season sorghum biomass, with additional traits not significantly improving the regression model. Mid-season plant height ($r = 0.58$) (Figure 4), late-season plant height ($r = 0.56$), and upper leaf angle ($r = -0.53$) were the three factors most correlated with yield stability. Mid-season plant height accounted for 33% of variation in yield stability, with additional traits not significantly improving the regression model.

Table 3. Phenotypic correlation coefficients between the means of 19 hybrids from a seven line diallel and Jubilee, a check, for all morphological and phenological traits and the means of traits related to weed competitiveness, measured in Arlington WI, 2007 and West Madison, WI, 2008. Means for all traits except early-season sorghum mass and late-season sorghum mass taken only from non-sorghum control blocks.

Trait	**Yield Stability**	**Early-season sorghum mass**	**Late-season sorghum mass**
Yield	0.51*	−0.60**	−0.61**
100 kernel mass	--	--	−0.62**
Ear length	--	--	--
Ear width	0.49*	--	−0.49*
GDD to anthesis	--	--	--
Early-season leaf area	--	−0.61**	−0.50*
Late-season leaf area	--	--	--
Early-season corn plant height	0.48*	−0.59**	−0.78**
Mid-season corn plant height	0.57**	−0.62**	−0.57**
Late-season corn plant height	0.56*	--	−0.45*
Corn tiller number	--	--	--
Upper leaf angle	−0.53*	--	--

*, ** Significant at 0.05 and 0.01 probability levels, respectively; -- = $p > 0.05$.

Figure 1. Means of sorghum-free control plot means of mid-season corn plant height *vs*. means of early sorghum biomass, at Arlington, WI 2007 and West Madison, WI 2008.

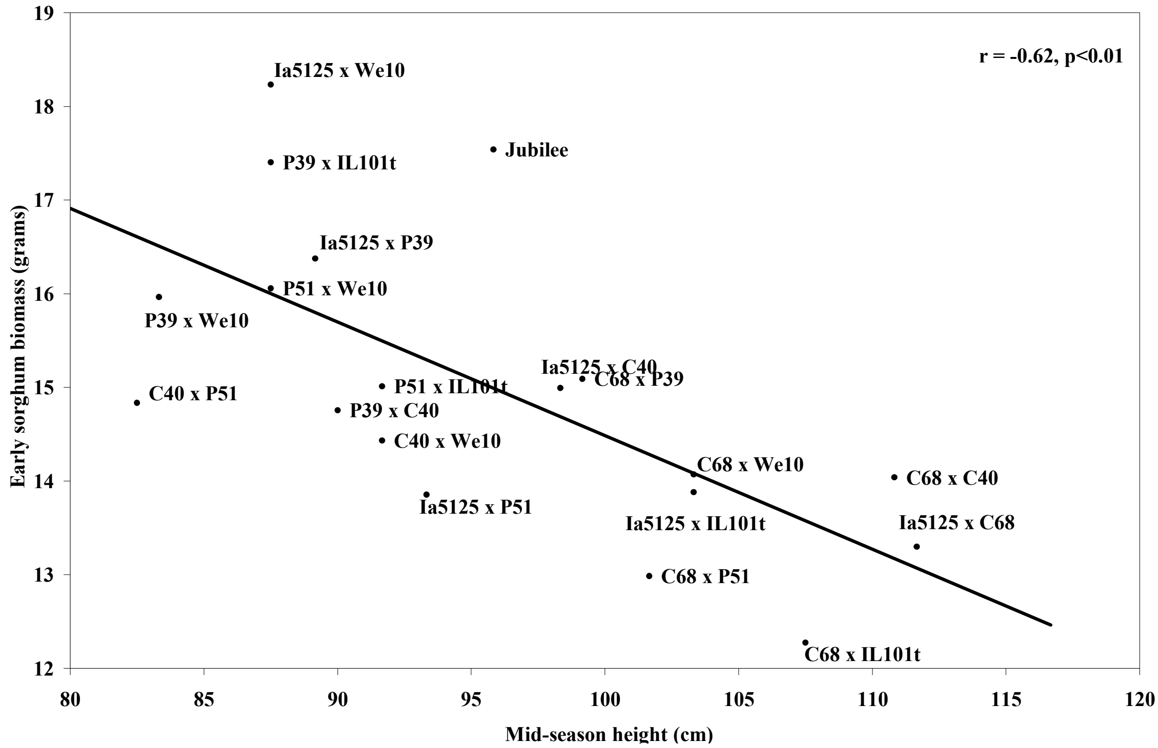


Figure 2. Means of sorghum-free control plot means of corn plant early leaf area *vs.* means of early sorghum biomass, at Arlington, WI 2007 and West Madison, WI 2008.

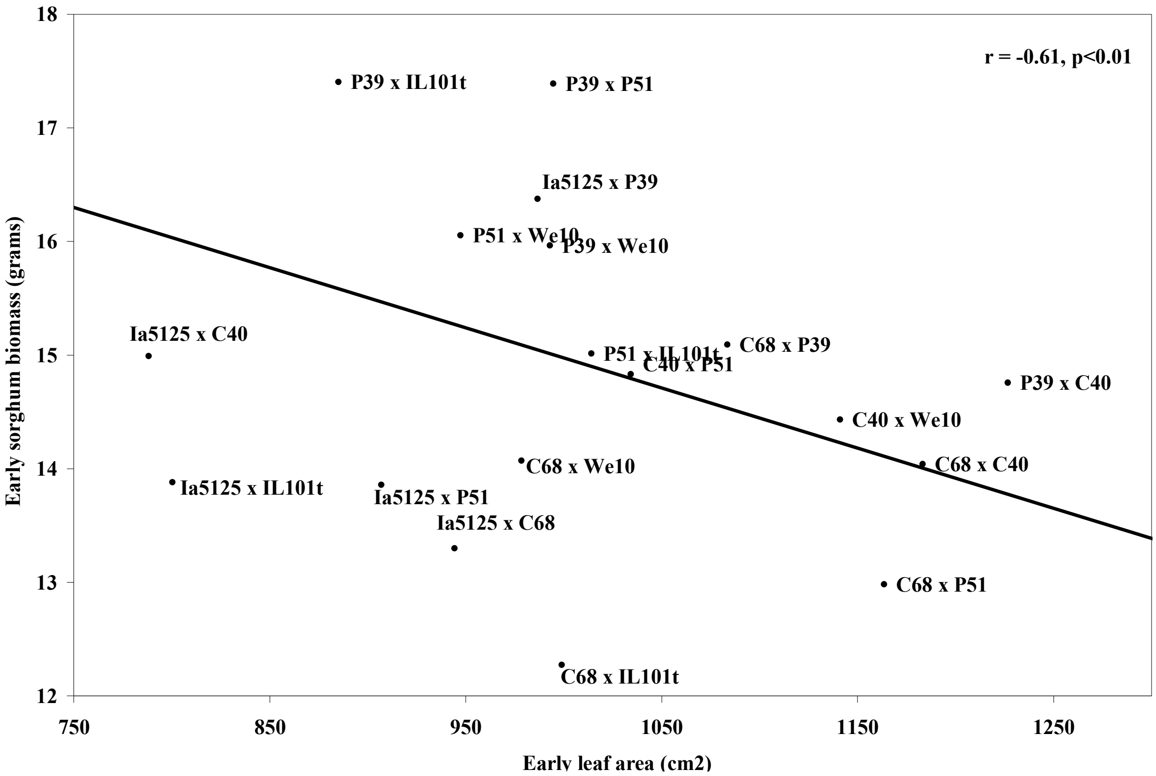


Figure 3. Means of sorghum-free control plot means of corn plant early height *vs.* means of late sorghum biomass, at Arlington, WI 2007 and West Madison, WI 2008.

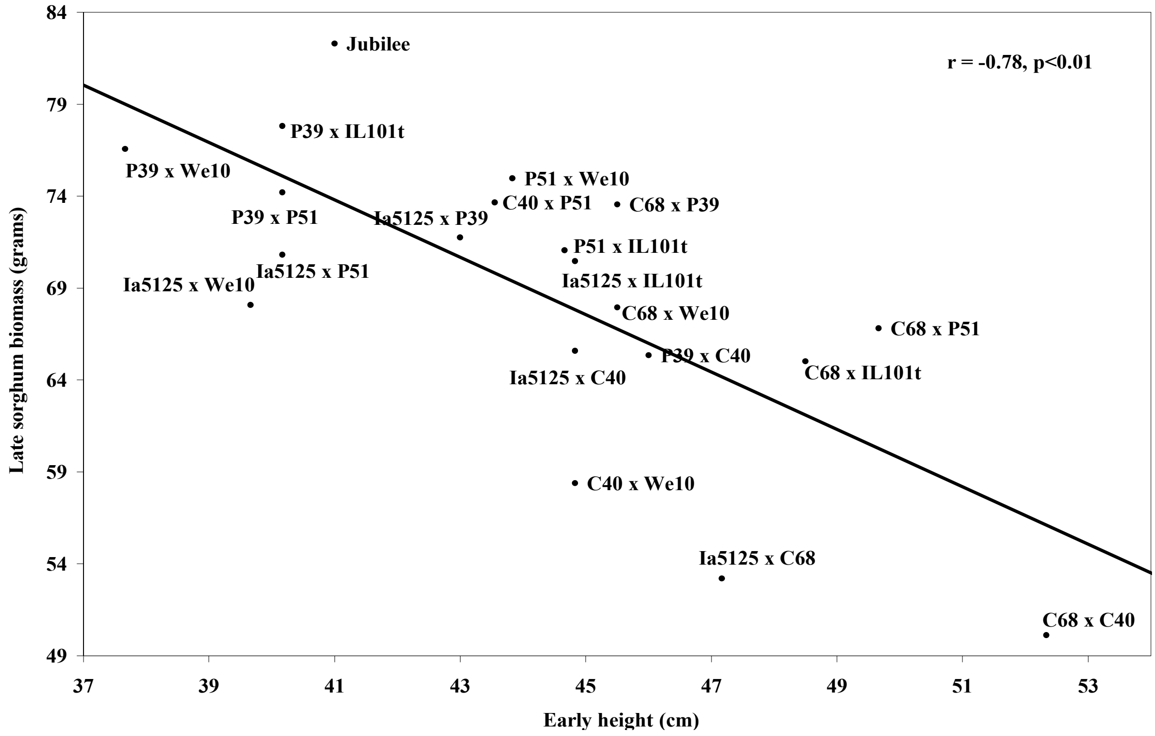
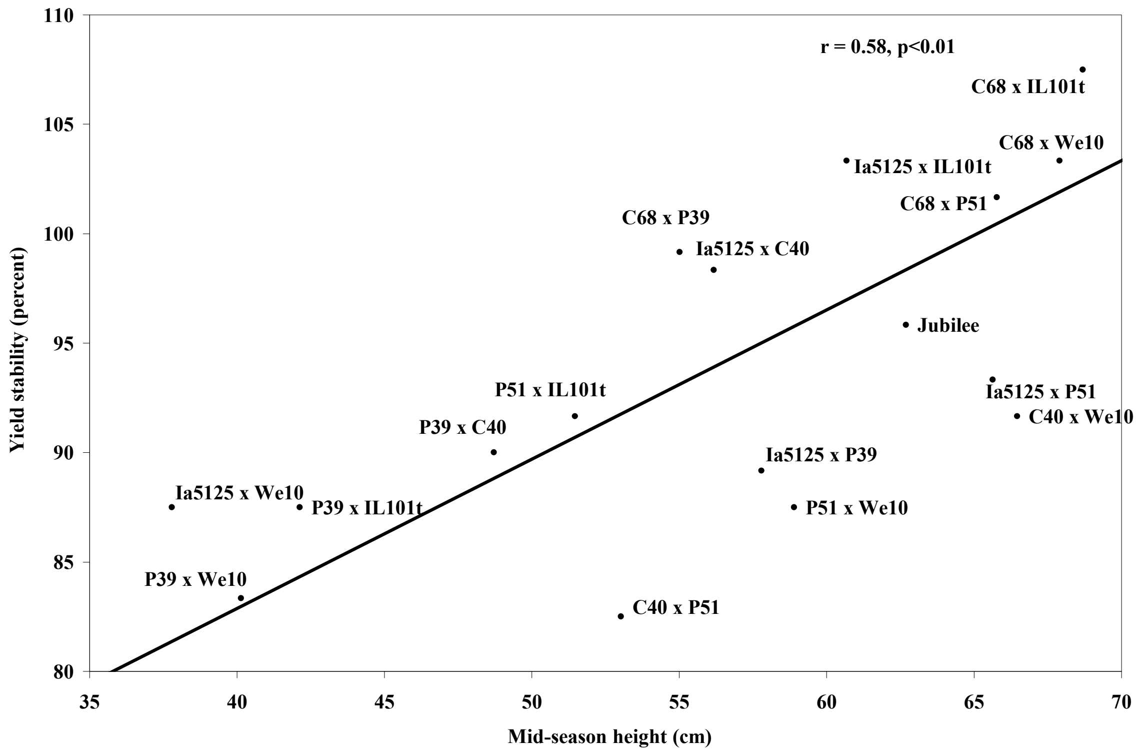


Figure 4. Means of sorghum-free control plot means of corn plant mid-season height *vs.* means of yield stability, at Arlington, WI 2007 and West Madison, WI 2008.



Large differences were seen in the potential combining abilities for the inbred parents both for the factors measuring competitive ability, and for the phenomorphological traits that correlate with competitive ability. For example, averaged across all environments, the range of GCA for yield, *i.e.*, the difference between the inbred with the highest GCA for yield and the inbred with the most negative GCA for yield, was 1341 kg ha^{-1} (Table 4), the range for early leaf area GCA was 256 cm^2 (Table 4), the range for late plant height GCA was 26 cm (Table 5), the range for early height was 8.4 cm (Table 5), the range for early sorghum biomass GCA was 3.0 grams (Table 6), the range for late sorghum biomass was 26 grams (Table 6), and the range for yield stability GCA was 21% (Table 7). By comparing the mean squares of GCA to total hybrid mean squares (2MSGCA: 2MSGCA + MSSCA), it can be shown that most of the variation in competitive ability and related traits is predictable based on inbred GCA alone (Table 8).

Table 4. General and specific combining abilities for corn grain yield† in kg ha^{-1} (above diagonal) and corn early leaf area‡ in cm^2 (below diagonal), from an incomplete half diallel among seven sweet corn inbreds, average was calculated from Arlington, WI 2007 and West Madison, WI 2008.

		SCA							GCA
		Ia5125	C68	P39	P51	We10	IL101t	C40	
SCA	Ia5125		52.61	156.82	372.51	−747.65	−44.28	209.99	204.18
	C68	37.10		110.12	87.39	7.96	−25.49	−232.60	704.20
	P39	81.57	−43.91		−412.51	−77.61	23.51	199.66	−636.58
	P51	28.69	43.20	−91.41		450.36	46.25	−544.00	−278.54
	We10	−92.64	−28.71	30.84	35.29		.	366.95	−504.13
	IL101t	36.25	27.51	−92.19	28.43	.		.	121.10
	C40	−90.96	−35.19	115.11	−44.19	55.23	.		389.76
GCA		−151.53	47.54	−0.76	16.54	−39.05	20.40	106.85	

† LSD (0.05) = 198.16 for GCA, 320.83 for SCA, ‡LSD (0.05) = 60.78 for GCA, 98.41 for SCA.

Table 5. General and specific combining abilities for corn plant late height† in cm (above diagonal) and corn plant early height‡ in cm (below diagonal), from an incomplete half diallel among seven sweet corn inbreds, measured in Arlington, WI 2007, West Madison, WI 2007, and West Madison, WI 2008.

		SCA							GCA
		Ia5125	C68	P39	P51	We10	IL101t	C40	
SCA	Ia5125		3.42	0.33	6.67	−14.35	−0.27	4.20	12.05
	C68	0.49		−1.70	1.38	2.95	−1.80	−4.25	16.25
	P39	1.16	−0.31		−4.20	0.20	3.87	1.50	−7.33
	P51	−0.41	1.13	−0.87		5.29	−1.80	−7.34	−8.41
	We10	−0.97	−0.19	−0.61	0.58		.	5.90	−0.98
	IL101t	1.18	−0.87	−1.37	1.06	.		.	−10.06
	C40	−1.45	−0.25	2.00	−1.49	1.20	.		12.05
GCA		−0.73	4.82	−3.59	−0.94	−2.54	0.39	2.65	

† LSD (0.05) = 2.49 for GCA, 4.02 for SCA; ‡LSD (0.05) = 1.04 for GCA, 1.68 for SCA.

Table 6. General and specific combining abilities for early sorghum dry weight† in g (above diagonal) and late sorghum dry weight‡ in g (below diagonal), from an incomplete half diallel among seven sweet corn inbreds, measured in Arlington, WI 2007 and West Madison, WI 2008.

		SCA							GCA
		Ia5125	C68	P39	P51	We10	IL101t	C40	
SCA	Ia5125		−0.21	−0.18	−1.33	2.22	−0.91	0.41	0.15
	C68	−6.76		0.31	−0.42	−0.17	−0.75	1.23	−1.62
	P39	−0.74	5.83		0.94	−1.32	1.34	−1.10	1.42
	P51	0.00	0.76	−4.37		0.14	0.32	0.35	0.05
	We10	−0.21	4.41	0.51	0.57		.	−0.88	0.88
	IL101t	2.23	0.97	1.25	−4.45	.		.	−0.34
	C40	5.49	−5.21	−2.49	7.48	−5.28	.		−0.54
GCA		−1.72	−6.50	6.02	4.37	1.84	2.36	−6.37	

† LSD (0.05) = 1.35 for GCA, NA for SCA, ‡LSD (0.05) = 5.56 for GCA, NA for SCA.

Table 7. General and specific combining abilities for yield stability in percent†, from an incomplete half diallel among seven sweet corn inbreds, measured in Arlington, WI 2007 and West Madison, WI 2008.

		SCA						GCA
		C68	P39	P51	We10	IL101t	C40	
SCA	Ia5125	5.39	7.86	5.49	−18.09	3.43	−4.07	2.85
	C68		−3.64	−3.08	3.30	2.72	−4.69	11.56
	P39			0.74	−3.26	−2.64	0.95	−9.64
	P51				5.30	−3.50	−4.94	0.57
	We10					.	12.75	−3.69
	IL101t						.	−2.33
	C40							0.67

† LSD (0.05) = 4.88 for GCA, 7.91 for SCA.

Table 8. Predictability, calculated as the ratio of (2 MSGCA):(2 MSGCA + MSSCA), of GCA for traits measured on 19 hybrids from an incomplete half-diallel, measured in Arlington, WI 2007, West Madison, WI 2007, and West Madison, WI 2008.

Trait	**Ratio of (2 MS_{GCA}):(2 MS_{GCA} + MS_{SCA})**
Yield	0.94
Ear width	0.98
Number of ears	0.89
GDD to anthesis	0.96
Early leaf area	0.91
Late leaf area	0.85
Early-season height	0.98
Mid-season height	0.98
Late-season height	0.96
Upper leaf angle	0.98
Yield stability	0.86

2.2. General Discussion

Some of the genotype by environment interaction effects seen in many of the traits may be due to the variable growing conditions experienced between environments. Rainfall and temperature may have contributed to creating these different growing environments.

Some previous conclusions about traits relating to competitive ability were supported by the results of this study. Although, unlike Roggenkamp *et al.* [20], upright leaves were not found to be correlated with WSA, upright leaves were found to be correlated with increased yield stability. While Makus [21] and Williams *et al.* [12,13] found greater WSA in late hybrids and Begna [22] found greater WSA in early hybrids, no differences in WSA based on maturity were observed in this study. Although late-season leaf area was not found to be correlated to WSA, early-season leaf area was, which supports Woolley and Smith's [23] finding that leafy corn had greater WSA. In contrast to Makus's [21] finding that yield was reduced more in a taller cultivar than a shorter one, this study found that, in general, plant height correlated with both increased CT and increased WSA. This study had more entries present than some previous work [8,12,13,19–22,24,25], allowing greater legitimacy to inferences made relating traits such as plant height to competitive ability.

If breeders are choose a few traits to use as a basis of selection for improved competitive ability, which should they be? Plant height, especially early- and mid-season plant height, showed the greatest correlation with both reduced sorghum biomass and yield stability (Table 3, Figures 1, 3 and 4), and that hybrid plant height was highly predictable based on the heights of the inbred parents (Table 8). Correlation is not causation and plant height may simply be the measured trait that is linked to other unmeasured factors that cause increases in competitive ability. For example, a recent modeling study [26] suggested that root characteristics may have been more important than canopy characteristics in the improvement of stress tolerance in commercial field corn hybrids. However, the results of this study suggest that regardless of the underlying factors responsible for competitive ability, selection for early- and mid-season plant height may lead to more competitive sweet corn.

Can a diallel analysis help breeders identify superior inbreds for competitive ability? Taking this study as an example, it can be shown that C68 stands out as a competitive inbred. It produced hybrids which on average had the highest yield, the highest yield stability, and the lowest early- and late-season sorghum biomass (Tables 4, 6 and 7). C68 also had the largest GCA in the positive direction for early- and late-season plant height and for vertical leaves (Table 5, data not shown). C68 produced both the tallest and the most tolerant hybrids, which is consistent with So *et al.*'s [27] finding that plant height, along with other 'late canopy and maturity' factors, was most effective in explaining the differences in CT in sweet corn.

While C68 stands out as most competitive, P39 stands out as least competitive. P39 produced hybrids which had the lowest yield, yield stability and the most early- and late-season sorghum biomass (Tables 4, 6 and 7). P39 also contrasts with C68 in that P39 produced hybrids which were, on average, shortest in the early season and had the most horizontal leaves (Table 5, data not shown).

Two key parameters influence the context of this study and should be considered when making inferences from this work about competitive ability in other systems. First, the interaction of two organisms depends partially on the relative fitness of each organism in a particular environment. The combination of the interactions that the two organisms have with each other, and the interactions that each have with the environment can make results obtained from evaluating the relationship between two organisms more sensitive to environmental variability than research focused on a single organism. In this study, competitive ability was most influenced by plant height. However, care must be taken when making any generalizations to other environments, especially those environments in which other resources, such as water or nutrients, may be more limited. In order to broaden the scope of the conclusions, similar experiments could be conducted in varied environments.

The second parameter that influences the context of this study is the choice of model weed. Forage sorghum is a good model due to its high competitiveness, accelerated growth and substantial biomass production and shading ability. It also offers the advantage of being able to be managed similarly to corn. However, can information gained from research with sorghum be applied to other weeds? Sorghum is a C4 grass similarly to corn. It has narrow, long leaves and has upright growth ability. But sorghum has a determinate flowering pattern, which limits plant height. Many broadleaf weeds have an indeterminate growth habit resulting in greater plasticity in plant height. Despite the differences between sorghum and broadleaf weeds, some inferences may be justifiable. Previous studies have found that, despite large differences in morphology, weed species can present similar competitive pressures. Moechnig *et al.* [28,29] found that common lambsquarters (*Chenopodium album*) and giant foxtail (*Setaria faberi*) had similar competitive abilities in corn, depending on the environment.

An additional difference between sorghum and wild weeds is that sorghum will germinate consistently. It is useful for a model weed, as it allows uniform pressure to be created. However, weeds and other wild plants generally have extended germination periods, emerging throughout the season. Corn competitive traits that act on young weed seedlings would only be important against sorghum at the beginning of the season, but would continue to be important through-out the season when in competition with wild weeds. Conducting a similar experiment with weeds which had different emergence patterns would allow broader conclusions to be made.

3. Experimental Section

3.1. Germplasm

Nineteen hybrids were developed from an incomplete seven-line half-diallel without parents (Griffing's Method 4) [30]. The following seven sugary1 (su1) inbreds served as parents: Ia5125, C40, C68, We10, Ill101t, P39, and P51. These inbreds were chosen to represent a wide range of morphologies, and a diversity of sweet corn ancestors. Jubilee, a commercial su1 hybrid, was also included as a check to provide a point of reference. The sorghum variety used was Silo 700D, a short-statured forage sorghum, chosen for its abundant biomass production and similarity in plant height to the sweet corn hybrids.

3.2. Experimental Design

The experiment was a split block randomized complete block design with three replications per environment. The main-block factor was presence or absence of sorghum and the sub-block factor was hybrid. Plots were four rows, with rows 3.5 m long, 0.76 m between rows, and 0.91 m alleys. Each plot consisted of one hybrid and each split block contained the set of nineteen hybrids and was interplanted either with or without sorghum. The experiment was conducted in 2007 at the Arlington Agricultural Research Stations in 2008 at the University of Wisconsin-Madison West Madison. The soil type at all locations was Plano silt loam (fine-silty, mixic mesic Typic Argiudoll).

The sweet corn hybrids were planted at Arlington, WI (ARL07) on 3 May in 2007 and at West Madison, WI (WM08) on 6 May in 2008. Because of limited seed, only 19 of the 21 possible diallel entries were planted in ARL07, with We10 x IL101t and C40 x IL101t not planted. Jubilee was planted in place of the missing entries.

The target density of sweet corn after emergence was approximately 93,600 plants ha^{-1} (25 seeds row^{-1}) Around V6 [31], the center two rows of each plot were thinned to 14 plants row^{-1} (52,400 plants ha^{-1}), while the outer two rows were thinned to 16 plants row^{-1} (59,900 plants ha^{-1}), leaving extra plants for destructive leaf area sampling. After leaf area sampling (V8-VT, see below) all rows had a final density of 14 plants row^{-1}, or 52,400 plants ha^{-1}.

In the sorghum treatment sub-blocks, after the corn had emerged (V1–V2), sorghum was hand planted in between the corn rows in two rows spaced 10 cm between sorghum rows and 20.5 cm away from the nearest corn row. The sorghum was thinned to a final density of 36 plants row^{-1} or 135,300 plants ha^{-1}. This density was chosen based on Myers *et al.* [32], which found that field corn yields were reduced 20% to 40% when sorghum was interplanted at a density of approximately 140,000 plants ha^{-1}.

3.3. Data Collection

Throughout the growing seasons of 2007 and 2008, phenomorphological, crop tolerance and weed suppressive traits were measured on the sweet corn hybrids and sorghum. Phenomorphological traits measured were: early-season, mid-season, and late-season plant height; height of tallest and second-tallest tillers; average tiller height; date of anthesis; leaf angle; leaf area; yield; ear length; ear width; mass of 100 kernels; and ears per plant. Traits measuring CT were: yield stability, 100 kernel mass stability, ear length stability, ear width stability, and ears per plant stability. The trait measuring WSA was sorghum biomass. Early-season [ARL07: V8, 519 growing degree days (GDD, 10°C/30° C); WM08: V6, 482 GDD] and mid-season (ARL07: V12, 762 GDD; WM08: V12, 814 GDD) sweet corn plant heights were visually estimated as an average of the center two rows of each plot from the soil surface to the height of the tallest leaf at its apex by placing a measuring stick in front of each plot. Late-season plant height was taken post anthesis (ARL07: 1630 GDD, WM08: 1509 GDD) and measured from the soil surface to the collar of the leaf subtending the tassel on five random plants from the third row of each plot. Number of tillers was recorded on the same plants as the late-season plant height and at the same time. Date of anthesis was recorded when 50 percent of tassels in the center two rows had exserted 50% of their anthers. Sweet corn leaf angles were measured post-anthesis (ARL07: 1630 GDD, WM08: 1141 GDD) on five random plants in the center two rows of each plot. The angle was measured with a protractor, with the zero center placed at the intersection of the leaf above the ear leaf and the stem, and the angle recorded as degrees from parallel to the stem [33]. Total leaf area was measured early in the season (ARL07: V6, 397 GDD; WM08: V4, 316 GDD) and later in the season (ARL07: VT, 990 GDD; WM08: V8, 557 GDD). Two sweet corn plants from each plot were harvested from each of the outer two rows during the early harvest and from each of the center two rows for the late harvest.

Sweet corn yield was measured on ears harvested from the center two rows after physiological maturity and dried to constant moisture. The following yield components were also measured for each plot: uppermost ear length, uppermost ear width, the mass of 100 kernels, number of ears per plant. The stability of yield and yield components (100 kernel mass, ear length, ear width, and ears per plant) were calculated as the value measured for a hybrid in the sorghum treatment divided by the value of the same hybrid in the non-sorghum treatment of the same block, and expressed as a percentage. Sorghum biomass was measured twice in each experiment, once near sweet corn anthesis (ARL07: 991 GDD, WM08: 1106 GDD) and once at physiological maturity (ARL07: 1876 GDD, WM08: 2045 GDD). Sorghum was taken from between sweet corn rows one and two during sweet corn anthesis and between rows three and four at sweet corn maturity. Sorghum was harvested by cutting all plants at 0.30 m from the soil surface and weighing in the field. A subsample was weighed, dried completely and weighed again to estimate dry mass for each plot.

3.4. Statistical Analysis

Linear mixed model analysis was conducted for all traits measured using the PROC MIXED in the SAS statistics package (SAS Institute, Cary, NC, USA). Block effects were considered random, with all other effects considered fixed. For all traits with H × E effects, Spearman rank correlations were calculated to determine if hybrid-by-environment effects were due to a change in magnitude or a change in rank. For each trait, environments were pooled if there were no environment-by-treatment or environment-by-hybrid effects, or if a Spearman rank correlation between environments for each trait or treatment condition demonstrated that the interaction was due to a change in magnitude and not a change in rank. Prior to calculating mean squares, residuals were analyzed to ensure they meet the normality and equal variance assumptions.

General combining ability (GCA) is the deviation of the mean performance of all crosses derived from an inbred line from the mean of all crosses in a diallel. GCA can be used to predict how a hybrid will perform based on the performance of the inbred parents. Specific combining ability (SCA) is the deviation in performance of a particular cross from its expected performance based on the mean of all crosses and the GCAs of its parents. If hybrid effects were significant, they were partitioned into GCA and SCA effects based on Griffing Model 2, Method IV [30]. Because a complete diallel of all seven lines was not represented in all environments, a design matrix for the SCA and GCA components was constructed based on the procedures in Wu and Matheson [34] and calculated based on Zhang and Kang [35] using CONTRAST and ESTIMATE statements in PROC MIXED in SAS (SAS Institute, Cary, NC, USA).

Means were compared using protected least significant differences (LSD) at $p < 0.05$ significance level. Correlations were calculated for traits with significant ($p < 0.05$) hybrid effects, as determined by the ANOVA. Correlations were done on phenotypic means using PROC CORR in SAS (SAS Institute, Cary, NC, USA). In order to remove the compounding effects of sorghum on phenomorphological traits that may affect weed competitiveness, sorghum plots were excluded from the means of the phenomorphological traits when calculating correlations between phenomorphological traits and competitive traits. Regressions between traits were calculated using stepwise regression with PROC REG in SAS (SAS Institute, Cary, NC, USA). The predictability of GCA for determining progeny performance was calculated based on the ratio of 2MSGCA to 2MSGCA + MSSCA [36].

4. Conclusions

Sweet corn hybrids can differ for competitive ability, both in terms of WSA and CT (Tables 1,2). Increased early- and mid-season plant height and increased early-season leaf area improved competitive ability and hybrids can differ for these morphological traits (Tables 1–3). These differences in hybrid competitive ability and morphology can be predicted based on the inbred GCAs (Table 8), allowing reliable selection to occur for improved competitive ability in sweet corn.

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Conflict of Interest

The authors declare no conflict of interest.

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