Principal Canopy Factors of Sweet Corn and Relationships to Competitive Ability with Wild-Proso Millet (*Panicum miliaceum*)

Yim F. So, Martin M. Williams II, Jerald K. Pataky, and Adam S. Davis*

Univariate analyses fail to account for covariance among phenomorphological traits implicated in crop competitive ability. A more complete analysis of cultivar–weed interactions would reduce a number of important traits to a few underlying principal factors responsible for sweet corn competitiveness. Twenty-three commercial sweet corn hybrids from nine seed companies were grown in the presence and absence of wild-proso millet to (1) quantify the extent to which phenomorphological traits vary in sweet corn, (2) identify underlying principal factors that describe variation in crop canopy development, and (3) determine functional relationships between crop canopy factors and competitive ability. A principal component factor analysis revealed that 7 of the 18 weed-free crop traits measured at silking loaded highly (0.65 to 0.90) into the first factor, including plant height, shoot biomass, per plant leaf area, leaf area index, and intercepted light, as well as thermal time from emergence to silking and emergence to maturity. All seven traits were highly correlated (0.38 to 0.93) and were interpreted as a "late canopy and maturity" factor. Another five traits formed two additional principal factors that were interpreted as an early "seedling quality" factor (e.g., kernel mass, seedling vigor, and height at two-leaf stage) and a mid-season "canopy closure" factor (e.g., leaf area index and intercepted photosynthetically active radiation at six-leaf stage). Relationships between principal factors and competitive abilities were quantified using least-squares linear regression. Cultivars with greater loadings in the late canopy and maturity and canopy closure factors were more competitive with wild-proso millet. In contrast, crop competitive ability declined with cultivars that loaded highly into the seedling quality factor. The analyses showed that sweet corn's ability to endure weed interference and suppress weed fitness relates uniquely to three underlying principal factors that capture crop canopy development around emergence and near canopy closure and during the reproductive phase.

Nomenclature: Wild-proso millet, *Panicum miliaceum* L.; sweet corn, *Zea mays* L. 'ACX1413BC', 'Beyond', 'Cahill', 'Code128', 'Code3', 'Code39', 'Coho', 'DMC2184', 'Dynamo', 'El Toro', 'EX 8716622', 'Harvest Gold', 'Incredible', 'Legacy', 'Luscious', 'Mystic', 'Precious Gem', 'Quickie', 'Rocker', 'SCH7006RR', 'Spirit', 'Spring Treat', and 'Sugar Buns'.

Key words: Competition, crop tolerance, cultural weed control, factor analysis, interference, integrated weed management, phenology, weed suppressive ability.

Deliberately increasing the ability of a crop to compete with weeds has been considered an approach to improving weed management for years (Callaway 1992; Jordan 1993). Crop competitive ability can be divided into two practical perspectives. Crop tolerance (CT) is defined as the ability of the crop to endure competitive stress from the presence of weeds without substantial reduction in growth or yield. Weed suppressive ability (WSA) is the ability of the crop to reduce weed growth and fecundity. In terms of economic goals, CT relates to crop yield under present weed conditions, whereas WSA relates to weed fecundity and the long-term cost of weed management (Jannink et al. 2000; Jordan 1993). Identifying commercial cultivars with greatest competitive ability or breeding for competitive ability has been pursued in rice (*Oryza sativa* L.), wheat (*Triticum aestivum* L.), and soybean [*Glycine max* (L.) Merr.] (Jannink et al. 2000; Lemerle et al. 2006; Zhao et al. 2006). Some researchers have sought to identify individual traits conferring improved competitive ability in dent corn (Begna et al. 2001a; Lindquist et al. 1998; Sankula et al. 2004). Use of competitive crop cultivars may be facilitated by advances in molecular research tools shedding

new light on the physiology of crop–weed interactions (Horvath et al. 2006, 2007).

Sweet corn is a dominant vegetable crop in the United States and is popular both as a fresh and processed vegetable. Among canned vegetables, sweet corn ranked second only to tomato (*Solanum lycopersicum* L.) in per capita consumption and was second only to potato (*Solanum tuberosum* L.) products by weight among frozen vegetables (Tracy 2001). Interest in sweet corn as a fresh vegetable has increased in some parts of the world such as Canada, Japan, Taiwan, and Korea (Tracy 2001). Sweet corn differs from dent corn in genes affecting starch synthesis and early plant growth, with the major endosperm mutations being *sugary1* (*su1*), *sugary enhancer1* (*se1*), and *shrunken2* (*sh2*) (Azanza et al. 1996; Tracy 2001). Williams et al. (2008c) reported 57% of sweet corn fields in the Midwest suffered yield loss due to weeds, despite extensive reliance on herbicides for weed control. Economic and environmental concerns call for fewer herbicide inputs while maintaining or increasing crop productivity (Swanton et al. 2007; Toler et al. 1999).

Wild-proso millet is one of the most problematic annual weeds in North American sweet corn production (Anderson 2000; Shenk et al. 1990; Williams and Harvey 2000). Wild-proso millet has prolonged germination and seedling emergence, tolerates many commonly used herbicides, grows rapidly, and produces many seeds. Wild-proso millet is a serious production constraint in the Pacific Northwest (Shenk et al. 1990), and in recent field surveys of the North Central region, wild-proso millet was one of the most frequent, dense, and fecund weed species at sweet corn harvest (Williams et al.

2008c). In addition to lowering crop yield, wild-proso millet seed can be difficult to remove from processed sweet corn.

Several phenomorphological traits relate to competitive ability of dent corn, including plant height, shoot growth rate, canopy density (Lindquist and Mortensen 1998), leaf uprightness (Sankula et al. 2004), crop maturity, leaf area growth rate (Begna et al. 2001a, b), canopy closure, and maximum leaf area index (LAI) (Lindquist et al. 1998). Canopy differences among commercial dent corn hybrids can be subtle and appear to have limited value in weed management (Ford and Pleasant 1994; Roggenkamp et al. 2000). In contrast, studies in sweet corn have revealed large competitive differences among a small number of modern commercial hybrids (Williams et al. 2006) and these differences have practical implications to weed management (Makus 2000; Williams et al. 2007, 2008a). Drawing robust inferences about corn competitive ability is often limited by the study of a relatively small number of cultivars or phenomorphological traits (Lindquist et al. 1998; Tollenaar et al. 1997; Williams et al. 2007, 2008b). When few cultivars are included in weed–crop interference studies, the narrow range and coarse grain of phenomorphological data do not allow for a functional interpretation of their role in CT or WSA. Nonetheless, interest from the seed industry has provoked recent research on heritability of sweet corn competitive ability (W. F. Tracy, personal communication).

Traits implicated in crop competitive ability can be numerous and are often correlated (e.g., crop height and maximum LAI), thereby limiting the usefulness of univariate analyses. A more comprehensive analysis of cultivar–weed interactions would reduce a number of important traits to a few underlying principal factors responsible for sweet corn competitive ability. Therefore, objectives of this work were to (1) quantify the extent to which phenomorphological traits vary in sweet corn, (2) identify underlying principal factors that describe variation in the crop canopy development, and (3) determine functional relationships between principal canopy factors and competitive ability with weeds.

Materials and Methods

Germplasm. Twenty-three commercial sweet corn hybrids were obtained from nine seed companies.[1] Breeders from each company were asked to provide up to three hybrids that differ in canopy architecture or stress tolerance. Each hybrid was derived from at least one parent carrying a dominant allele for metabolism of several cytochrome P450–metabolized herbicides, including bentazon (Nordby et al. 2008; Pataky et al. 2006). All major endosperm types were included, with one heterozygous *se1su1* hybrid, 11 homozygous *su1* hybrids, four homozygous *se1* hybrids, and seven homozygous *sh2* hybrids. In addition, seed of a local biotype of wild-proso millet was collected from a sweet corn field the previous year, stored at room temperature, and used in the following experiments.

Experimental Approach. Field experiments were conducted in 2006 and 2007 at the University of Illinois Vegetable Crop Research on a Flanagan silt loam (fine, smectic, mesic Aquic Argiudoll) soil averaging 3.8% organic matter and pH of 5.8. A single field was divided into two halves, whereby one half was used each year. The previous crop was soybean. In April prior to planting, experimental sites were fertilized with

129 kg N ha^{-1}, 113 kg P ha^{-1}, and 135 kg K ha^{-1}, in the form of urea, concentrated super phosphate, and ground potash. The experimental area was then prepared for planting by two passes each of a field cultivator and disk harrow. The study was sprinkler irrigated three times in 2006 and 2007.

The experimental design was a split plot with four replicates. Hybrid was the main plot factor, whereby eight-row by 9.2-m-long main plots were planted on a 76-cm row spacing at 10 seed per meter of row using a cone planter. Presence or absence of wild-proso millet was randomly assigned to subplots measuring four rows by 9.2 m. Since the field had no history of wild-proso millet, subplots assigned to have wild-proso millet were shallowly seeded at 115 viable seed per meter of row directly into the center two rows using a cone planter immediately after crop planting. A weedy monoculture (crop-free) treatment was included. Sweet corn and wild-proso millet were planted on May 29, 2006, and on May 14, 2007. After crop emergence, sweet corn was thinned to 5 plants m^{-1} of row. In addition, two permanent 1-m row quadrats per subplot were established, providing the location where wild-proso millet was counted within 16 d of emergence and where biomass was taken immediately after crop harvest.

The study area was kept free of all weeds except wild-proso millet. Atrazine was applied preemergence to the entire study area at 1.68 kg ai ha^{-1}, and *S*-metolachlor was applied preemergence at 1.78 kg ai ha^{-1} to weed-free plots. Three weeks after emergence an application of *S*-metolachlor at 1.78 kg ai ha^{-1} was applied to all plots and was incorporated with interrow cultivation. Weeds other than wild-proso millet that escaped herbicides were controlled with a single application of bentazon at 0.56 kg ai ha^{-1} (2006 only) and handweeding.

Data Collection. Kernel mass of each hybrid was determined prior to planting and 17 additional variables were measured in center two rows in weed-free subplots throughout the season. Growth stages were determined by the number of visible leaf collars and appearance of reproductive organs (Ritchie et al. 1993). Seedling vigor was rated visually approximately at the two-leaf (V2) stage on a 1 to 5 scale, with 5 being most vigorous. Plant height was measured from the soil surface to the apex near V2, V6, and silk emergence (R1). At V6 and R1, leaf chlorophyll index was measured on the fifth leaf and primary ear leaf, respectively, using a portable chlorophyll meter.[2] Measurements were taken on the leaf 8 cm from the stem and 4 cm from the leaf edge. A visual rating of the leaf uprightness at V6 and R1 was used to describe the relative vertical position of the uppermost, fully emerged leaves as described by So et al. (2009). Leaf area index and intercepted photosynthetically active radiation (IPAR) were quantified at V6 and R1 using a line quantum sensor[3] as described by Williams et al. (2006). At R1, two plants per subplot were cut at the soil surface, leaves were separated at the lamina, and total leaf area was determined using an area meter.[4] Plants were then dried at 65 C and weighed. Date of silk emergence and maturity (R3) were recorded for each hybrid.

Marketable ears, measuring ≥ 4.5 cm in diameter, were hand-harvested at R3 of each hybrid from the two center rows over 6 m of row, and ear mass and number were recorded. Immediately after crop harvest, shoots of wild-proso millet were harvested from permanent quadrats in weedy plots.

Table 1. Monthly water supply and average daily temperature for the months of May, June, July, and August in 2006 and 2007 in Urbana, IL. Departure from 30-yr average water supply and mean air temperature are included for reference.

Year	Month	Water supply		Average daily temperature			Departure from average	
		Rainfall	Irrigation	Minimum	Maximum	Mean	Water supply	Mean air temperature
		——————— mm ———————		——————————C ——————————			mm	C
2006	May	77.7	0.0	11.0	22.4	16.7	−44.2	−0.3
	June	41.9	25.4	15.8	27.9	21.9	−39.6	−0.2
	July	199.4	7.6	19.0	30.7	24.8	88.4	0.9
	August	76.2	0.0	18.4	28.3	23.3	−34.8	0.6
2007	May	41.4	0.0	13.0	27.1	20.1	−80.5	3.0
	June	144.3	50.8	16.9	29.1	23.1	88.1	1.0
	July	87.4	0.0	17.0	28.4	22.7	−31.2	−1.2
	August	37.6	0.0	19.7	31.6	25.7	−73.4	2.9

Some seed had matured and was beginning to disperse. Seed was separated using a mechanical thresher and air dried at room temperature and enumerated. Shoot biomass was determined after drying samples at 65 C. Daily minimum and maximum temperature and rainfall data were obtained from a nearby weather station with water supply from irrigation added to the data. Growing degree days (GDD) accumulated after crop emergence were calculated with a base temperature of 10 C.

Statistical Analyses. Crop tolerance was characterized in terms of marketable ear mass (CT_{mass}) and marketable ear number (CT_{num}), which are most relevant to the processing and fresh market crops, respectively. Hybrid CT_{mass} and CT_{num} were calculated as the fraction of weedy corn yield divided by weed-free corn yield. Weed suppressive ability was measured in terms of total shoot biomass (WSA_{shoot}) and seed production (WSA_{seed}). Hybrid WSA_{shoot} and WSA_{seed} were calculated as

$$WSA = 1 - \frac{Yld_{hybrid}}{Yld_{monoculture}} \quad [1]$$

where Yld_{hybrid} is yield of wild-proso millet within a hybrid and $Yld_{monoculture}$ is wild-proso millet yield in monoculture.

All data were examined with Levene's test for homogeneity (Ott and Longnecker 2001). Variances were found to be homogenous for all variables and met ANOVA assumptions of normality. In order to determine if hybrids differed in phenomorphological traits and competitive ability, ANOVA was conducted on each response variable. In addition, associations between years for each response variable were quantified using Pearson correlation coefficients. A principal component factor analysis can be used to describe the covariance relationships among many variables in terms of a few underlying, yet unobservable, quantities called factors (Johnson 1998). For instance, principal component factor analysis could reduce various phenomorphological traits to a small number of factors describing variation in the crop canopy.

Therefore, a principal component factor analysis with varimax rotation was conducted and factors were retained using Cattell's Scree Plot Test (Johnson 1998). Relationships among variables loading into each factor were quantified using Pearson correlation coefficients. An advantage of principal component factor analysis is that loadings of each factor can be used in further analyses, such as elucidating relationships between principal canopy factors and competitive ability with weeds. Therefore, CT_{mass}, CT_{num}, WSA_{shoot}, and WSA_{seed}

were fitted to a linear model as functions of weed-free factor loadings of each crop canopy factor using least-squares regression. All analyses were performed in SAS software (2002).

Results and Discussion

Experiments were conducted under warm, dry conditions compared to the 30-yr average. Below normal water supply was observed in three of four months for both years of the study and total shortfalls were 31 and 97 mm in 2006 and 2007, respectively (Table 1). Above-normal moisture in July of 2006 and June of 2007 enabled sweet corn to avoid severe drought stress during pollination. The mean temperatures were above normal; mean monthly temperature was 0.3 and 1.4 C above the 30-yr average in 2006 and 2007, respectively (Table 1).

Sweet corn population density was similar in both years, averaging 4.7 plants per meter of row after thinning. Weed-free yields range from 7.2 to 19.9 Mg ha^{-1} in 2006 and 11.2 to 26.3 Mg ha^{-1} in 2007, which were representative of weed-free yields for central Illinois (Williams et al. 2006). Wild-proso millet population density averaged 72 and 126 plants m^{-2} in 2006 and 2007, respectively. Observed wild-proso millet population densities were within a range that caused differential crop yield loss among three commercial sweet corn hybrids (Williams et al. 2008b). More favorable growing conditions the second year of the study in 2007 favored wild-proso millet germination and growth over the first year in 2006, as evidenced by mean shoot biomass in weedy monoculture plots of 317 g m^{-2} in 2007 and 149 g m^{-2} in 2006, respectively. In addition, mean seed production in weedy monoculture plots was 3,320 seed m^{-2} and 4,120 seed m^{-2} in 2006 and 2007, respectively (data not shown).

Variation in Phenomorphological Traits. Sweet corn hybrids differed significantly in early season morphological traits. Mass of 100 kernels ranged from 4.3 to 14.5 g, and seedling vigor, leaf number, and plant height at V2 varied ($P \le 0.03$) among hybrids (Table 2).

As plants began autotrophic growth, canopy development continued to vary among hybrids, as evidenced by significant P-values ($P \le 0.05$) for the effect of hybrid on phenomorphological traits throughout the season (Table 2). For instance at V6, some hybrids intercepted 13 to 26% more light than other hybrids, and plant height among hybrids ranged from 41.1 to 54.0 cm and from 31.8 to 44.5 cm in 2006 and 2007, respectively. While chlorophyll index, leaf

Table 2. Summary statistics of 18 weed-free phenomorphological traits and four measures of crop competitive ability among 23 sweet corn hybrids grown in Urbana, IL in 2006 and 2007. Crop growth stage in parentheses indicates when each trait was measured.[a]

		Mean		SD		Range of hybrid means		P-value[b]		
	Units	2006	2007	2006	2007	2006	2007	2006	2007	Correlation between years[c]
Phenomorphological trait										
Kernel mass	g 100 seed^{-1}	8.4	8.8	2.2	2.7	5.0–12.2	4.3–14.5	< 0.01	< 0.01	0.55*
Seedling vigor	—	3.8	1.6	0.7	0.3	2.3–4.8	1.0–2.4	< 0.01	< 0.01	0.64*
Leaf no. (V2)	no. plant^{-1}	2.6	1.9	0.5	0.1	2.0–3.0	1.6–2.2	< 0.01	0.03	0.75*
Chlorophyll (V6)	—	48.5	42.5	1.8	2.6	45.6–52.5	38.3–47.7	< 0.01	0.85	0.44*
Chlorophyll (R1)	—	54.8	58.4	2.4	2.9	50.7–60.4	52.5–63.8	< 0.01	< 0.01	0.39
Leaf up (V6)	—	2.2	1.8	0.4	0.2	1.3–2.9	1.4–2.2	< 0.01	0.30	0.41
Leaf up (R1)	—	1.7	2.2	0.5	0.4	1.0–3.0	1.5–2.9	< 0.01	< 0.01	0.77*
Height (V2)	cm	19.2	10.7	3.5	1.5	12.3–25.3	8.0–14.3	< 0.01	< 0.01	0.72*
Height (V6)	cm	48.5	39.7	3.5	3.2	41.1–54.0	31.8–44.5	< 0.01	< 0.01	0.34
Height (R1)	cm	175	197	20	27	124–201	127–228	< 0.01	< 0.01	0.90*
LAI (V6)	m^2 m^{-2}	1.5	0.3	0.3	0.1	0.9–1.9	0.2–0.5	< 0.01	0.12	0.59*
LAI (R1)	m^2 m^{-2}	4.1	5.0	0.8	1.0	2.1–5.0	3.0–6.6	< 0.01	< 0.01	0.92*
IPAR (V6)	%	49.9	10.2	6.0	3.4	36.2–62.2	4.9–17.6	< 0.01	0.03	0.48*
IPAR (R1)	%	84.7	87.2	8.6	7.5	56.9–93.6	67.3–95.3	< 0.01	< 0.01	0.86*
Biomass (R1)	g plant^{-1}	96.4	111.0	30.3	38.2	50.5–140.5	42.0–187.2	< 0.01	< 0.01	0.68*
Leaf area (R1)	cm^2 plant^{-1}	2,115	3,831	506	1349	1,104–3,055	1,294–8,058	< 0.01	< 0.01	0.72*
Silking	GDD	626	641	65	57	504–688	525–721	< 0.01	< 0.01	0.91*
Maturity	GDD	868	877	79	54	752–979	760–941	< 0.01	< 0.01	0.88*
Competitive ability										
CT$_{mass}$	—	0.55	0.52	0.13	0.14	0.25–0.76	0.18–0.73	< 0.01	< 0.01	0.76*
CT$_{num}$	—	0.50	0.53	0.12	0.22	0.25–0.65	0.02–0.89	< 0.01	< 0.01	0.75*
WSA$_{shoot}$	—	0.64	0.59	0.07	0.11	0.46–0.74	0.38–0.77	< 0.01	< 0.01	0.33
WSA$_{seed}$	—	0.67	0.83	0.12	0.10	0.28–0.85	0.61–0.94	0.01	< 0.01	0.06

[a] Abbreviations: Leaf up, leaf uprightness; LAI, leaf area index; IPAR, intercepted photosynthetically active radiation; CT$_{mass}$, crop tolerance in terms of ear mass; CT$_{num}$, crop tolerance in terms of ear number; WSA$_{shoot}$, weed suppressive ability in terms of wild-proso millet shoot biomass; WSA$_{seed}$, weed suppressive ability in terms of wild-proso millet seed production; GDD, growing degree days.
[b] P-values report significance in variation among hybrids for each trait.
[c] Correlation coefficients of traits in 2006 and 2007. An asterisk denotes coefficients that are significant at $\alpha = 0.05$.

uprightness, and LAI at V6 varied among hybrids in 2006, unusually droughty conditions prior to sampling in 2007 resulted in hybrids that appeared similar ($P \geq 0.12$) for these traits in 2007 (Table 2). By R1, some hybrids were 89 cm taller and intercepting 32% more light than other hybrids, averaged over years. Differential light interception among hybrids at R1 was attributed to large differences that per plant leaf area had on LAI (e.g., 120 to 138% differences in LAI among hybrids). In addition, leaf uprightness varied considerably among hybrids, with some hybrids having leaves oriented entirely below the point of attachment versus other hybrids with leaves oriented upright.

Phenology also varied among hybrids. Thermal time from crop emergence to silking ranged from 504 to 688 GDD and 525 to 721 GDD in 2006 and 2007, respectively (Table 2). Likewise, days to silking varied among hybrids, and averaged over years, hybrids required 67 to 81 calendar days from planting to harvest.

Hybrids were relatively consistent in canopy development over years, as evidenced by positive associations between responses in 2006 and 2007 for most phenomorphological traits. The highest correlation coefficient (0.92) was observed for LAI at R1 (Table 2). Significant correlations for other traits had coefficients that ranged from 0.44 (chlorophyll index at V6) to 0.91 (thermal time from emergence to silking). Results are in general agreement with previous research on canopy development of two or three sweet corn hybrids; however, a greater range of values were observed in this work for most traits. Despite differences in crop height, LAI, and IPAR among environments, rankings of hybrids (e.g., least to greatest) for these traits were largely consistent across primary sweet corn production regions (Williams et al. 2006, 2008a).

Sweet corn hybrids differed in their ability to tolerate wild-proso millet interference and suppress weed growth and fecundity. As an example, mean CT$_{mass}$ was 0.55 in 2006, ranging from 0.25 to 0.76 (Table 2). Therefore, wild-proso millet interference reduced sweet corn yield 75% in one hybrid, but only 24% in another hybrid. Similar results were observed in 2007, as well as for CT$_{num}$. Hybrid mean WSA$_{shoot}$ was 0.64 and 0.59 in 2006 and 2007, respectively, and ranged from a low of 0.38 to a high of 0.77 (Table 2). Suppression of wild-proso millet seed may have been slightly higher than suppression of biomass (e.g., average WSA$_{seed}$ of 0.75); yet like WSA$_{shoot}$, all hybrids provided some weed suppression and no hybrid outright killed wild-proso millet. Details of individual hybrid growth and yield responses to weed interference are reported by So et al. (2009).

Principal Plant Canopy Factors. Factor analysis reduced the 18 phenomorphological traits to three principal plant canopy factors that accounted for as much as 80% of the variation among traits. The first factor for both years loaded highly (≥ 0.65) for the following traits measured at R1: height, LAI, IPAR, biomass, leaf area, thermal time to silking, and thermal time to maturity (Table 3). The first factor accounted for 38 and 48% of the variation in 2006 and 2007, respectively. Because the first factor described the canopy within 3 wk of crop harvest, factor 1 was interpreted as a "late canopy and maturity" factor. Differential maturity among hybrids had a significant influence on these morphological traits, as later-maturing hybrids had a longer vegetative phase than earlier-maturing hybrids. Consequently, increases in final plant height, LAI, IPAR, biomass, and leaf area were positively correlated (0.38 to 0.75) to thermal time to maturity (Table 4).

Table 3. Mean varimax-rotated factor loadings and cumulative variance accounted for by 18 weed-free phenomorphological traits. Crop growth stage in parentheses indicates when each trait was measured.

| Phenomorphological trait | Year | | | | | |
| | 2006 | | | 2007 | | |
	Factor 1	Factor 2	Factor 3	Factor 1	Factor 2	Factor 3
Kernel mass	—	0.75	—	—	0.64	—
Seedling vigor (V2)	—	0.81	—	—	0.74	—
Leaf no. (V2)	—	0.80	—	—	—	—
Chlorophyll (V6)	—	—	—	—	—	—
Chlorophyll (R1)	—	—	—	—	—	—
Leaf up (V6)	—	—	—	—	—	—
Leaf up (R1)	—	—	—	—	—	—
Height (V2)	—	0.88	—	—	0.73	—
Height (V6)	—	—	—	—	0.60	—
Height (R1)	0.78	—	—	0.79	—	—
LAI (V6)	—	—	0.96	—	—	0.91
LAI (R1)	0.82	—	—	0.86	—	—
IPAR (V6)	—	—	0.96	—	—	0.89
IPAR (R1)	0.85	—	—	0.84	—	—
Biomass (R1)	0.70	—	—	0.82	—	—
Leaf area (R1)	0.65	—	—	0.75	—	—
Silking (R1)	0.88	—	—	0.90	—	—
Maturity (R3)	0.79	—	—	0.89	—	—
Cumulative variance (%)	38	62	77	48	69	80

[a] Abbreviations: Leaf up, leaf uprightness; LAI, leaf area index; IPAR, intercepted photosynthetically active radiation.

Variables that loaded into factor 2 for both years were kernel mass, seedling vigor, and height at V2 (Table 3). In addition, the factor was loaded by leaf number at V2 in 2006 and height at V6 in 2007. Variables that loaded into factor 2 largely described seed reserves and seedling growth as the plant began autotrophic growth. Factor 2 was interpreted as a "seedling quality" factor that accounted for an additional 21 to 24% of the variation in canopy development. Kernel mass, seedling vigor, and height at V2 were positively correlated (0.45 to 0.68) (Table 5). Reduced starch content of *se1* and *sh2* endosperm types, relative to *su1*, resulted in lower kernel mass, seedling vigor, and seedling growth rate (Azanza et al. 1996). In the present study, endosperm phenotype had a significant effect on early season crop growth and initial canopy development.

Leaf area index and IPAR at V6 loaded highly (0.89 to 0.96) into factor 3. Both LAI and IPAR described the density of the canopy and its ability to capture light near the time of canopy closure. Factor 3 was interpreted as a "canopy closure" factor that accounted for 11 to 15% of the total variation. Leaf area index and IPAR at V6 were significantly correlated, as evidenced by correlation coefficients ≥ 0.93 (data not shown). Few differences in LAI and IPAR at V6 were observed among three sweet corn hybrids grown in Illinois and Washington (Williams et al. 2006), perhaps because hybrids were not as diverse as the hybrids in this experiment.

The canopy closure factor defined morphological traits that have been linked to competitive ability of both dent and sweet corn. Lindquist et al. (1998) found that maximum LAI and rate of canopy closure in dent corn was important to light competition with velvetleaf and proposed that improving these traits would improve crop competitive ability. After V6, Williams et al. (2007) found that sweet corn leaf area at the 120- to 150-cm height was important to wild-proso millet suppression. The present study provides evidence that, during the mid-vegetative phase, the crop canopy differed among a broad pool of sweet corn germplasm and that the canopy closure factor is highly consistent across two environments.

Relationships between Canopy Factors and Competitive Ability. Regression analyses quantified functional relationships between principal plant canopy factors and measures of crop competitive ability. Regressions were significant ($P < 0.05$) between each canopy factor and at least one measure of crop competitive ability (Table 6).

The late canopy and maturity factor was associated with all measures of crop competitive ability (Table 6). Positive slope coefficients ranging from 0.07 to 0.12 indicated that each unit increase in the late canopy and maturity factor corresponded to a 7 to 12% improvement in the crop's ability to tolerate weed interference or suppress wild-proso millet. Hybrids with longer vegetative phases and greater height, LAI, IPAR,

Table 4. Correlation coefficients among the seven phenomorphological traits that loaded into the "late canopy and maturity" factor (factor 1) for 2006 (below diagonal) and 2007 (above diagonal). Crop growth stage in parentheses indicates when each trait was measured. All coefficients are significant at α = 0.05.[a]

	Height (R1)	LAI (R1)	IPAR (R1)	Biomass (R1)	Leaf area (R1)	Silking	Maturity
Height (R1)	—	0.63	0.61	0.52	0.48	0.74	0.75
LAI (R1)	0.45	—	0.93	0.51	0.63	0.65	0.66
IPAR (R1)	0.57	0.89	—	0.52	0.56	0.66	0.65
Biomass (R1)	0.45	0.66	0.58	—	0.78	0.70	0.74
Leaf area (R1)	0.38	0.61	0.59	0.62	—	0.55	0.58
Silking	0.67	0.65	0.68	0.73	0.62	—	0.93
Maturity	0.38	0.64	0.65	0.65	0.61	0.84	—

[a] Abbreviations: LAI, leaf area index; IPAR, intercepted photosynthetically active radiation.

Table 5. Correlation coefficients among the five phenomorphological traits that loaded into the "seedling quality" factor (factor 2) for 2006 (below diagonal) and 2007 (above diagonal). Crop growth stage in parentheses indicates when each trait was measured. Except noted by "ns," all coefficients are significant at $\alpha = 0.05$.

	Kernel mass	Seedling vigor (V2)	Leaf no. (V2)	Height (V2)	Height (V6)
Kernel mass	—	0.49	ns	0.45	0.39
Seedling vigor (V2)	0.68	—	0.29	0.58	0.44
Leaf no. (V2)	0.61	0.38	—	0.72	0.18
Height (V2)	0.58	0.54	0.41	—	0.34
Height (V6)	0.45	0.33	ns	0.29	—

biomass, and per plant leaf area at silking produced a denser canopy that was more competitive with weeds, compared to earlier-maturing and smaller-canopy hybrids.

Improvements in traits driving light interception, such as height, LAI, and canopy diameter, increased competitiveness of several crops (Bennett and Shaw 2000; Callaway 1992; Lindquist and Mortensen 1998; Lindquist et al. 1998). When the crop can avoid interference from weeds, which is sometimes the case with early-maturing cultivars (Begna et al. 2001a, b), the aforementioned traits become less important to crop competitive ability. However, our results showed that when wild-proso millet competes with sweet corn, hybrids with a large canopy were best equipped to tolerate the weed and suppress wild-proso millet growth and seed production, even for late-maturing hybrids that competed the longest period of time.

The seedling quality factor was associated with all measures of competitive ability (Table 6). Negative slope coefficients ranging from -0.08 to -0.17 indicated that each unit increase in the loading of seedling quality factor was associated with an 8 to 17% decrease in crop competitive ability. Jannink et al. (2000) observed earlier-maturity soybean cultivars displayed greater initial growth and weed suppression, compared to later-maturity cultivars, but were less able to sustain weed suppression throughout the season due to senescence. Differences in crop seedling growth were driven by larger seed of earlier-maturing cultivars; with conditions of the maternal environment favoring large seed mass (Jannink et al. 2001). However in the present work, only weak, negative relationships were observed between maturity and seed mass or vigor (data not shown). In commercial sweet corn production, early vigor and seedling growth rate are largely attributed to endosperm phenotype, specifically, the result of starch concentration of the endosperm (Azanza et al. 1996).

Hybrids with the *su1* endosperm phenotype, which spanned the full range of hybrid maturities studied here, had greater seed mass than *se1* and *sh2* hybrids, and had higher seedling quality factor loadings than *sh2* hybrids (data not shown). The negative relationship between the seedling quality factor and competitive ability appeared to be influenced by maturity-induced early growth characteristics as well as endosperm phenotype.

Since maturity does not limit the use of endosperm phenotype in hybrid development, conceptually there is unlikely to be a biological trade-off between seedling quality and late canopy and maturity factors. Compared to improving a single canopy factor, exploitation of both canopy factors in breeding programs may optimize competitive ability of future sweet corn hybrids.

The canopy closure factor identified at V6 was less robust across measures of crop competitive ability than the other factors. The canopy closure factor related only to CT_{num} and WSA_{shoot} (Table 6). Positive slope coefficients indicated that each unit increase in the canopy closure factor corresponded to a 7% greater ability of the crop to produce marketable ears and a 4% improvement in wild-proso millet growth suppression. Maximum LAI and rate of canopy closure in dent corn was important to light competition with velvetleaf (*Abutilon theophrasti* Medik.) (Lindquist et al. 1998). Weak or inconsistent relationships between crop competitive ability and canopy traits measured at V6 may be in part the result of poor plant growth caused by drought conditions preceding this sampling time in 2007. Correlations between years for several variables measured at V6 were insignificant, despite associations between years for the same variables at other sampling times (Table 2). Hybrids with greater LAI and IPAR at V6 were better equipped to produce marketable ears in the presence of weed interference and suppress wild-proso millet growth.

Table 6. Significance (P-values) of analysis of crop tolerance variables regressed on canopy factor loadings derived from factor analysis (see Table 3). Linear regression parameter estimates, standard errors of estimates, and root mean square error (RMSE) are included.[a]

Canopy factor	Variable	P-value	Intercept	SE	Slope	SE	RMSE
Late canopy and maturity	CT_{mass}	< 0.01	0.54	0.02	0.10	0.02	0.16
	CT_{num}	< 0.01	0.56	0.02	0.12	0.02	0.22
	WSA_{shoot}	< 0.01	0.61	0.01	0.07	0.01	0.11
	WSA_{seed}	< 0.01	0.85	0.01	0.08	0.01	0.08
Seedling quality	CT_{mass}	0.01	0.53	0.02	−0.13	0.05	0.18
	CT_{num}	0.02	0.55	0.03	−0.17	0.07	0.24
	WSA_{shoot}	0.01	0.60	0.01	−0.09	0.04	0.13
	WSA_{seed}	0.01	0.83	0.01	−0.08	0.03	0.11
Canopy closure	CT_{mass}	0.21	0.52	0.02	0.03	0.02	0.18
	CT_{num}	0.02	0.55	0.03	0.07	0.03	0.24
	WSA_{shoot}	0.02	0.60	0.01	0.04	0.02	0.13
	WSA_{seed}	0.77	0.83	0.01	< 0.01	0.02	0.11

[a] Abbreviations: CT_{mass}, crop tolerance in terms of ear mass; CT_{num}, crop tolerance in terms of ear number; WSA_{shoot}, weed suppressive ability in terms of wild-proso millet shoot biomass; WSA_{seed}, weed suppressive ability in terms of wild-proso millet seed production.

Competitive ability is unknown for all but a few of the 600 commercial sweet corn hybrids. The present work suggests that identifying hybrids most competitive with weeds does not necessarily need to focus on an individual phenomorphological trait. Covariance among traits important to competitive ability can be captured in the underlying principal canopy factors.

Several weed-free traits loading into a canopy factor, rather than a single trait, may provide flexibility in identifying competitive hybrids. For instance, information on any of the seven traits in the late canopy and maturity factor could be useful in predicting relative performance of hybrids with unknown competitive abilities. Conceivably, hybrids with traits that load highly into multiple factors would be even better suited for weed management. Product quality and yield currently drive sweet corn hybrid development with additional emphasis on disease resistance. Whether breeding programs explicitly select for superior competitive ability with weeds remains to be seen. Nonetheless, expanding herbicide resistance, limited herbicide registrations, rising costs of external inputs, yield loss due to weeds in most fields, and poor competitive ability of some hybrids are persistent challenges to sweet corn production. Weeds are particularly problematic in organic production and further growth in this market segment eventually could buoy interest in identifying which commercial hybrids are competitive, and perhaps development of hybrids with superior competitive ability.

This work showed commercial sweet corn exhibits greater variation in phenomorphological traits important to crop–weed interactions than previously reported (Makus 2000; Williams et al. 2006, 2008a). Consequently, the crop's ability to tolerate weed interference or provide weed suppression is highly cultivar specific. Three principal crop canopy factors derived from 12 phenomorphological traits accounted for much of the variation in canopy development and related to competitive ability with weeds. Functional relationships between crop canopy factors and competitive ability revealed that rapid canopy closure and a large, late-maturing canopy were positively associated with competitive ability. The data also reveal more work is needed to fully understand the role of endosperm phenotype and seedling growth on early competitive ability. Recently, gene expression studies show promise in revealing physiological processes and signaling pathways altered in crops and weeds under competition (Horvath et al. 2006, 2007). Identifying mechanisms to exploit crop competitive ability, from the level of the cropping system to the genome, could refine the ability to improve several facets of weed management, ranging from competitive cultivars to more accurate crop–weed competition models.

Sources of Materials

[1] Sweet corn seed, Abbot & Cobb, Inc., Feasterville, PA; Crookham Company, Caldwell, ID; Del Monte USA, Rochelle, IL; Green Giant Agricultural Research, LeSueur, MN; Harris Moran Seed Company, Nampa, ID; Illinois Foundation Seeds Inc., Champaign, IL; Mesa Maize, Olathe, CO; Rogers Seeds/Syngenta, Nampa, ID; Seminis Vegetable Seeds, DeForest, WI.

[2] Chlorophyll meter SPAD-502, Spectrum Technologies Inc., Plainfield, IL.

[3] Accu PAR model LP-80, Decagon Devices, Inc., Pullman, WA.

[4] LI-3100 Area Meter, LI-COR, Inc., Lincoln, NE.

Literature Cited

Anderson, R. L. 2000. Ecology and interference of proso millet (*Panicum miliaceum*) in semi-arid corn. Weed Technol. 14:45–50.

Azanza, F., A. B. Zur, and J. Juvik. 1996. Variation in sweet corn characteristics associated with stand establishment and eating quality. Euphytica 87:7–18.

Begna, S. H., R. I. Hamilton, L. M. Dwyer, D. W. Stewart, D. Cloutier, L. Assemat, K. Foroutan-Pour, and D. L. Smith. 2001a. Weed biomass production response to plant spacing and corn (*Zea mays*) hybrids differing in canopy architecture. Weed Technol. 15:647–653.

Begna, S. H., D. L. Smith, R. I. Hamilton, L. M. Dwyer, and D. W. Stewart. 2001b. Corn genotypic variation effects on seedling emergence and leaf appearance of short-season areas. J. Agro. Crop Sci. 186:267–271.

Bennett, A. C. and D. R. Shaw. 2000. Effect of *Glycine max* cultivar and weed control on weed seed characteristics. Weed Sci. 48:431–435.

Callaway, B. M. 1992. A compendium of crop varietal tolerance to weeds. Am. Alt. Agric. 7:169–180.

Ford, G. T. and J. M. Pleasant. 1994. Competitive ability of six corn (*Zea mays*) hybrids with four weed control practices. Weed Technol. 8:124–128.

Horvath, D. P., R. Gulden, and S. A. Clay. 2006. Microarray analysis of late-season velvetleaf (*Abutilon theophrasti*) effect on corn. Weed Sci. 54:983–994.

Horvath, D. P., D. Llewellyn, and S. A. Clay. 2007. Heterologous hybridization of cotton microarrays with velvetleaf (*Abutilon theophrasti*) reveals physiological response due to corn competition. Weed Sci. 55:546–557.

Jannink, J. L., N. R. Jordan, and J. H. Orf. 2001. Feasibility of section for high weed suppressive ability in soybean: absence of tradeoffs between rapid initial growth and sustained later growth. Euphytica 120:291–300.

Jannink, J. L., J. H. Orf, N. R. Jordan, and R. G. Shaw. 2000. Index selection for weed suppressive ability in soybean. Crop Sci. 40:1087–1094.

Johnson, D. E. 1998. Applied Multivariate Methods for Data Analysts. Pacific Grove, CA: Brooks/Cole. Pp. 191–212.

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

Lemerle, D., A. Smith, B. Verbeek, E. Koetz, P. Lockley, and P. Martin. 2006. Incremental crop tolerance to weeds: a measure for selecting competitive ability in Australian wheats. Euphytica 149:85–95.

Lindquist, J. L. and D. A. Mortensen. 1998. Tolerance and velvetleaf (*Abutilon theophrasti*) suppressive ability of two old and two modern corn (*Zea mays*) hybrids. Weed Sci. 46:569–574.

Lindquist, J. L., D. A. Mortensen, and B. E. Johnson. 1998. Mechanisms of corn tolerance and velvetleaf suppressive ability. Agron. J. 90:787–792.

Makus, D. J. 2000. Performance of two sweet corn cultivars grown under conservation tillage and with-in-row weed pressure. Subtropical Plant Sci. 52:18–22.

Nordby, J. N., M. M. Williams II, J. K. Pataky, and D. E. Riechers. 2008. A common genetic basis in sweet corn inbred Cr1 for cross sensitivity to multiple cytochrome P450-metabolized herbicides. Weed Science 56:376–382.

Ott, R. L. and M. Longnecker. 2001. An Introduction to Statistical Methods and Data Analysis. 5th ed. Pacific Grove, CA: Duxbury. Pp. 368–371.

Pataky, J. K., J. N. Nordby, M. M. Williams II, and D. E. Riechers. 2006. Inheritance of cross-sensitivity in sweet corn to herbicides applied postemergence. Journal of the American Society for Horticultural Science 131:744–751.

Ritchie, S. W., J. J. Hanway, G. O. Benson, and J. C. Herman. 1993. How a Corn Plant Develops. http://www.biologie.uni-hamburg.de/b-online/library/maize/www.ag.iastate.edu/departments/agronomy/corngrows.html. Accessed: December 16, 2008.

Roggenkamp, G. J., S. C. Mason, and A. R. Martin. 2000. Velvetleaf (*Abutilon theophrasti*) and green foxtail (*Setaria viridis*) response to corn (*Zea mays*) hybrid. Weed Technol. 14:304–311.

Sankula, S., M. J. VanGessel, and R. R. Mulford. 2004. Corn leaf architecture as a tool for weed management in two production systems. Weed Sci. 52:1026–1033.

SAS Institute. 2002. User's Guide: Statistics. Cary, NC: SAS Institute.

Shenk, M. D., W. S. Braunworth Jr., R. J. Fernandez, D. W. Curtis, D. McGrath, and R. D. William. 1990. Wild-proso millet (*Panicum miliaceum*) control in sweet corn (*Zea mays*). Weed Technol. 4:440–445.

So, Y. F., M. M. Williams II, and J. K. Pataky. 2009. Weed interference differentially affects canopy architecture and yield components of 25 sweet corn hybrids. HortScience. In press.

Swanton, C. J., R. H. Gulden, and K. Chandler. 2007. A rationale for atrazine stewardship in corn. Weed Sci. 55:75–81.

Toler, J. E., E. C. Murdock, G. S. Stapleton, and S. U. Wallace. 1999. Corn leaf orientation effects on light interception, intraspecific competition, and grain yields. J. Prod. Agric. 12:369–399.

Tollenaar, M., A. Aguilera, and S. P. Nissanka. 1997. Grain yield is reduced more by weed interference in an old than in a new maize hybrid. Agron. J. 89:239–246.

Tracy, W. F. 2001. Sweet corn. Pages 155–197 *in* A. R. Hallauer, ed. Specialty Corns. 2nd ed. Boca Raton, FL: CRC.

Williams, B. J. and R. G. Harvey. 2000. Effect of nicosulfuron timing on wild-proso millet (*Panicum miliaceum*) control in sweet corn (*Zea mays*). Weed Technol. 14:377–382.

Williams, M. M. II, R. A. Boydston, and A. S. Davis. 2006. Canopy variation among three sweet corn hybrids and implications for light competition. HortScience 41:1449–1454.

Williams, M. M. II, R. A. Boydston, and A. S. Davis. 2007. Wild proso millet (*Panicum miliaceum*) suppressive ability among three sweet corn hybrids. Weed Sci. 55:245–251.

Williams, M. M. II, R. A. Boydston, and A. S. Davis. 2008a. Crop competitive ability contributes to herbicide performance in sweet corn. Weed Res. 48:58–67.

Williams, M. M. II, R. A. Boydston., and A. S. Davis. 2008b. Differential tolerance in sweet corn to wild-proso millet (*Panicum miliaceum*) interference. Weed Sci. 56:91–96.

Williams, M. M. II, R. L. Rabaey, and C. M. Boerboom. 2008c. Residual weeds of sweet corn in the north central region. Weed Technol. 22:646–653.

Zhao, D. L., G. N. Atlin, L. Bastiaans, and J.H.J. Spiertz. 2006. Cultivar weed-competitiveness in aerobic rice: heritability, correlated traits, and the potential for indirect selection in weed-free environments. Crop Sci. 46:372–380.