

Why Early Season Weed Control Is Important in Maize

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Control of early-emerging weeds is essential to protect the yield potential of maize. An understanding of the physiological changes that occur as a result of weed interference is required to address variability in yield loss across sites and years. Field trials were conducted at the University of Guelph (UG), the Ohio State University (OSU), and Colorado State University (CSU) during 2009 and 2010. There were six treatments (season-long weedy and weed-free, and weed control at the 1st-, 3rd-, 5th-, and 10th-leaf-tip stages of maize development) and 20 individual plants per plot were harvested at maturity. We hypothesized that, as weed control was delayed, weed interference in the early stages of maize development would increase plant-to-plant variability in plant dry-matter accumulation, which would result in a reduction of grain yield at maturity. The onset of the critical period for weed control (CPWC) occurred on average between the third and fifth leaf tip stages of development (i.e., V1 to V3, respectively). Rate of yield loss following the onset of the CPWC ranged from 0.05 MG ha⁻¹ d⁻¹ at UG 2009 to 0.22 MG ha⁻¹ d⁻¹ at CSU 2010 (i.e., 0.5 and 1.6% d⁻¹, respectively). On average, reductions in kernel number per plant accounted for approximately 65% of the decline in grain yield as weed control was delayed. Biomass partitioning to the grain was stable through early weed removal treatments, increased and peaked at the 10th-leaf-tip time of control, and decreased in the season-long weedy treatment. Plant-to-plant variability in dry matter at maturity and incidence of bareness increased as weed control was delayed. As weed control was delayed, the contribution of plant-to-plant variability at maturity to the overall yield loss was small, relative to the decline of mean plant dry matter. **Nomenclature:** Atrazine; glyphosate; mesotrione; *S*-metolachlor; maize, *Zea mays* L.

Key words: Zea mays, corn, weed interference, yield loss, harvest index, kernel number, kernel weight, plant-to-plant variability, reproductive allometry.

Weed interference remains one of the major limitations to crop productivity in North America (Rajcan and Swanton 2001; Subedi and Ma 2009). It has been estimated that, at their peak, yield losses from weed interference can range from 0.03 to 0.21 MG ha⁻¹ d⁻¹ in maize (Hall et al. 1992). Timing of weed emergence relative to the crop, weed density, and weed competitive ability are variables that will influence the onset and rate of yield loss (Kropff and Spitters 1991; O'Donovan et al. 1985; Swanton et al. 2008). The onset and severity of yield losses from weed interference, however, can vary across sites and years, often with little apparent connection to the level of weed pressure or to the timing of weed management practices (Evans et al. 2003b; Hall et al. 1992). To address this variability, integrated weed management strategies have often incorporated knowledge of the critical period for weed control (CPWC; Swanton et al. 2008). The CPWC has provided generalized guidelines for the timing of weed control practices based on the mean yield losses observed during several site years (Hall et al. 1992; Knezevic et al. 1994, 2002; Swanton et al. 1999; Van Acker et al. 1993). Although these studies have made significant contributions toward optimizing the timing of weed management practices, they have often overlooked the critical information required to explain the inconsistency in yield losses that they have summarized.

In a review of the concept and analysis of the CPWC, Knezevic et al. (2002) suggested that there is a minimum amount of data in addition to grain yield that should be collected in order to address the inherent variability in cropweed interference relationships. The authors suggested that data on important variables, such as weed species and density, date of weed and crop emergence, and weekly staging and height measurements, should be collected in order to quantify the competitive environment and extrapolate the results beyond the scope of the experiment in question. We advocate that, in order to take a further step toward understanding the physiological mechanisms underlying the observed yield losses, weed control studies should also collect data on crop yield components (i.e., seed number and weight) and biomass partitioning at physiological maturity. To date, only a few weed control studies have collected such data (Cox and Cherney 2010; Cox et al. 2006; Evans et al. 2003a,b; Tollenaar et al. 1997).

Although yield losses from weed interference are reported on per-unit-area basis, they are in fact the direct result of changes in biomass accumulation and partitioning of the individuals that comprise the crop stand. Therefore, an understanding of how resources are allocated and yield is formed by individuals of a given crop species is required in order to identify commonalities in the patterns of yield losses observed across sites and years. In maize, the proportion of total aboveground biomass at maturity allocated to grain (i.e., harvest index [HI]) is relatively stable for large and midsize plants, but then declines rapidly in smaller, stressed individuals (Vega et al. 2000). The variation in HI among smaller individuals with similar biomasses is indicative of a breakdown in reproductive allometry, where reproductive growth is uncoupled from vegetative growth (Vega and Sadras 2003). The decline in HI for individuals with low plant dry matter (PDM) is often associated with a reduction in kernel number per plant (KNP). Kernel number is associated with the rate of plant dry-matter accumulation and partitioning to

DOI: 10.1614/WS-D-11-00183.1

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the ear during a critical period of 3 to 4 wk centered on and bracketing silking (Andrade et al. 1999; Echarte and Tollenaar 2006; Tollenaar et al. 1992; Tollenaar and Daynard 1978). If the plant growth rate around silking (PGR_S) falls below a threshold, then these individuals fail to set kernels and are barren at maturity (i.e., HI = 0). Thus, reductions in maize grain yield (GY) caused by biotic and abiotic stresses are associated primarily with declining PGR_S, leading to lower kernel set and, to a lesser extent, lighter kernel weights (KW).

Stresses experienced during the vegetative or reproductive phases of the life cycle of a crop can also increase the plant-toplant variability within a crop stand (Tollenaar and Wu 1999). In maize, this reduction in stand uniformity is often manifested in the number of days to silking, KNP, and HI, and is frequently associated with yield losses (Fasoula and Tollenaar 2005). For example, Liu et al. (2004) demonstrated that the increase in plant-to-plant variability in dry matter caused by a two-leaf-stage delay in emergence, in one out of every six plants, and reduced maize GY by 4%. When this delay in emergence increased to four leaf stages, the yield loss increased to 8%. Similarly, Page et al. (2010) demonstrated that the expression of shade avoidance in response to the presence of neighboring weeds doubled the plant-to-plant variability in KNP and HI of maize. When plants expressing a shade-avoidance response were exposed to a subsequent stressor, the increased plant-to-plant variability magnified the severity of yield losses as the mean plant dry matter et al. maturity approached the threshold when HI declines (Page et al. 2011). Thus, increases in plant-to-plant variability caused by weed interference can persist even after weed control practices have been applied. This reduction in stand uniformity may contribute to the yield losses caused by secondary stressors (i.e., drought, nutrient limitations, etc).

This study was undertaken to highlight the importance of early weed management in protecting the yield potential of maize. We explored the effects of time of weed control on biomass accumulation and partitioning, GY, and yield components of maize (i.e., KNP and KW). We tested the hypothesis that, as weed control was delayed, weed interference in the early stages of maize development would increase plant-to-plant variability in dry-matter accumulation that would result in a reduction of grain yield at maturity. A surrogate weed (i.e., winter wheat, Triticum aestivum L.) was used in this study to ensure that the period of weed interference began at or near the time of crop emergence and that this variable was held constant across all environments. We evaluated the effects of weed interference at the level of the individual and the crop stand as a whole in order to better understand the role that plant-to-plant variability plays in influencing yield loss in maize.

Materials and Methods

A field trial was conducted over 2 yr (2009, 2010) and at three locations (University of Guelph [UG], Ohio State University [OSU], and Colorado State University [CSU]) in order to investigate the impact of weed interference on plant to plant variability in maize GY, yield components, and reproductive partitioning. The soil type at UG was a London loam soil (Aquic Hapluddaf) with tile drainage and soil organic matter content of 3.8 to 4.0%. At OSU, the soil type was a Kokomo silty clay loam (fine, mixed, superactive, mesic Typic Argiaquolls) with organic matter 2.2 to 3.1%. At CSU, the soil type was Fort Collins loam (fine-loamy, mixed, mesic Ustollic Haplargid) with organic matter of 1.8%. Maize hybrids were selected for each geographic region and planted at a conventional planting density (i.e., 75,000 to 80,000 plants per ha) according to the best management practices for each area. In 2009, maize was planted on May 13, 11, and 20 at UG, CSU, and OSU, respectively. In 2010, maize was planted on May 5 and 6 and April 30 at UG, CSU, and OSU, respectively. All hybrids were glyphosate tolerant. Trials conducted at CSU were under center pivot irrigation, and UG and OSU were nonirrigated, rain-fed systems. Irrigation at CSU began in late June of each year, and approximately 2.54 cm of water was applied per week through the end of September. Following maize planting, winter wheat was seeded at a density of 150 seeds m^{-2} in rows (spacing 13 to 18 cm) perpendicular to those of the maize in order to act as a surrogate weedy competitor. Winter wheat was selected as a surrogate weedy competitor in order to standardize the competitive pressure across sites and years. Moreover, winter wheat was planted such that wheat seedlings emerged at or near the time of maize emergence, thus ensuring this critical aspect of crop-weed interference was also held constant. Each plot consisted of four rows of maize (row spacing of 0.76 m), 8 to 10 m long, and the entire experiment was bordered by four rows of maize on all sides. Within a plot, the two exterior rows served as borders and only the center two rows were used for all measurements and analyses.

The experiment was designed as a randomized complete block design with six replications. Time of weed control was the main factor and there were six treatments: (1) weed-free control (WF), (2) weed control at the 1-leaf-tip stage (WC1), (3) weed control at the 3-leaf-tip stage (WC3), (4) weed control at the 5-leaf-tip stage (WC5), (5) weed control at the 10-leaf-tip stage (WC10), and (6) season-long weedy (W). Developmental stages were based on the number of visible leaves per plant, including the tip of the youngest leaf emerging from the whorl (Tollenaar et al. 1979). In the WF treatment, a pre-emergence herbicide application consisting of mesotrione ($\overline{0.140}$ kg ai ha⁻¹), *S*-metolachlor (1.6 kg ai ha⁻¹), and atrazine (1.28 kg ai ha⁻¹) was used to control the surrogate weedy competitor (i.e., the winter wheat). In-crop weed-removal timings were achieved with the use of an application of mesotrione (0.105 kg ai ha^{-1}), S-metolachlor $(1.05 \text{ kg ai } ha^{-1})$, and glyphosate $(1.05 \text{ kg ae } ha^{-1})$. Plots were maintained weed-free for the remainder of the season by manually controlling newly emerged weeds or by applying glyphosate (0.84 kg ae ha^{-1}). Prior to each time of weed control, the biomass of the surrogate weed was assessed by harvesting a 0.5-m² area. Weed biomass samples were dried at 80 C to a constant weight.

Measured Traits and Harvest Procedures. Shortly after emergence, 10 consecutive maize seedlings were selected and marked in each of the two center rows of each plot. A 1-m border was left to separate these seedlings from the front edge of the plot. At maturity, the aboveground biomass of theses 20 plants per plot were harvested, separated into ears and stover (i.e., stem and leaves), and dried at 80 C to a constant weight. Ears were then shelled and KNP was determined with the use of a seed counter. Kernel weight was calculated by dividing grain yield by KNP. Ears on the remaining plants in the center two rows of each plot were harvested in bulk, dried, shelled, and weighed. These GY were then added to the yield from the 20 focal plants to obtain a bulk plot yield. The individual grain and stover weights were used to determine the harvest index (HI = GY/[stover + GY]) for each of the 20 focal plants.

Statistical Analysis. A mixed model (PROC MIXED [SAS Institute, Cary, NC]) was used to conduct a two-way analysis of variance (ANOVA) on the mean of the 20 maize plants harvested per plot. Site years were considered to be unique environments and were treated as a fixed effect along with time of weed control in the ANOVA. Replicate and replicate within environments were treated as random effects. The traits analyzed included GY, KNP, KW, PDM, and HI. Weed biomass at each time of control (i.e., WC1, WC3, WC5, and WC10) was also analyzed as a two-way ANOVA with the use of the same fixed and random effects. The results of these ANOVAs indicated a significant interaction with environment for all analyzed traits and, therefore, data sets for each trait were split by environment and least significant differences at $\alpha = 0.05$ (LSD 0.05) were determined (Saxton 1998). Furthermore, regression analyses for grain yield losses were also conducted separately for each environment.

Yield loss, as a percent of the weed-free control, was modeled with the use of a logistic regression equation (Evans et al. 2003b; Knezevic et al. 2002). Separate regressions were conducted for the GY harvested from the 20 focal plants and for the bulk plot yield to ensure that detailed results generated from the harvest of individual plants was representative of the whole-plot response to weed interference (data not presented). The adjusted coefficient of determination (R^2_{Adj}) was calculated for each regression in accordance with Zar (1996). Growing degree days (GDD) were calculated as in Campbell and Norman (1998), with the use of daily minimum and maximum air temperatures recorded at each location. GDD accumulation began on the day of planting using a base temperature (T_b) for maize growth of 10 C (Gilmore and Rodgers 1958; Tollenaar et al. 1979).

Results and Discussion

Delaying Weed Control Reduced Yield Despite Variability in Weed Biomass. Yield losses from weed interference varied across environments (P < 0.0001; Figure 1A, Table 1). Weed-free GY ranged from 8.5 Mg ha⁻¹ at UG 2009 to 15.3 Mg ha⁻¹ at OSU 2009, and yield losses from seasonlong weed interference ranged from 72% at CSU 2010 to 17% at OSU 2009. Based on the regressions of relative yield over time, the onset of the CPWC (defined as the point where yield losses exceed 5% of the weed-free control) ranged from 60 GDD at UG 2009 to 245 GDD at OSU 2009 ($T_{\rm b} = 10$ C; 23 and 25 d after planting [DAP], respectively). When averaged across the six environments, a 5% yield loss was reached between the third- and fifth-leaf-tip stages of development (i.e., V1 to V3), which were reached on average at 121 and 182 GDD, respectively. During the subsequent phase of linear yield losses (i.e., from WC3 to WC10), the rate of loss from weed interference ranged from approximately $0.05 \text{ MG ha}^{-1} \text{ d}^{-1}$ at UG 2009 to $0.22 \text{ MG ha}^{-1} \text{ d}^{-1}$ at CSU 2010. These rates represent losses of 0.5 and 1.6% d^{-1} , respectively. When averaged across the six environments, the



Figure 1. (A) Relative yield loss as a function of growing degree days and (B) wheat biomass at the time of weed control from the University of Guelph (UG), the Ohio State University (OSU), and Colorado State University (CSU) in 2009 and 2010. Relative yield losses were calculated from the samples of 20 focal plants per plot and were fitted to following the logistic response equation: $Y_i = c + (d - c)/1 + \exp[b(\log GDD) - \log I_{50})]$. Equation parameters and adjusted $R^2 (c; d; b; I_{50}; R^2_{Adj})$ for each site year were as follows: UG, 2009 (33.2, 98.5, 2.7, 185.2, 0.99), 2010 (36.1, 100.9, 1.72, 665.9, 0.99); CSU, 2009 (30, 101.8, 2.6, 252.6, 0.99); 2010 (24.4, 101.9, 3.7, 292.6, 0.98).

overall rate of yield loss following the onset of the CPWC was approximately $1.2\% \text{ d}^{-1}$.

Previous studies of maize-weed interference have reported the onset of the CPWC with the use of a variety of thermal and developmental scales. For example, Hall et al. (1992) reported that the CPWC began as early as the third-leaf tip stage, whereas Norsworthy and Oliveira (2004) reported that it began as early as V1 to V2 (i.e., the third-leaf-tip stage). Gower et al. (2003) reported that weeds needed to be removed before they reached 10 cm in height, at no more than 23 DAP and prior to the V4 stage of maize development. Similarly, Cox et al. (2006) reported that the onset of the CPWC began after the V3 to V4 stage of development but prior to V5 to V6. These stages were reached on average at 202 and 357 GDD ($T_{\rm b}$ = 8 C), respectively. Finally, Evans et al. (2003b) reported that, at a nitrogen rate of 120 kg N ha⁻¹, the CPWC began on average at 317 GDD ($T_b = 10$ C), which corresponded roughly to the V7 stage of maize development and was reached at approximately 25 d after emergence (DAE). The interpretation and comparison of these results with those of the current study are, however, complicated by the use of natural weed populations and by variability in the type of data collected on the timing, density, species, and biomass of these populations at the time of weed removal. For instance, although Evans et al. (2003b) concluded that the CPWC began most often at V7, there was one of their four site years during which the CPWC began at V4 (200 GDD, 14 DAE) because of the presence of Pennsylvania smartweed (*Polygonum*) pensylvanicum L.) that emerged 4 d prior to the crop. Thus, the authors concluded that the time of weed emergence relative to the crop was the primary factor determining the onset of the CPWC in maize in their study.

The surrogate weed methodology used in our study helped to ensure that the period of weed interference began at or near the time of crop emergence and that this variable was held constant across all environments. Nevertheless, the level of biomass produced by the surrogate weed at each time of weed control did vary across environments (P < 0.0001; Figure 1B). For example, at the 10th leaf tip of maize (i.e., V5 to V6), the surrogate weed biomass ranged from 139 g m⁻²

Table 1. Effect of time of weed control on grain yield, yield components, reproductive partitioning, and plant-to-plant variability at UG, OSU, and CSU in 2009 and 2010.^a

Location	Treatment	2009						2010							
		GY	PDM	KNP	KW	HI	$\mathrm{CV}_{\mathrm{PDM}}$	GY	PDM	KNP	KW	HI	CV_{PDM}		
		g plant $^{-1}$	g plant ⁻¹	kernel plant ⁻¹	g kernel $^{-1}$	%	%	g plant $^{-1}$	g plant ⁻¹	kernel plant ⁻¹	g kernel $^{-1}$	%	%		
UG	WF	114	238	500	0.23	47.7	15.0	155	288	550	0.28	53.8	18.2		
	WC1	113	243	495	0.23	46.7	14.0	162	299	575	0.28	54.4	13.4		
	WC3	106	230	485	0.22	46.1	14.8	152	286	542	0.28	53.4	22.8		
	WC5	109	239	465	0.23	45.5	15.1	155	285	552	0.28	54.5	20.8		
	WC10	87	164	442	0.20	53.2	19.5	128	223	500	0.25	57.3	26.4		
	W	40	83	284	0.14	48.4	34.1	98	172	377	0.26	56.8	24.8		
LSD _{0.05}		14	26	49	0.02	3.5		14	29	37	0.01	1.6			
OSU	WF	204	327	*p	*	62.5	16.5	198	350	588	0.34	56.7	20.0		
	WC1	199	317	*	*	62.7	17.9	199	341	586	0.34	58.4	24.1		
	WC3	197	316	*	*	62.3	18.6	192	326	577	0.33	58.8	22.2		
	WC5	191	309	*	*	61.9	16.5	184	305	557	0.33	60.2	24.6		
	WC10	171	275	*	*	62.4	20.6	154	254	478	0.32	60.8	32.4		
	W	169	270	*	*	62.8	23.4	95	160	320	0.29	59.3	39.7		
LSD _{0.05}		15	26	*	*	3.0		19	36	58	0.01	3.0			
CSU	WF	155	279	529	0.29	55.7	10.5	176	295	590	0.30	59.7	10.1		
	WC1	155	277	524	0.30	56.0	11.0	173	294	572	0.30	58.7	15.9		
	WC3	151	269	508	0.30	55.9	23.0	169	293	561	0.30	57.9	15.2		
	WC5	126	209	483	0.26	60.4	22.1	151	258	515	0.29	58.9	20.2		
	WC10	86	137	385	0.22	62.6	31.9	94	156	360	0.26	60.4	21.9		
	W	49	85	260	0.19	57.6	43.8	50	84	253	0.20	58.6	32.9		
LSD _{0.05}		14	21	40	0.01	2.5		13	25	49	0.01	3.9			
Mean	WF	158	282	514	0.26	55.3	14.0	176	311	576	0.31	56.7	16.1		
	WC1	156	279	509	0.26	55.1	14.3	178	311	578	0.31	57.1	17.8		
	WC3	151	272	496	0.26	54.8	18.8	171	302	560	0.31	56.7	20.1		
	WC5	142	252	474	0.25	55.9	17.9	163	283	541	0.30	57.9	21.9		
	WC10	115	192	413	0.21	59.4	24.0	125	211	446	0.28	59.5	26.9		
	W	86	146	272	0.16	56.3	33.8	81	139	317	0.25	58.2	32.5		

^a Abbreviations: UG, University of Guelph; OSU, Ohio State University; CSU, Colorado State University; GY, grain yield; PDM, plant dry matter at maturity; KNP, kernel number per plant; KW, kernel weight; HI, harvest index; CV_{PDM} , coefficient of variation of PDM; WF, weed-free; WC1, 1-leaf-tip weed control; WC3, 3-leaf-tip weed control; WC5, 5-leaf-tip weed control; WC10, 10-leaf-tip weed control; W = weedy.

^b Asterisks indicate missing data.

at OSU 2009 to 321 g m $^{-2}$ at CSU 2010. For comparison, at a similar stage of maize development (V6), Evans et al. (2003b) reported that the biomass from their natural weed population ranged from 11 g m⁻² to 166 g m⁻² (N rate = 120 kg N ha-1). In fact, the site years where Evans et al. (2003b) reported that the CPWC began at V7 averaged only 23 g m^{-2} of weed biomass at V6, whereas the site year where the CPWC began at V4 had 166 g m^{-2} of weed biomass at V6. Because the density and timing of surrogate weed emergence were held constant across the six environments used in the current study, the variability in weed biomass accumulation is likely related to differences in temperature and precipitation shortly after crop and weed emergence (Table 2). For example, weed biomass accumulation at OSU was greater at all times of weed removal in 2010 than in 2009 (Figure 1B). The precipitation received at OSU during the period of weed biomass accumulation (i.e., from emergence to 10th-leaf-tip stage of development; Table 2) in 2009 was 47% of that received in 2010 during the same period of time. Although this difference in precipitation likely contributed to the disparity in weed biomass accumulation between years, it is interesting to note that yield losses in the treatments bracketing the onset of the CPWC (i.e., the third- and fifthleaf-tip stages) were similar in 2009 and 2010 (Table 1). It was only in the WC10 and W treatments where the yield loses at OSU 2010 greatly exceeded those from OSU 2009. Similarly, weed biomass sampled from CSU at the fifth-leaftip stage of weed removal was 47% greater in 2010 than in

2009, yet the yield loss from this level of weed interference was 5% less in 2010 than 2009. These results suggest that, at early times of weed control, increases in weed biomass do not necessarily result in greater yield losses.

Delaying Weed Control Reduced Biomass Accumulation and Shifted Partitioning. Maize PDM at maturity, KNP, KW, and HI were influenced by time of weed control, environment, and their interaction (P < 0.0001; Table 1). The PDM at maturity in the WF treatment ranged from 238 to 350 g plant⁻¹ at UG 2009 and OSU 2010, respectively. As the time of weed control was delayed, PDM at maturity decreased. When averaged across the six environments, the relative reductions in PDM (expressed as a percentage of the WF treatment) for the WC1, WC3, WC5, WC10, and W treatments were 0, 3, 10, 32, and 52%, respectively. In contrast to PDM, HI was generally stable through early weed control treatments (i.e., WC1 to WC5), after which it peaked in WC10 and decreased in W. The reductions in PDM as weed control was delayed were, however, consistently greater than any increases in HI, which resulted in a net reduction in GY despite the increased partitioning to the ear.

The decline in GY as weed control was delayed was attributable to reductions in both KNP and KW (Table 1). On average, the relative contributions of KNP and KW to the observed reductions in GY were approximately 65 and 35%, respectively. These contributions varied among times of weed control and across environments. For example, the contribu-

Table 2. Mean daily air temperature, precipitation, and radiation during periods of maize development at UG, OSU, and CSU in 2009 and 2010.^a

		Duration			Temperature			Precipitation			Radiation		
Year	Period of maize development	UG	OSU	CSU	UG	OSU	CSU	UG	OSU	CSU	UG	OSU	CSU
			d		C			mm			MJ m ⁻²		
2009	30 d pre-emergence	30	30	30	*p	17	12.3	*	49	29	*	610	608
	Emergence to the 10th leaf tip	35	45	40	14.9	20.8	16.3	88.4	91.2	158.5	754	961	749
	10th leaf tip to 1 wk presilking	43	10	23	16.8	20.5	20.7	130.4	55	95.8	824	208	548
	1 wk presilking to 2 wk postsilking	21	21	21	18.3	20.9	19.9	61.2	94	98.6	387	411	473
	2 wk postsilking to maturity	46	69	47	11.9	17	17.2	104.2	200	185.4	621	1,089	801
2010	30 d pre-emergence	30	30	30	12	13.5	5	95.9	45.6	113.8	583	536	569
	Emergence to the 10th leaf tip	27	43	41	17.4	20.2	17.8	108	195	91.2	550	848	1,143
	10th leaf tip to 1 wk presilking	40	6	30	19.6	24.3	21.5	161	147	123.4	869	138	711
	1 wk presilking to 2 wk post silking	21	21	21	19.5	23.5	21.4	12.3	141.4	85.9	378	530	451
	2 wks postsilking to maturity	60	68	57	12.4	22.5	16.6	155	75.6	239.8	790	1,428	1,074

^a Abbreviations: UG, University of Guelph; OSU, Ohio State University; and CSU, Colorado State University.

^b Asterisks indicate missing data.

tion of KNP to GY reductions ranged from 52% at UG 2009 to 82% at UG 2010. Yield losses in maize have often been attributed to reductions in KNP (Cirilo and Andrade 1994; Echarte et al. 2000; Otegui et al. 1995; Pagano and Maddoni 2007; Tollenaar et al. 1992). In fact, many of these studies have documented concomitant declines in maize GY and KNP in response to increases in plant population density. Of the weed-interference studies that have reported KNP and KW, several have also reported that reductions in GY were attributable primarily to declines in KNP (Cox et al. 2006; Evans et al. 2003b). Conversely, Cerrudo et al. (2011) reported that KNP and KW declined in similar proportions when comparing early- and late-season weed control treatments. Although our study supports the conclusion that yield losses from weed interference are more frequently the result of reductions in KNP, the considerable variability among sites and years suggests that environmental conditions may play a role in determining the trade-off between reductions in KNP and KW.

In maize, KNP and KW at maturity are influenced strongly by the PGR_S (Andrade et al. 1999; Borrás and Westgate 2006; Tollenaar et al. 1992). Several authors have suggested that the sink capacity (i.e., potential KNP and KW) is set in response to source strength during the critical period bracketing silking (i.e., PGR_S; Borrás and Gambín 2010; Lee and Tollenaar 2007; Tollenaar and Lee 2006). This yield potential can then be realized or reduced based on the environmental conditions that influence assimilate supply during the subsequent grain filling period (GFP; Borrás and Westgate 2006). Weed interference can influence both the PGR_S and the assimilate supply during the GFP. For example, Cerrudo et al. (2011) reported that increasing durations of weed interference reduced PGR_S and delayed the onset of the GFP by increasing the number of days from emergence to silking. Though it is likely that a reduction in PGR_S is the primary factor leading to yield losses from weed interference, the resulting delay in silking may also contribute by reducing the number of days from silking to maturity during which the environmental conditions are suitable for photosynthesis and grain filling.

In the current study, increasing durations of weed interference delayed silking. This effect was most evident in the later weed control timings, WC10 and W, where silking was delayed on average 4.1 and 7.1 d, respectively. Although yield losses from weed interference tended to increase as silking was delayed within an environment, the largest yield losses were observed in environments where silking was delayed across all treatments. For instance, yield losses at UG 2009 and 2010 were notably different in spite of similar levels of weed biomass at all times of weed control (Figure 1). The percent reductions in KNP and KW at UG in 2009 and 2010 were generally similar in all weed control treatments with the exception of the W treatment (Table 1). Relative to the WF treatment, KNP and KW in the W treatment in 2009 were reduced by 43 and 39%, respectively, and the overall yield loss was 65%. In 2010, the relative reductions in KNP and KW in this same treatment were 32 and 7%, respectively, and the yield loss was only 37%. It is clear from these results that the contributions of KNP and KW to the overall yield loss were nearly equal in 2009 (52 and 48%, respectively), whereas in 2010, the contribution of KNP was far greater than that of KW (81 and 19%, respectively).

In spite of the fact that the growing seasons at UG were of similar length in 2009 and 2010 (175 vs. 178 d, respectively; Table 2), the durations of the vegetative and reproductive periods of crop growth were notably different among years. In particular, maize plants reached the critical period bracketing silking (i.e., 1 wk pre- to 2 wk postsilking) on average 11 d later in 2009 than in 2010. Because the developmental stage of silking is correlated with whole plant and ear biomass accumulation (Borràs et al. 2007), this delay suggests that maize plants in 2009 had a lower plant growth rate leading up to the critical period bracketing silking. This conclusion is further supported by the reductions in the vegetative and reproductive biomass accumulation across all treatments in 2009 vs. 2010 (Table 2). The delayed silking in 2009 also reduced the length of the GFP, and maize plants received 21% less radiation during this period in 2009 than in 2010 (Table 2). It is possible that this reduction in the length of the GFP in 2009 vs. 2010 may have contributed to the lower KW and the disparity in HIs that are apparent when comparing the results from these 2 yr.

In general, increasing durations of weed interference had little impact on the HI. Harvest index was stable through early weed control treatments (i.e., WC1–WC5), after which it increased and peaked in WC10 and finally, decreased in W (Table 1). With the exception of OSU 2009, the relative increase in HI in WC10 was consistent across environments and ranged from 0.7 to 6.9%. These results are similar to that reported by Cerrudo et al. (2011) who documented an average increase of 6% in HI as weed control was delayed from the 3rd- to the 10th-leaf-tip stage of development. Cerrudo et al. (2011) hypothesized that the increase in HI was related to the differential impact of weed pressure on plant dry matter accumulated at early stages of maize development (i.e., emergence to 1 wk before silking) versus that accumulated during the critical period for KNP determination and grain filling period (i.e., 1 wk before silking to maturity). Because PDM at maturity represents the total biomass accumulated during both early and late periods of development, and HI is the ratio of GY (which his mainly determined from 1 wk before silking to maturity) to PDM at maturity (including GY), a disproportionate reduction in PDM relative to GY would result in an increase in HI.

Delaying Weed Control Increased Plant-to-Plant Variability. Plant-to-plant variability in PDM (as measured by the coefficient of variation or CV_{PDM}) increased as weed control was delayed (Table 1). When averaged across the six environments, the CV_{PDM} increased by 0.7, 4.1, 4.6, 10.2, and 17.8%, (relative the WF treatment) for the WC1, WC3, WC5, WC10, and W treatments, respectively. Increases in plant-to-plant variability in a maize canopy have often been observed as a result of biotic and abiotic stress (Cerrudo et al. 2011; Pagano et al. 2007). Moreover, it has been suggested that increases in plant-to-plant variability negatively impact canopy productivity and yield stability in maize (Andrade and Abbate 2005; Ford and Hicks 1992; Glenn and Daynard 1974; Liu et al. 2004; Maddonni and Otegui 2004; Pendleton and Seif 1962; Tollenaar and Wu 1999). It is important to note that, as a standardized measure of variability, CV is a ratio of the mean and the standard deviation (SD) and the mean of a population and changes in CV can be related to shifts in either one of these components. For example, the CV_{PDM} in the WC1, WC3, and WC5 treatments at CSU 2009 were 11, 23, and 22, respectively (Figure 2). The doubling of CV_{PDM} from WC1 to WC3 was associated primarily with a doubling of SD and, to a lesser extent, a 3% reduction in the mean PDM. It is evident from Figure 2 that the increase in SD in the WC3 treatment was caused by a group of individuals that achieved notably lower PDM at maturity than the mean of this treatment. If we consider these three weed control treatments (i.e., WC1, WC3, and WC5) to be points on a continuum, then the increase in SD in WC3 is an indicator of the future impact of weed interference on PDM in the WC5 treatment. From WC3 to WC5, the SD declined as a greater proportion of the WC3 population shifted toward the mean PDM of the WC5 population. As a result of this concurrent decline in the mean and SD, the CV_{PDM} changed little between the WC3 and WC5 treatments and thus, the onset of the CPWC was not associated with an increase in plant-to-plant variability. Rather, the increase in plant-to-plant variability preceded significant yield losses and, in this case, should be viewed as an indicator of future reductions in GY.

The shift in the maize population from high to low PDM as weed control was delayed can also be described in terms of the skewness of the frequency distributions (Figure 2). Skewness is a measure of the symmetry of a population about the mean and has a value of zero for symmetrical distributions, such as the normal distribution (Hara 1988). Across all of our environments, skewness of PDM at maturity generally increased and became more negative as weed control was delayed up to the WC5 treatment, after which skewness decreased toward zero and in some cases became positive (data not presented). For example, the progressive shift in the skewness of the CSU 2009 population began with a delay in



Figure 2. Aboveground plant biomass at maturity and harvest index of maize plants that developed under six durations of weed interference (WF = season-long weed-free; WC1 = 1-leaf-tip weed control; WC3 = 3-leaf-tip weed control; WC5 = 5-leaf-tip weed control; WC10 = 10-leaf-tip weed control; W = season-long weedy). The mean plant dry matter (M_{PDM}), mean harvest index (M_{HI}); standard deviation of plant dry matter (SD), coefficient of variation of plant dry matter (CV), skewness of plant dry matter (S), and kurtosis of plant dry matter (K) are also presented.

weed control from the WF to the WC1 treatment and a decrease in S from 0.24 to -0.25 (Figure 2). Although this brief duration of weed interference did not result in a significant yield loss, the subtle shift in the skewness of the population frequency distribution marked the beginning of a trend toward an increasing proportion of the population achieving progressively lower PDM at maturity. This trend continued in the WC3 treatment, where skewness was largest and most negative, and yield losses approached the 5% level. During the subsequent period of rapid linear yield loss, which stretched roughly from 150 to 400 GDD at CSU 2009 (Figure 1), skewness increased and became positive as the entire population progressively shifted to lower values of PDM at maturity.

Delaying Weed Control Increased Bareness. As PDM at maturity decreased, an increasing proportion of the population approached the threshold PDM where HI declines and bareness occurred (Figure 2). When individuals fall below this threshold, the decline in GY not only reflects the reduction in PDM but also the reduction in the partitioning of dry matter to the ear (i.e., HI). As a result, the inequality in reproductive

output among individuals near this threshold is not mirrored by inequality in their PDM (Vega and Sadras 2003). Previous studies of plant population density in maize have suggested that increases in the CV_{PDM} when the mean PDM is near this threshold can result in significant yield losses by increasing the frequency of bareness (Liu and Tollenaar 2009; Vega and Sadras 2003). In the current study, the threshold PDM varied among the environments and this variability was likely attributable to differences in hybrid selection and in the temperature, precipitation, and radiation across sites and years (Table 2). Based on all of the treatments from CSU 2009, the threshold PDM for HI was approximately 100 g plant (Figure 2). In this environment, and in all other environments examined in this study, the mean PDM only approached the threshold in the WC10 and W treatments. At these levels of PDM, the proportion of plants falling below the threshold contributed little to the overall yield loss when compared to the contribution of the relative reduction in PDM. Not unlike the tolerance to high plant population densities, a maize hybrid with a low PDM threshold for HI and low CV_{PDM} near this threshold will ultimately have lower yield losses from weed interference than hybrids with higher values for these parameters. However, given that most weed management practices prevent the mean PDM from ever approaching this threshold, it is unlikely that selecting a hybrid with these traits will play a significant role in reducing the yield losses from weed interference.

The results of this study demonstrate the importance of early-season weed control. When weeds emerge at or near the time of crop emergence, the onset of the CPWC consistently occurred between the third- and fifth-leaf-tip stages of development. In spite of the consistency in emergence timing and seedling density provided by our surrogate weed methodology, the level of weed biomass produced at each time of weed removal varied across environments. Although this variability appeared to influence the level of crop yield losses in later weed control timings (i.e., WC10, W), increases in weed biomass at early times of weed control (i.e., WC1, WC3, WC5) did not necessarily result in greater yield losses. This result is in agreement with the well-established principle that the timing of weed emergence often has a greater impact on crop yield losses than does weed density or biomass (Kropff and Spitters 1991; O'Donovan et al. 1985).

Plant-to-plant variability increased as the timing of weed control was delayed. At early times of weed control, increases in the CV_{PDM} were driven by an increase in the SD, often with little change in the mean PDM. As a result, yield losses leading up to the onset of the CPWC were associated with a shift in the frequency distribution of the population toward more negative skewness values, which are characterized by a pronounced tail to the left of the distribution. Following the onset of the CPWC, the linear decline phase of the logistic response curve was associated with concurrent decreases in the mean and SD of PDM and thus, little change in the CV_{PDM}. In later weed control treatments the mean PDM approached the threshold where HI declined and bareness occurred. Although increases in CV_{PDM} near this threshold can increase crop yield losses, the contribution of this effect was small compared to that of the decline in PDM at maturity.

This study has focused on the contribution of plant-toplant variability at maturity to crop-yield losses that occurred as a result of weed interference. It is evident from these results that yield losses were primarily associated with a reduction in the mean PDM and that increases in CV_{PDM} could only make a small contribution to these losses until the mean PDM approached the threshold for HI. What is not clear from these results is whether increases in plant-to-plant variability in traits associated with vegetative biomass accumulation or the timing of the transition to reproductive growth may underlie the observed decline in the mean PDM at maturity. Future studies should endeavour to examine the connections between changes in physiological and phenological development of the individuals in the crop stand during the period of weed interference and the resulting impact on grain yield and partitioning in order to produce a more complete picture of how early interspecific interference may influence subsequent intraspecific interference within a crop stand.

Acknowledgments

The authors gratefully acknowledge the funding support of Syngenta Crop Protection and the assistance of A. Dobbels, J. Bullington, and K. Chandler in conducting this experiment. The authors also acknowledge the constructive input of V. H. Gonzalez and two anonymous reviewers.

Literature Cited

- Andrade, F. H. and P. A. Abbate. 2005. Response of maize and soybean to variability in stand uniformity. Agron. J. 97:1263–1269.
- Andrade, F. H., C. Vega, S. Uhart, A. Cirilo, M. Cantarero, and O. Valentinuz. 1999. Kernel number determination in maize. Crop Sci. 39:453–459.
- Borrás, L. and B. L. Gambín. 2010. Trait dissection of maize kernel weight: toward integrating hierarchical scales using a plant growth analysis. Field Crops Res. 118:1–12.
- Borrás, L. and M. E. Westgate. 2006. Predicting maize kernel sink capacity early in development. Field Crops Res. 95:223–233.
- Borrás, L., M. E. Westgate, J. P. Astini, and L. Echarte. 2007. Coupling time to silking with plant growth rate in maize. Field Crops Res. 102:73–85.
- Campbell, G. S. and J. M. Norman. 1998. An Introduction to Environmental Biophysics. New York: Springer-Verlag. Pp. 28–34.
- Cerrudo, D., E. R. Page, M. Tollenaar, G. Stewart, and C. J. Swanton. 2012. Mechanisms of yield loss in maize caused by weed competition. Weed Sci. 60:225-232.
- Cirilo, A. G. and F. H. Andrade. 1994. Sowing date and kernel weight in maize. Crop Sci. 36:325–331.
- Cox, W. J. and J. H. Cherney. 2011. Growth and yield response of soybean to row spacing and seeding rate. Agron J. 103:123–128.
- Cox, W. J., R. R. Hahn, and P. J. Stachowski. 2006. Time of weed removal with glyphosate affects corn growth and yield components. Agron. J. 98:349–353.
- Echarte, L., S. Luque, F. H. Andrade, V. O. Sadras, A. Cirilo, M. E. Otegui, and C.R.C. Vega. 2000. Response of maize kernel number to plant density in Argentinean hybrids released between 1965 and 1993. Field Crops Res. 68:1–8.
- Echarte, L. and M. Tollenaar. 2006. Kernel set in maize hybrids and their inbred lines exposed to stress. Crop Sci. 46:870–878.
- Evans, S. P., S. V. Knezevic, J. L. Lindquist, and C. A. Shapiro. 2003a. Influence of nitrogen and duration of weed interference on corn growth and development. Weed Sci. 51:546–556.
- Evans, S. P., S. V. Knezevic, J. L. Lindquist, C. A. Shapiro, and E. E. Blankenship. 2003b. Nitrogen application influences the critical period for weed control in corn. Weed Sci. 51:408–417.
- Fasoula, V. A. and M. Tollenaar. 2005. The impact of plant population density on crop yield and response to selection in maize. Maydica 50:39-48.
- Ford, J. H. and D. R. Hicks. 1992. Corn growth and yield in uneven emerging stands. J. Prod. Agric. 5:185–188.
- Glenn, F. B. and T. B. Daynard. 1974. Effects of genotype planting pattern and planting density on plant-to-plant variability and grain yield of corn. Can. J. Plant Sci. 54:323–330.
- Gilmore, E. C. and J. S. Rodgers. 1958. Heat units as a method of measuring maturity in corn. Agron. J. 50:611–615.

Gower, S. A., M. M. Loux, J. Cardina, S. K. Harrison, P. L. Spankle, N. J. Probst, T. T. Bauman, W. Bugg, W. S. Curran, R. S. Currie, R. G. Harvey, W. G. Johnson, S. J. Kells, M.D.K. Owen, D. L. Regehr, C. H. Slack, M. Spaur, C. L. Sprague, M. VanGessel, and B. G. Young. 2003. Effect of postemergence glyphosate application timing on weed control and grain yield in glyphosate resistant corn: results of a 2-yr multistate study. Weed Tech. 17:821–828.

- Hall, M. R., C. J. Swanton, and G. W. Anderson. 1992. The critical period of weed control in grain corn (*Zea mays*). Weed Sci. 40:441-447.
- Hara, T. 1988. Dynamics of size structure in plant populations. Trends Ecol. Evol. 3:129-133.
- Knezevic, S. V., S. P. Evans, E. E. Blankenship, R. C. Van Acker, and J. L. Lindquist. 2002. Critical period for weed control: concept and data analysis. Weed Sci. 50:773–786.

Knezevic, S. V., S. F. Weise, and C. J. Swanton. 1994. Interference of redroot pigweed (Amaranthus retroflexus) in corn (Zea mays). Weed Sci. 42:568–573.

- Kropff, M. J. and C.J.T. Spitters. 1991. A simple model of crop loss by weed competition from early observations on relative leaf area of the weed. Weed Res. 31:97–105.
- Lee, E. A. and M. Tollenaar. 2007. Physiological basis of successful breeding strategies for maize grain yield. Crop Sci. 47(S3):S202–S215.
- Liu, W. and M. Tollenaar. 2009. Response of yield to increasing plant density in maize. 2009. Crop Sci. 49:1807–1816.
- Liu, W., M. Tollenaar, G. Stewart, and W. Deen. 2004. Response of corn grain yield to spatial and temporal variability in emergence. Crop Sci. 44:847–854.
- Maddonni, G. A. and Otegui, M. E. 2004. Intra-specific competition in maize: early establishment of hierarchies among plants affects final kernel set. Field Crops Res. 85:1–13.
- Norsworthy, J. K. and M. J. Oliveira. 2004. Comparison of the critical period for weed control in wide- and narrow-row corn. Weed Sci. 52:802–807.
- O'Donovan, J. T., A. E. De St Remy, P. A. O'Sullivan, D. A. Dew, and A. K. Sharma. 1985. Influence of relative time of emergence of wild oat (*Avena fatua*) on yield loss in barley (*Hordeum vulgare*) and wheat (*Triticum aestivum*). Weed Sci. 33:498–503.
- Otegui, M. E., M. G. Nicolini, R. A. Ruiz, and P. A. Dodds. 1995. Sowing date effects on grain yield components for different maize genotypes. Agron. J. 87:29–33.
- Pagano, E. and G. A. Maddoni. 2007. Intra-specific competition in maize: early establishment hierarchies differ in plant growth and biomass partitioning to the ear around silking. Field Crops Res. 101:306–320.
- Page, E. R., D. Cerrudo, W. Liu, E. A. Lee, and C. J. Swanton. 2011. Shade avoidance influences stress tolerance in maize. Weed Sci. 59:326–334.
- Page, E. R., M. Tollenaar, E. A. Lee, L. Lukens, and C. J. Swanton. 2010. Shade avoidance: an integral component of crop-weed competition. Weed Res. 50:281–288.
- Pendleton, J. W. and R. D. Seif. 1962. Role of height in corn competition. Crop Sci. 2:154–156.

- Rajcan, I. R. and C. J. Swanton. 2001. Understanding maize-weed competition: resource competition, light quality and the whole-plant. Field Crops Res. 71:139–150.
- Saxton, A. M. 1998. A macro for converting mean separation output to letter groupings in Proc Mixed. Pages 1243–1246 in Proceedings of the 23rd SAS Users Group International, SAS Institute, Cary, NC.
- Subedi, K. D. and B. L. Ma. 2009. Assessment of some major yield-limiting factors on maize production in a humid temperate environment. Field Crops Res. 110:21–26.
- Swanton, C. J., K. J. Mahoney, K. Chandler, and R. H. Gulden. 2008. Integrated weed management: knowledge based weed management systems. Weed Sci. 56:168–172.
- Swanton, C. J., S. Weaver, P. Cowan, R. Van Acker, W. Deen, and A. Shresthta. 1999. Weed thresholds: theory and applicability. J. Crop. Prod. 2:9–29.
- 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.
- Tollenaar, M. and T. B. Daynard. 1978. Kernel growth and development at two positions on the ear of maize (*Zea mays*). Can. J. Plant Sci. 58:189–197.
- Tollenaar, M., T. B. Daynard, and R. B. Hume. 1979. Effect of temperature on rate of leaf appearance and flowering date in maize. Crop Sci. 19:363–366.
- Tollenaar, M., L. M. Dwyer, and D. W. Stewart. 1992. Ear and kernel formation in maize hybrids representing three decades of grain yield improvement in Ontario Crop Sci. 33:432–438.
- Tollenaar, M. and E. A. Lee. 2006. Dissection of physiological processes underlying grain yield in maize by examining genetic improvement and heterosis. Maydica 51:399–408.
- Tollenaar, M. and J. Wu. 1999. Yield improvement in temperate maize is attributable to greater stress tolerance. Crop Sci. 39:1597–1604.
- Van Acker, R. C., C. J. Swanton, and S. F. Weise. 1993. The critical period for weed control in soybean [*Glycine max* (L.) Merr.]. Weed Sci. 41:194–200.
- Vega, C. R. and V. O. Sadras. 2003. Size-dependent growth and the development of inequality in maize, sunflower and soybean. Ann. Bot. (Lond.) 91:795– 805.
- Vega, C.R.C., V. O. Sadras, F. H. Andrade, and S. A. Uhart. 2000. Reproductive allometry in soybean, maize and sunflower. Ann. Bot. (Lond.) 85:461–468.

Zar, J. H. 1996. Biostatistical Analysis. 3rd ed. Upper Saddle River, NJ: Prentice-Hall. 417 p.

Received November 4, 2011, and approved March 19, 2012.