Weed Science 2014 62:326–337

Delaying Weed Control Lengthens the Anthesis-Silking Interval in Maize

Andrew Reid, Victor Gonzalez, Peter H. Sikkema, Elizabeth A. Lee, Lewis Lukens, and
Clarence J. Swanton*

Stress caused by early weed competition is known to delay the rate of maize development which may result in a decrease in kernel number. Kernel number in maize is correlated negatively with the length of the anthesis-silking interval (ASI). A short ASI has been identified as an easily measured, visual trait which may identify enhanced drought tolerance in maize. Field studies were conducted to test whether: (1) delaying weed control would result in a lengthening of ASI in both a drought tolerant and non-drought tolerant maize hybrid and (2) the presence of drought tolerance genetics comes at a physiological cost, resulting in a greater yield reduction under weedy conditions. In this study, the response of a drought tolerant hybrid with its non-drought tolerant near-isoline was compared to seven different timings of weed control using wheat as a surrogate competitor. Results confirmed that there was no treatment by hybrid interaction at any site–yr for any of the parameters evaluated. Delaying weed control reduced plant height, leaf tip number, shifted and reduced biomass accumulation, kernel number and grain yield and lengthened ASI for both hybrids. Although yield losses occurred with the delay in weed control timing, no yield differences were observed between hybrids suggesting that there was no additional physiological cost associated with the drought tolerant traits. The drought tolerant hybrid, however, was found to have a shorter ASI, lower kernel number and higher kernel wt compared to the non-drought tolerant hybrid. This study confirmed that delaying weed control can influence the length of ASI, which is an important drought tolerant trait. The lengthening of ASI by early weed competition resulted in a rate of yield loss of 0.13 T ha^{-1} growing degree days (GDD)$^{-1}$ when averaged across both hybrids and all treatments.

Nomenclature: Maize, *Zea mays* L.

Key words: Corn, drought tolerance, kernel number, kernel wt, reproductive development, yield loss.

Timing of weed control is a critical management decision in protecting yield potential in maize. It is well established that early emerging weeds relative to crop emergence are the most competitive (Hall et al. 1992; Kropff and Spitters 1991; Page et al. 2012; Swanton et al. 2008). When weeds emerged with maize, a 2% yield reduction was observed when weed control was delayed until the third-leaf stage of maize development (Hall et al. 1992). Page et al. (2012) reported a 5% yield loss in maize when the control of early emerging weeds was delayed until the third to fifth-leaf tip stage (V1 to V3). When seedlings of redroot pigweed (*Amaranthus retroflexus* L.) were allowed to emerge with maize and not controlled throughout the season, Knezevic et al. (1994) observed a 5% yield loss at a density as low as 0.5 redroot pigweed seedling m^{-1} of crop row. Similarly, Bosnić and Swanton (1997) reported a maximum yield loss in maize ranged from 26 to 35% for early emerging barnyard grass [*Echinochloa crus-galli* (L.) Beauv.] and less than 6% yield loss when barnyardgrass seedlings emerged later than the four-leaf stage of maize growth. Recently, Fickett et al. (2013) observed that if weed control was delayed until weeds were 5 to 10 cm tall (approximately the 4-leaf stage of maize) a yield reduction of 4.5% was predicted to have already occurred.

Several mechanisms by which this yield loss occurs in response to weed interference have been reported. These mechanisms include a decrease in root volume and biomass, above ground dry matter accumulation, harvest index, kernel number plant^{-1} and kernel wt (Afifi and Swanton 2011; Cerrudo et al. 2012; Page et al. 2012). Page et al. (2012) observed as weed control was delayed, yield loss in maize occurred as a result of a reduction in kernels plant^{-1} and kernel wt. Cerrudo et al. (2012) suggested that this reduction in kernels plant^{-1} and kernel wt was caused by a decrease in total dry matter and the inability of the plant to accumulate dry matter during the maturation process. A recent study by Afifi and Swanton (2012) reported that the presence of neighboring weeds could alter several

---

DOI: 10.1614/WS-D-13-00099.1

* First, second, fourth, fifth and sixth authors: Department of Plant Agriculture, University of Guelph, 50 Stone Road E., Guelph, ON, N1G 2W, Canada; third author: Department of Plant Agriculture, Ridgetown Campus, Ridgetown, Ontario N0P 2C0. Corresponding author's E-mail: cswanton@uoguelph.ca

important physiological pathways within the maize seedling, which included the synthesis of lignin, anthocyanins, and ethylene and the alteration of auxin transport genes. They suggested that these changes may result in a physiological cost that would contribute to the yield loss observed under field conditions. The modulation of these physiological pathways would suggest that molecular changes have occurred, thereby, altering the genetic expression of maize (see also Moriles et al. 2012).

One of the most recent genetic improvements in maize has been the introduction of drought tolerant hybrids. Drought is the single largest cause of yield reduction worldwide in agricultural production (Ribaut et al. 2009). By introducing maize hybrids that are more tolerant to water stress, it may be possible to reduce risk with regards to water availability, increase yield stability and thereby stabilize worldwide maize production (Campos et al. 2004). General mechanisms of drought tolerance have been identified; a few examples include rapid seedling establishment, greater density and depth penetration of roots, improved root conductance and osmoregulation (Bruce et al. 2002; McCully 1999; Parry et al. 2005; Passioura 1996). For a more thorough review of drought tolerance, see Campos et al. (2004) and Araus et al. (2012). Specifically for maize, improved drought tolerance has been associated with such traits as ears plant^{-1}, decreased tassel branching, anthesis-silking interval (ASI; the length of time between pollen shed and receptive silk emergence), kernel number, and kernel wt (Bolaños and Edmeades 1996; Edmeades et al. 1993,1999). These traits are easy to measure and select for, and have been identified in maize to be correlated highly with grain yield in plants grown in water stressed conditions (Bolaños and Edmeades 1996).

The primary determinants of grain yield in maize are kernel number plant^{-1} and kernel wt (Tollenaar and Lee 2006). Bolaños and Edmeades (1996) observed that under water stressed conditions, loss of grain yield could be attributed to a decrease in both kernels plant^{-1} and kernel wt. In addition, the length of ASI was observed to be associated negatively with kernel number plant^{-1} (r^2 = 0.74) (Bolaños and Edmeades 1993). They suggested that the observed yield reduction in grain yield was almost mediated entirely by the decrease in kernel number as ASI lengthened from −0.4 to 10 d as a result of water stress. Stress caused by high plant density and low nitrogen was observed by Monneveux et al. (2005) to cause a lengthening of ASI. Lafitte and Edmeades (1994) found that length of ASI and grain yield had a negative correlation of −0.55 under low nitrogen conditions. Similarly, Buren et al. (1974) observed a lengthening of ASI with increasing maize density and a correlation of −0.92 between ASI and grain yield. In addition, Tollenaar et al. (1997) found weed pressure which occurred after the three- to four -leaf tip stage of corn development resulted in a delay of 2.5 d in silking and a 28% yield reduction. Thus, evidence to date suggests that as ASI is lengthened by abiotic or biotic stresses, the risk of kernel reduction and subsequent yield loss increases in maize.

In this study, we explore the interaction of ASI and stress created by early emerging weeds. To accomplish this, we obtained an Agrisure® Artesian® maize hybrid from Syngenta Crop Protection, Inc. (USA). One hybrid contained drought tolerance genetics and the other was a near-isogenic conventional non-drought tolerant hybrid, reported to be 95% homologous with the drought tolerant hybrid. These two hybrids differed primarily in the presence or absence of genes conferring drought tolerance. We hypothesized that delaying weed control would cause ASI to lengthen in both the drought tolerant and non-drought tolerant maize hybrid. If ASI was observed to lengthen, particularly in the drought tolerant hybrid, this would suggest that a critical mechanism for drought tolerance had been compromised. We also hypothesized that stress caused by the presence of early emerging weeds would reduce yield to a greater extent in the drought tolerant maize hybrid. This hypothesis was predicated on the fact that under non-drought conditions, the genes conferring drought tolerance would not be advantageous for maize growth and yield. As a result, these genetics would be carried within the drought tolerant maize hybrid at a physiological cost resulting in a greater yield reduction when grown under weedy conditions.

Materials and Methods

Field experiments were conducted in 2011 and 2012. In 2011, the experiment was located at the Ridgetown campus of the University of Guelph (42°26′26″N 81°53′3″W); in 2012, experiments were located at Ridgetown and at the Woodstock Research Station University of Guelph (43°8′45″N 80°47′2″W). The soil at Ridgetown was a loam soil, containing 40% sand, 35% silt, 25% clay and 7.1% organic matter. The soil at Woodstock was a silt loam, containing 40% sand, 43% silt, 17% clay and

Table 1. Number of days, daily average temperature, growing degree day accumulation (GDD) and precipitation which occurred during the selected maize development periods at Ridgetown in 2011 and 2012 and Woodstock in 2012.

	No. of days				Temperature				Accumulation of GDD				Precipitation		
Period of maize development	R11[a]	R12	W12	Avg	R11	R12	W12	Avg	R11	R12	W12	Avg.	R11	R12	W12
					°C				GDD				mm		
Planting to the 10th leaf tip	27	34	43	17	19	18	16	305	257	295	314	77	74	117	155
10th leaf tip to tassel emergence	27	24	27	21	23	23	23	319	352	297	325	82	37	55	42
Tassel emergence to 2 wk post silking	21	21	47	22	22	22	21	205	249	219	528	93	77	168	142
2 wk post-silking to maturity	71	84	51	15	15	16	14	519	424	580	299	193	219	187	120

[a] Abbreviations: R11 refers to Ridgetown 2011; R12 refers to Ridgetown 2012; W12 refers Woodstock 2012; Avg refers to 15-yr average monthly rainfall recorded by Environment Canada at Ridgetown.

4.8% organic matter. Growing degree days were calculated following Campbell and Norman (1998) using daily minimum and maximum air temperatures recorded at each location. Number of days, daily average temperature, GDD, and precipitation which occurred during the selected maize development periods at Ridgetown in 2011 and 2012 and Woodstock in 2012 is reported in Table 1. Growing degree day accumulation began on the day of seeding at each location using a base temperature of 10 C (Tollenaar et al. 1979).

Prior to seeding at Ridgetown, the plot area was moldboard plowed in the fall, followed by two passes with an S-tine cultivator with rolling basket harrows in the spring. At Woodstock, the plot area was cultivated twice with a tine cultivator with rolling basket harrows in the spring. Depending on current weather conditions, winter wheat was seeded 24 to 72 h prior to the seeding of maize. The winter wheat was seeded at a density of 150 seeds m^{-2} in rows (spacing 0.18 m) perpendicular to the maize rows in order to act as a surrogate weedy competitor. This was done in order to ensure consistent competitive pressure across all site–yr.

Two glyphosate resistant Syngenta maize hybrids (X58945WP and SK5069WP) were selected for study. One hybrid (X58945WP) was a non-drought tolerant line, whereas the second (SK5069WP) hybrid was classified as an Agrisure® Artesian® hybrid containing genes conferring drought tolerance. These two hybrids were considered as near-isogenic lines, differing only in the presence or absence of the drought tolerance genetics (i.e. 95% genetic similarity; personal communication, Syngenta Canada, 2011). The drought tolerance traits were selected for by screening for several QTLs known to be associated with water use efficiency. The non-drought tolerant isoline was derived from backcrossing with the parent until a genetically similar line was developed that did not have the drought tolerant genes present. As these hybrids were very similar, this allowed for the effects of the genes of interest (i.e. the drought tolerance genetics) and the influence they may have upon whole plant physiology under different weed control timings to be studied. Hereafter, these two hybrids will be referred to as non-drought tolerant and drought tolerant, respectively.

These hybrids were planted on June 2, 2011 in Ridgetown and on May 1 (Woodstock) and May 15 (Ridgetown), 2012 resulting in established maize populations of approximately 80,000 plants ha^{-1} at Ridgetown and 73,000 plants ha^{-1} at Woodstock. All trials were conducted under nonirrigated, rain-fed systems. Each plot consisted of four rows of maize (spacing 0.76 m) 8m long in Ridgetown, 9.25m long in Woodstock. Within each plot, the exterior two rows served as border rows and only the center two rows were used for measurements and analyses.

The experiment was a split-plot design arranged in a randomized complete block with four replications. The two maize hybrids were the sub-plot factor, and time of weed control was the whole-plot factor, and consisted of seven treatments: (1) full season weed free (WF), (2) weed control at the one leaf tip stage (WR1 or VE), 3) weed control at the three leaf tip stage (WR3 or V1), (4) weed control at the five leaf tip stage (WR5 or V3), (5) weed control at the seven leaf tip stage (WR7 or V5), (6) weed control at the 10 leaf tip stage (WR10 or V7 to V8), and (7) full season weedy (WD). Developmental stages were based on number of visible leaf tips $plant^{-1}$, including the tip of the youngest leaf emerging from the whorl. A split-plot design was utilized to have greater precision and power for statistical analysis to quantify any difference between the non-drought and drought tolerant hybrids. To ensure even competition across treatments, bromoxynil was sprayed at 0.38 kg ai ha^{-1} to control broadleaf weeds and leave grassy weeds to compete. Weed control was achieved with glyphosate applied at 0.9 kg ae ha^{-1} at the specified timings. In the WF treatment, glyphosate was applied prior to the emergence of maize seedlings. Once glyphosate was applied at the specified growth stage of maize, plots were maintained weed-free for the remainder of the season by manually controlling newly emerged weeds or by applying glyphosate when necessary in order to ensure weed-free conditions.

Shortly after maize seedling emergence, 10 consecutive plants within each of the two center rows (20 plants plot^{-1} treatment^{-1}, $n = 80$) were selected and marked in each plot in both 2011 and 2012. A one meter border was left to separate these seedlings from the front and back edges of the plot. Leaf tip number and seedling height, measured to the highest visible leaf collar were recorded until tassel emergence was observed in the WF treatment in 2011. In 2012, leaf tip number and heights were recorded twice weekly until the 10 leaf tip stage of crop growth in the WF treatment. After this stage of crop development, measurements were recorded once weekly until tassel emergence was observed in the WF treatment. The dates of tasseling (defined as tassel emergence from the whorl), anthesis (the release of pollen from the tassel) and silking (emergence of silk) were recorded daily for each of the selected plants. Anthesis-silking interval was calculated for individual plants using the following formula (see Bolaños and Edmeades 1996):

$$\mathrm{ASI} = \text{date of silking} - \text{date of anthesis} \qquad [1]$$

At physiological crop maturity (i.e., appearance of black layer within the seed), all remaining aboveground biomass of each selected plant was harvested and separated into ears and stover (i.e., stems and leaves). Each plant component was bagged separately and then dried at 60°C to a constant wt. Kernel number, kernel wt and grain yield plant were determined. Harvest index for individual plants was calculated as follows:

$$\mathrm{HI}(\%) = (\text{total grain yield}/\text{total plant dry matter at maturity}) \times 100 \qquad [2]$$

The remaining plants within the center two rows were machine harvested using a small plot combine. This harvested seed yield was then added to the yield of the 20 selected plants plot^{-1} that were harvested previously, in order to obtain yield. Total maize yield treatment^{-1} was calculated at 15.5% moisture.

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 individual maize plants harvested plot^{-1} ($n = 80$) for all parameters measured. Time of weed control and hybrid were treated as fixed effects in the ANOVA. Replicate within environment, environment, weed control timing by environment and weed control timing by hybrid by environment were treated as random effects. Leaf tip number and plant height were analyzed as repeated measures. Because of differences in environments during the early part of the growing seasons, all site–yr were analyzed separately for height and leaf tip numbers. Treatment effects on ASI, grain yield, kernel number plant^{-1}, kernel wt, plant dry matter, and harvest index were analyzed using a two-way ANOVA with the same fixed and random effects as described above, and pooled across all site–yr for analysis. Log transformations were performed on height in all 3 site–yr, leaf number for Ridgetown in 2012, as well as ASI and harvest index to meet the assumptions of normality required for analysis. For the ASI-grain yield loss model, coefficients were fitted through the iterative process equation using PROC NLIN SAS (SAS Institute, Cary, NC). A Student's *t*-test was used to contrast the difference between the WF and timing of weed control treatments (WR1 through WD) for calculated means of ASI.

Population distribution comparisons between hybrids were conducted under all different weed control timings using a Kolmogorov-Smirnov Two-Sample Test. Analysis of frequency distributions was used for plant dry matter (PDM) (Edmeades and Daynard 1979). Coefficient of variation (CV %) was used as a measure of variability of individuals (e.g., Edmeades and Daynard 1979; Glenn and Daynard 1974; Vega et al. 2001). The CV is calculated as the percentage of the standard deviation (SD) over the mean of the population. Asymmetric competition for aboveground resources among plant categories (e.g. smaller ones vs. larger ones) was studied using skewness (S) and kurtosis (K) coefficients to analyze changes relative to the population mean of a normal distribution (e.g. Weiner 1990). Skewness is a measure of departure from normality for a population distribution (See Equation 3). A negative S value indicates that the population is left of center of an expected normal population (i.e., J shaped distribution) and a positive value the opposite. Kurtosis measures

Table 2. Maize height (cm) measured to the highest visible leaf collar and leaf tip number averaged for both non-drought tolerant and drought tolerant maize hybrids under seven weed control timings, recorded prior to tasseling at Ridgetown in 2011 and 2012, and Woodstock in 2012.

	Ridgetown 2011		Ridgetown 2012		Woodstock 2012	
	Height	Leaf tip no.	Height	Leaf tip no.	Height	Leaf tip no.
	cm		cm		cm	
Timing	**	**	**	**	**	**
WF[a]	117 ab*	16 ab	98 a	16 a	132 a	16 a
WR1	132 a	16 a	96 a	16 a	131 a	16 a
WR3	122 a	16 ab	100 a	16 a	123 a	16 a
WR5	110 ab	16 ab	90 a	16 a	83 b	15 b
WR7	111 ab	16 ab	58 b	15 b	43 c	14 c
WR10	77 bc	13 bc	33 c	13 c	23 d	12 d
WD	67 c	13 c	24 d	11 d	20 d	9 e
Hybrid	NS	NS	**	NS	NS	NS
DT	105	16	64 a	15	62	14
NDT	100	16	60 b	15	62	14
Interactions						
T X H	NS	NS	NS	NS	NS	NS

[a] Abbreviations: WF, full season weed free; WD, full season weedy; WR1-WR10, weed removal at 1 leaf tip through 10 leaf tips of maize development; NDT, non-drought tolerant maize hybrid (X58945WP); DT, drought tolerant maize hybrid (SK5069WP); T, timing of weed control; H, hybrid.

** Significant at $P < 0.05$; NS, not significant at $P < 0.05$.

* Means followed by the same letter within a column do not differ significantly ($P < 0.05$).

peakness of the frequency distribution (See Equation 4). A negative K indicates that the peak is lower than expected for a normal population. The S and K coefficients are considered herein as symmetry parameters in each hybrid for PDM.

$$\text{(Skewness) } S = \sum\nolimits_i (Xi\text{-}X)^3 / nS^3 \qquad [3]$$

$$\text{(Kurtosis) } K = \sum\nolimits_i (Xi\text{-}X)^4 / nS^4 - 3 \qquad [4]$$

The numerators are the sum of the deviation from the mean (X) plant dry matter value and the denominators are the product of the number of samples (plants) and the variance of the mean PDM.

Results and Discussion

Delaying Weed Control Reduced Maize Height and Leaf Tip Number. Delaying weed control reduced height and leaf tip number (Table 2). There was no significant treatment by hybrid interaction at any site–yr for height or leaf tip number, indicating that both hybrids responded similarly to each delay in the timing of weed control. For example, in 2011 at Ridgetown, plant height was reduced from 117 cm in the weed free to 67 cm in the full season weedy treatment (Table 2). The decrease in maize height was more pronounced at both Ridgetown and Woodstock in 2012. At Ridgetown in 2012, the drought tolerant hybrid was taller than the non-drought tolerant hybrid (Table 2). The average leaf tip number plant^{-1} also decreased from 16 to 13 leaf tips at Ridgetown in 2011. This decrease in leaf tip number was greater in 2012 for both Ridgetown and Woodstock. The loss in plant height and leaf number as weed control was delayed has also been reported in previous studies (Cerrudo et al. 2012; Liu et al. 2009; Page et al. 2009). This reduction in height and leaf number in maize under late weed control timings was attributed to direct weed competition for limiting resources.

Delaying Weed Control Lengthened ASI for both Maize Hybrids. There was no significant treatment by hybrid interaction for ASI, indicating that both hybrids responded similarly to each delay in the timing of weed control (Table 3). Delaying weed control until the 10 leaf tip stage lengthened the ASI for both the non-drought tolerant and drought tolerant maize hybrids. When weeds were allowed to compete up to the 10th leaf tip (i.e., V7 to V8) an increase in ASI of 0.9 d (1.8 d to 0.9 d) was observed when compared to the season long weed free treatment. The ASI was lengthened by 3.8 d in the full season weedy treatment compared to the weed free treatment.

There was a difference in ASI between hybrids pooled across all weed control timings. The non-drought tolerant maize hybrid had a longer ASI

Table 3. Anthesis-silking interval (ASI) averaged for both a non-drought tolerant and drought tolerant maize hybrids. ASI was measured on a daily basis on 80 individual plants plot^{-1} yr^{-1} and pooled across 3 site–yr (n = 240). P-values for preplanned contrasts (*t*-test) are also presented.

	ASI	Preplanned	
	days	Contrasts	P-value
Timing	**		
WF[a]	0.9 *c*	WF vs. WR1	0.7027
WR1	0.9 *c*	WF vs. WR3	0.7743
WR3	0.8 *c*	WF vs. WR5	0.3601
WR5	1.1 *c*	WF vs. WR7	0.148
WR7	1.2 *c*	WF vs. WR10	0.0061
WR10	1.8 *b*	WF vs. WD	$<$0.0001
WD	4.7 *a*		
Hybrid	**		
DT	1.5 *b*	DT vs. NDT	0.0004
NDT	1.8 *a*		
Interactions			
T X H	NS		

[a] Abbreviations: WF, full season weed free; WD, full season weedy; WR1-WR10, weed removal at 1 through 10 leaf tips of maize development; NDT, non-drought tolerant maize hybrid (X58945WP); DT, drought tolerant maize hybrid (SK5069WP); T, timing of weed control; H, hybrid.

** Significant at $P < 0.05$; NS, not significant at $P<0.05$.

* Means followed by the same letter do not differ significantly ($P < 0.05$).

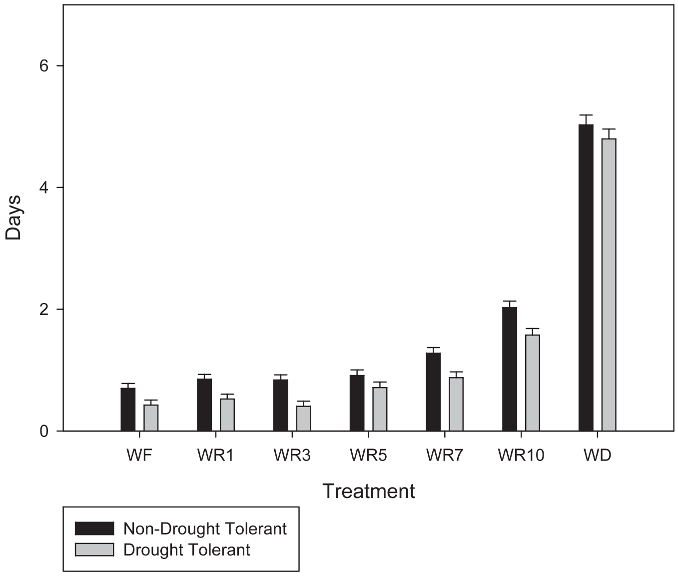

Figure 1. Anthesis-silking interval (ASI) expressed in days at Ridgetown in 2012 for a non-drought tolerant (X58945WP) and a drought tolerant (SK5069WP) maize hybrids. For each hybrid, ASI was measured on a daily basis. The calculations of average ASI (± SE) were based on 80 individual plants treatment^{-1}.

than the drought tolerant maize hybrid of 0.3 d (Table 3). To further illustrate this point, at Ridgetown in 2012, ASI was observed to increase as weed control was delayed from 0.7 in the weed free to 5.0 d in the full season weedy, and 0.4 in the weed free to 4.8 d in the full season weedy treatment for the non-drought and drought tolerant hybrids, respectively (see Figure 1). Similar results were observed at Ridgetown in 2011 and Woodstock in 2012 (data not shown). The shorter ASI observed in the drought tolerant hybrid may be indicative of the selection for improved ear biomass partitioning under water stress by using ASI as a selection tool, as reported by Bolaños and Edmeades (1993).

Influence of Weed Control Timing on Yield Components of Maize. There was no significant treatment by hybrid interaction for plant dry matter (PDM), harvest index, kernel number, kernel wt, grain yield plant^{-1} or grain yield ha^{-1} (Table 4). For example, a difference in PDM was observed only under the full season weedy treatment. Plant dry matter declined from 272 in the weed free to 102 g plant^{-1} in the full season weedy treatment. No differences were detected between hybrids. As weed control was delayed, however, plant-to-plant variability increased as measured by the coefficient of variation in plant dry matter (CV_{PDM}). CV_{PDM} has been reported to be a useful parameter to indicate plant-to-plant variability among treatments when their means differ (Edmeades 1976). For example, CV_{PDM} increased from 22 in the weed free to 80% in the full season weedy treatment, but no differences between hybrids was observed. An increase in CV_{PDM} is an indicator that impending weed competition is causing the maize population to shift plant dry matter distribution, and could be a sign of future grain yield loss (Page et al. 2012).

Kernel wt remained constant across weed control timings despite a decline in kernel number and grain yield plant^{-1} for both hybrids. Kernel wt ranged from 0.301 to 0.289 g kernel^{-1} despite a loss in kernel number from 497 in the weed free to 211 in the full season weedy treatment (Table 4). In previous studies, it has also been observed that kernel number is more sensitive to weed interference than kernel wt (Cox et al. 2006; Evans et al. 2003; Page et al. 2012). Differences were, however, detected between the hybrids in terms of kernel number and kernel wt. The drought and non-drought tolerant hybrid had an average kernel number of 421 and 466 kernels plant^{-1}, respectively. In contrast, the drought and non-drought

Table 4. Main effects and interactions for yield components averaged for both non-drought tolerant and drought tolerant maize hybrids resulting from seven weed control timings and pooled across 3 site–yr PDM, KW and GY plant^{-1} are reported as dry wt; GY (T ha^{-1}) is reported at 15.5% moisture.

	PDM[a]	CV_{PDM}	HI	KN	KW	GY	
	g plant^{-1}	%	%	kernels plant^{-1}	g kernel^{-1}	g plant^{-1}	T ha^{-1}
Timing	**	—	NS	**	NS	**	**
WF	272 *a**	22	54	497 *a*	0.301	156 *a*	15.9 *a*
WR1	268 *a*	19	56	501 *a*	0.305	153 *a*	15.0 *a*
WR3	265 *a*	21	56	499 *a*	0.302	152 *a*	15.2 *a*
WR5	251 *a*	25	57	487 *a*	0.299	145 *a*	14.8 *a*
WR7	227 *a*	25	59	458 *a*	0.294	136 *a*	13.9 *a*
WR10	181 *ab*	31	62	383 *ab*	0.293	112 *ab*	11.7 *ab*
WD	102 *b*	80	22	211 *b*	0.289	59 *b*	6.7 *b*
Hybrid	NS	—	NS	**	**	NS	NS
DT	223	38	50	421 *b*	0.306 *a*	131	13.4
NDT	224	38	50	446 *a*	0.291 *b*	130	13.2
Interactions							
T X H	NS	—	NS	NS	NS	NS	NS

[a] Abbreviations: PDM, plant dry matter; HI, harvest index; CV_{PDM}, coefficient of variation of plant dry matter; KN, kernel number; KW, kernel wt; GY, grain yield; WF, full season weed free; WR1-WR10, weed removal at 1 leaf tip through 10 leaf tips; WD, full season weedy; NDT, non-drought tolerant maize hybrid (X58945WP); DT, drought tolerant maize hybrid (SK5069WP); T, timing of weed control; H, hybrid.

** Significant at $P < 0.05$; NS, not significant at $P < 0.05$.

* Means followed by the same letter do not differ significantly ($P < 0.05$).

tolerant hybrid had a kernel wt of 0.306 and 0.291 g kernel^{-1}, respectively. The difference in kernel number observed between the hybrids in this study was compensated for by the difference in kernel wt, thus negating any differences in grain yield between the hybrids.

Delaying Weed Control Shifted Plant Dry Matter Distribution from High to Low, and Increased Barrenness for both Maize Hybrids. As weed control was delayed, there was a shift in PDM distribution to a higher frequency of smaller plants with fewer kernel numbers. This shift in distribution of PDM was also accompanied by a change in kurtosis, which is the measure of the width of the peak of the frequency distribution, and skewness, which is the measure of symmetry of a population compared to a normal distribution (Figure 2). These measurements can be used as indicators of change in population dynamics (Page et al. 2012; Weiner 1990). This shift in PDM caused by a delay in weed control resulted in a decrease in kurtosis. The reference value for K in a normally distributed population is 3; the degree of spread in PDM will be a function of the departure from this value. For example, a reduction from 1.86 in the full season weed free to −1.21 in the full season weedy treatments was observed. An increase in skewness was also observed, ranging from −0.92 in the weed free to 0.25 in the full season weedy treatment. These changes in population dynamics are indicative of the bulk of the population shifting towards lower PDM accumulation, resulting in increased barrenness (i.e. 32% barren plants in the full season weedy treatment) as weed control was delayed.

This study was undertaken to address two hypotheses: (1) delaying weed control will lengthen the ASI for both a non-drought tolerant and drought tolerant maize hybrid; and (2) the drought tolerance genes contained within the maize hybrid will come at a physiological cost, resulting in a greater yield reduction under weed competition. The first hypothesis was supported, as delayed weed control did lengthen ASI for both maize hybrids. The second hypothesis was not supported by the data collected.

A shorter ASI is correlated highly with the expression of drought tolerance in maize (Araus 2012; Bolaños and Edmeades 1993, 1996), and has been identified as a crucial trait in the selection for drought tolerance (Duvick 1996). ASI is a heritable trait, easy to select for, and correlated highly to grain yield under water stress conditions (Araus et al. 2012; Bolaños and Edmeades 1993; Edmeades et al. 1999; Ribaut et al. 2009). Bolaños and Edmeades (1993) found that as ASI increased from −0.4 to 10 d because of water stress, there was a corresponding decrease in grain yield of 90%

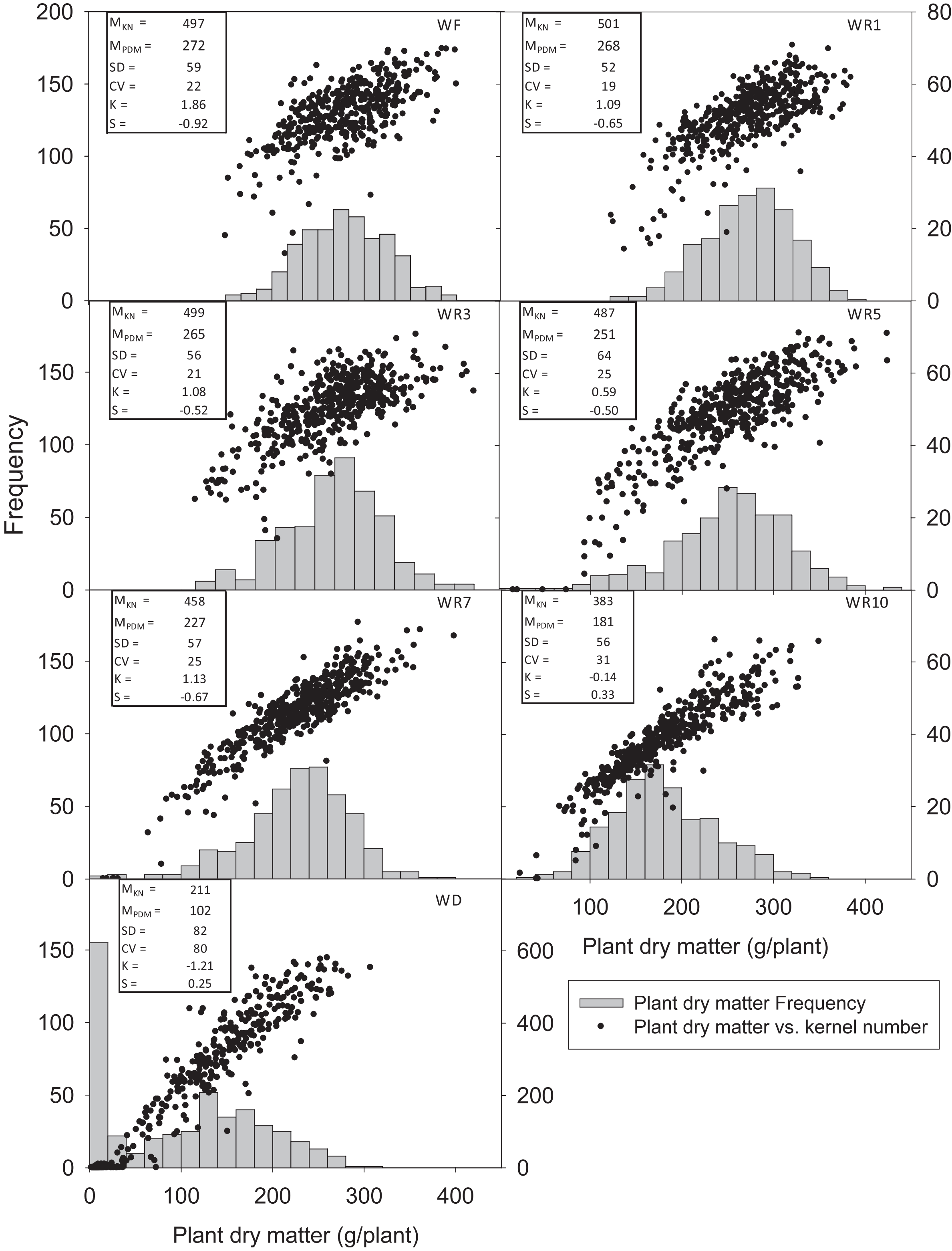

Figure 2. Aboveground plant dry matter at physiological maturity and kernel number under seven weed control timings (WF, season long weed free; WR1-WR10, weed removal at 1 through 10 leaf tips; WD, full season weedy) averaged for both drought tolerant and non-drought tolerant maize hybrids, combined across 3 site–yr. Grey bars indicate frequency distribution of plant dry matter *n* = 480). Mean kernel number (M_{KN}), mean plant dry matter (M_{PDM}), standard deviation of plant dry matter (SD), coefficient of variation of plant dry matter (CV), kurtosis of plant dry matter (K) and skewness of plant dry matter (S) are also presented.

Table 5. Regression analyses of potential yield loss based on equations published from three separate studies conducted by Bolaños and Edmeades (1996) ($n = 50$) and Bruce et al. (2002) ($n = 12$), and Reid et al. (2013) ($n = 156$) with lengthening of the anthesis-silking interval (ASI). ASI values used in each equation were obtained from this study. GDD were calculated using daily average GDD accumulated during each ASI at all 3 site–yr for the Bruce et al, and Reid et al. equations.

				Estimated Yield Loss (%)			
				ASI			
				0.3 days	0.6 days	0.9 days	
Reference	Genotype	Stress	Equation	3.5 GDD	6.9 GDD	10.4 GDD	R^2
Bolaños and Edmeades (1996)	Tropical maize hybrids	Midseason drought	$GY = e^{(2.45 - 1.16 \sqrt{(ASI + 1)})}$	15	26	36	0.70
Bruce et al. (2002)	Elite temperate maize hybrids	Midseason drought	$GY = -0.6189 + 7.906e^{(-0.01338[ASI])}$	5	10	14	0.65
Reid et al. (2013)	Ontario temperate hybrids	Weed competition	$GY = 17.67e^{-0.019(ASI)}$	6	12	18	0.98

compared to the well watered control treatment. To further illustrate this point, Bolaños and Edmeades (1996) reported that an increase in ASI of 2 d resulted in a yield loss of 2.1 T ha^{-1} (57% yield loss), for a selection of tropical maize hybrids grown under highly water stressed conditions. Similarly, Bruce et al. (2002) observed with elite temperate maize hybrids that a lengthening of ASI by 23 GDD (corresponding to approximately 2 d) resulted in a yield loss of 2.1 T ha^{-1} (29% yield loss). Using these same formulas, we estimated potential yield loss using ASI values obtained from our own study (Table 5). A lengthening of ASI by 0.3 (difference between drought tolerant and non-drought tolerant $P < 0.05$, Table 3), 0.6 (intermediate value) and 0.9 d (difference between WF and WR10, $P < 0.05$, Table 3) or 3.5, 6.9 and 10.4 GDD, respectively, resulted in an estimated yield loss ranging from 5 to 36%. These results suggested that yield was very sensitive to any increase in the length of ASI. Our model equation predicted a decrease from 6 to 18% in grain yield using a delay in ASI of 0.3 to 0.9 d. Our estimated yield loss values compared favorably to those predicted using the model proposed by Bruce et al. (2002) (see Table 5). Based on data from this study, the lengthening of ASI by early weed competition resulted in an estimated rate of yield loss of 0.13 T ha^{-1} GDD^{-1}.

This increase in the length of ASI has been attributed to a delay in ear development, silk growth and subsequent silk extrusion (Bassetti and Westgate 1994; Bolaños and Edmeades 1993). This delay in ear development and silk growth is critical in the period leading up to and surrounding silking (R1), as it is the time when final kernel number is determined (Ritchie et al. 1992). Mechanisms associated with ASI can be traced back in the season in maize. Lower rates of leaf initiation can result in lower rates of leaf appearance (Padilla and Otegui 2005) and delays in ear initiation (Lejeune and Bernier 1996). Moreover, the onset of silk's linear growth starts after ear-spikelet differentiation (V6 to V7 or around 200 GDD) (Carcova et al. 2003). Therefore any stress factor that operates during this critical window can delay normal silk growth and/or development (Fuad-Hassan et al. 2008). The WR10 treatment (32% yield reduction, $P < 0.05$, Table 4) covered the onset of this window of early reproductive initiation (V6 to V7). Weeds presence resulted in reduced rate of leaf appearance and final leaf tip across genotypes (Table 2). Shorter ASI in the drought tolerant genotype ($P < 0.05$, Table 4), however, may not be associated with rate of leaf appearance since genotypes did not differ in rates of leaf appearance or final leaf tip number (Table 2). Therefore, mechanisms driving ASI synchrony in the drought tolerant hybrids were likely related to the actual tassel-ear-silks initiation phase and the presilking extrusion phase.

Close synchrony of tassel and ear development is critical in order to optimize kernel set and yield potential (Bassetti and Westgate 1993, 1994). The loss of this synchrony during the reproductive period of maize can account for a reduction in kernel number. Under nitrogen stressed conditions, Lemcoff and Loomis (1986) observed a delay in silk emergence which increased median silking date and resulted in a decrease in kernel number. As well, Jacobs and Pearson (1991) observed an increase in asynchronous flowering which led to a reduction in kernel number when maize was grown under nitrogen stress. A lengthening of the interval between anthesis and silking has also been reported to be an indicator of stress, particularly, when maize was grown at high density (Buren et al. 1974; Dow et al. 1984; Monneveux et al. 2005) or under drought stressed conditions (Bruce et al. 2002).

Under weedy conditions as described in this study, the drought tolerant hybrid had a lower kernel number but heavier kernel wt compared to the non-drought tolerant hybrid. It has been reported previously, that drought tolerant hybrids may have reduced kernel number (Bruce et al. 2002; Edmeades et al. 1993). A reduction in kernel number has been suggested to be an adaptation of maize to drought stress (Bruce et al. 2002; Edmeades et al. 1993). This reduction in kernel number may increase resource allocation to individual spikelets, thereby causing increased individual spikelet growth and subsequent rate of silk extrusion (Edmeades et al. 1993). Weed competition may have also contributed to the occurrence of lower kernel number. Similar results have been reported in other weed control studies (Cerrudo et al. 2012; Page et al. 2012). This possible reduction in kernel number caused by weed competition may have been the result of a reduction in the number of viable spikelets during reproductive development. This would increase the amount of photoassimilates available kernel^{-1}, thus allowing for an increase in wt gain kernel^{-1} (see also Edmeades et al. 1993). The ability to increase kernel wt can compensate for a reduction in kernel number, thereby maintaining grain yield (Borrás and Otegui 2001; Borrás et al. 2004; Kiniry et al. 1990). It should be noted, however, that the ability for kernel wt to compensate for lower kernel number is dependent upon the environment that occurs during the effective grain filling period which is defined from 3 wk after silking to physiological maturity (Daynard et al. 1971; Tollenaar 1977).

In conclusion, this study found that as weed control was delayed there was a decrease in maize plant height, leaf number, dry matter plant^{-1}, kernels plant^{-1} and grain yield in both hybrids. A fair degree of similarity in response to weed pressure would be expected from near isogenic lines. The drought tolerant hybrid, however, had a shorter ASI and fewer but heavier kernels compared to the non-drought tolerant hybrid. Delaying weed control lengthened ASI for both hybrids. Since the lengthening of ASI is negatively correlated with kernel number, the increase in ASI observed by delaying weed control would invariably influence kernel number and final yield in both hybrids. The lengthening of ASI caused by weed competition further suggests that molecular and physiological changes were triggered within the plant well before phenological expression was evident. Thus, yield potential can be altered well before detection at the whole plant level. As a result of the strong association of ASI length and drought tolerance, a delay in weed control can result in molecular and physiological changes that may compromise the full expression of a critical mechanism for drought tolerance. Further research is required to continue to explore the interactions between weed management and novel trait expression in maize.

Acknowledgments

The financial support of the Natural Science and Engineering Research Council of Canada (File CRDPJ 425128-11), Syngenta Crop Protection Inc. and Ontario Ministry of Agriculture, Food, and Rural Affairs are gratefully acknowledged. The authors also wish to express their appreciation to H. Wright from Syngenta Crop Protection Canada Inc., and K. Chandler from the University of Guelph for their assistance throughout the course of this study. A special thank you to C. Shropshire for her assistance with field work and statistical analyses.

Literature Cited

Afifi M, Swanton CJ (2011) Maize seed and stem roots differ in response to neighbouring weeds. Weed Res. 51:442–450

Afifi M, Swanton CJ (2012) Early physiological mechanisms of weed competition. Weed Sci 60:542–551

Araus JL, Serret MD, Edmeades GO (2012) Phenotyping maize for adaptation to drought. Front Physiol 3: (Article 305), 1–20

Bassetti P, Westgate ME (1993) Emergence, elongation, and senescence of maize silks. Crop Sci 33:271–275

Bassetti P, Westgate ME (1994) Floral asynchrony and kernel set in maize quantified by image analysis. Agron J 86:699–703

Bolaños J, Edmeades GO (1993) Eight cycles of selection for drought tolerance in lowland tropical maize. II. Responses in reproductive behavior. Field Crops Res 31:253–268

Bolaños J, Edmeades GO (1996) The importance of the anthesis-silking interval in breeding for drought tolerance in tropical maize. Field Crops Res 48:65–80

Borrás L, Otegui ME (2001) Maize kernel wt response to post flowering source–sink ratio. Crop Sci 49:1816–1822

Borrás L, Slafer GA, Otegui ME (2004) Seed dry wt response to source–sink manipulations in wheat, maize and soybean: a quantitative reappraisal. Field Crops Res 86:131–146

Bosnić A, Swanton CJ (1997) Influence of barnyardgrass (*Echinochloa crus-galli*) time of emergence and density on corn (*Zea mays*). Weed Sci 45:276–282

Bruce WB, Edmeades GO, Barker TC (2002) Molecular and physiological approaches to maize improvement for drought tolerance. J Exp Biol 53:366 13–25

Buren LL, Mock JJ, Anderson IC (1974) Morphological and physiological traits in maize associated with tolerance to high plant density. Crop Sci 14:426–429

Campbell GS, Norman JM (1998) An introduction to environmental biophysics. New York: Springer-Verlag. Pp 28–34

Campos H, Cooper M, Habben JE, Edmeades GO, Schussler JR (2004) Improving drought tolerance in maize: a view from industry. Field Crops Res 90:19–34

Carcova J, Andrieu B, Otegui ME (2003) Silk Elongation in Maize: Relationship with Flower Development and Pollination. Crop Sci 43:914–920

Cerrudo D, Page ER, Tollenaar M, Stewart G, Swanton CJ (2012) Mechanisms of yield loss in maize caused by weed competition. Weed Sci 60:225–232

Cox WJ, Hahn RR, Stachowski PJ (2006) Time of weed removal with glyphosate affects corn growth and yield components. Agron J 98:349–353

Daynard TB, Tanner JW, Duncan WG (1971) Duration of the grain filling period and its relation to grain yield in corn (*Zea mays* L.). Crop Sci 11:45–48

Dow EW, Daynard TB, Muldoon JF, Major DJ, Thurtell GW (1984) Resistance to drought and density stress in Canadian and European maize (*Zea mays* L.) hybrids. Can J Plant Sci 64:575–585

Duvick DN (1996) Review of the symposium on developing drought and low N tolerant maize. Pages 554–556 *in* Developing Drought- and Low N-Tolerant Maize, Proceedings of a Symposium. El Batán, Mexico: CIMMYT

Edmeades GO (1976) Aspects of plant-to-plant variability in maize (*Zea mays* L.). Ph.D Dissertation. Ontario, Canada: University of Guelph. 174 p

Edmeades GO, Bolaños J, Chapman SC, Lafitte HR, Bänziger M (1999) Selection improves drought tolerance in tropical maize populations: I. Gains in biomass, grain yield, and harvest index. Crop Sci 39:1306–1315

Edmeades GO, Bolaños J, Hernandez M, Bello S (1993) Causes for silk delay in a lowland tropical maize. Crop Sci 33:1029–1035

Edmeades GO, Daynard TB (1979) The development of plant to plant variability in maize at different planting densities. Can J Plant Sci 59:561–576

Evans SP, Knezevic SZ, Lindquist JL, Shapiro CA, Blankenship EE (2003) Nitrogen application influences the critical period for weed control in corn. Weed Sci 51:408–417

Fickett ND, Boerboom CM, Stoltenberg DE (2013) Predicted corn yield loss due to weed competition prior to postemergence herbicide application on Wisconsin farms. Weed Tech 27:54–62

Fuad-Hassan A, Tardieu F, Turc O (2008) Drought-induced changes in anthesis-silking interval are related to silk expansion: a spatio-temporal growth analysis in maize plants subjected to soil water deficit. Plant Cell Environ 31:1349–1360

Glenn FB, Daynard TB (1974) Effects of genotype, planting pattern, and plant density onplant-to-plant variability and grain yield corn. Can J Plant Sci 54:323–330

Hall MR, Swanton CJ, Anderson GW (1992) The critical period of weed control in grain corn (*Zea mays*). Weed Sci 40:441–447

Jacobs BC, Pearson CJ (1991) Potential yield of maize, determined by rates of growth and development of ears. Field Crops Res 27:281–298

Kiniry JR, Wood CA, Spanel DA, Bockholt AJ (1990) Seed wt response to decreased seed number in maize. Agron J 54:98–102

Knezevic SF, Weise SF, Swanton CJ (1994) Interference of redroot pigweed (*Amaranthus retroflexus*) in corn (*Zea mays*). Weed Sci 42:568–573

Kropff MJ, Spitters CJT (1991) A simple model of crop loss by weed competition from early observations on relative leaf area of the weeds. Weed Res 31:97–105

Lafitte HR, Edmeades GO (1994) Improvement for tolerance to low soil nitrogen in tropical maize I. Selection criteria. Field Crops Res 39:1–14

Lejeune P, Bernier G (1996) Effect of environment on the early steps of ear initiation in maize (Zea mays L.). Plant Cell Environ 19:217–224

Lemcoff JH, Loomis RS (1986) Nitrogen influences on yield determination in maize. Crop Sci 26:1017–1022

Liu JG, Mahoney KJ, Sikkema PH, Swanton CJ (2009) The importance of light quality in crop–weed competition. Weed Res 49:217–224

McCully ME (1999) Roots in soil: unearthing the complexities of roots and their rhizospheres. Ann Rev Plant Physiol Plant Mol Biol 50:695–718

Monneveux P, Zaidi PH, Sanchez C (2005) Population density and low nitrogen affects yield-associated traits in tropical maize. Crop Sci 45:535–545

Moriles J, Hansen S, Horvath DP, Reicks G, Clay DE, Clay SA (2012) Microarray and Growth Analyses Identify Differences and Similarities of Early Corn Response to Weeds, Shade, and Nitrogen Stress. Weed Sci 60:158–166

Padilla JM, Otegui ME (2005) Co-ordination between leaf initiation and leaf appearance in field-grown maize (Zea mays): genotypic differences in response of rates to temperature. Ann Bot 96:997–1007

Page ER, Cerrudo D, Westra P, Loux M, Smith K, Foresman C, Wright H, Swanton CJ (2012) Why early season weed control is important in maize. Weed Sci 60:423–430

Page ER, Tollenaar M, Lee EA, Lukens L, Swanton CJ (2009) Does the shade avoidance response contribute to the critical period for weed control in maize (*Zea mays*)? Weed Res 49:563–571

Parry MAJ, Flexas J, Medrano H (2005) Prospects for crop production under drought: research priorities and future directions. Ann Appl Biol 147:211–226

Passioura JB (1996) Drought and drought tolerance. Plant Growth Regul 20:79–83

Ribaut J, Betran J, Monneveux P, Setter T (2009) Drought tolerance in maize. Pages 311–344 *in* Bennetzen JL and Hake SC, eds. Handbook of Maize: Its Biology. New York: Springer

Reid A (2013) Timing of weed control influences the anthesis-silking interval in maize. Master's thesis. University of Guelph. 57 p

Ritchie SW, Hanway JJ, Benson GO (1992). How a corn plant grows. Iowa State Univ Sci Tech Coop Ext Serv Rep 48

Swanton CJ, Mahoney KJ, Chandler K, Gulden RH (2008) Integrated weed management: knowledge-based weed management systems. Weed Sci 56:168–172

Tollenaar M (1977) Sink–source relationships during reproductive development in maize. A review. Maydica 22:49–75

Tollenaar M, Aguilera A, Nissanka SP (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, Daynard TB, Hunter RB (1979) Effect of temperature on rate of leaf appearance and flowering date in maize. Crop Sci 19:363–366

Tollenaar M, Lee EA (2006) Dissection of physiological processes underlying grain yield in maize by examining genetic improvement and heterosis. Maydica 51:399–408

Vega CRC, Andrade FH, Sadras VO (2001) Reproductive partitioning and seed set efficiency in soybean, sunflower and maize. Field Crops Res 72:163–175

Weiner J (1990) Asymmetric competition in plant populations. Trends Ecol Evol 5:360–364

Received June 19, 2013, and approved November 17, 2013.