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Influence of nitrogen and duration of weed interference on corn growth and development

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An improved understanding of the effects of nitrogen (N) on crop–weed interactions is needed for the development of integrated weed management systems where responsible use of N fertilizers is considered. Field experiments conducted in 1999 and 2000 at two locations in eastern Nebraska quantify the effects of N and increasing duration of weed interference on corn growth and development. A naturally occurring population of weeds was allowed to compete with the corn crop for increasing lengths of time and at three rates of N application (0, 60, and 120 kg N ha⁻¹). Weed interference and withholding applied N increased the time to 50% silking by an average of 3.9 and 2.9 d, respectively. Regardless of treatments, relative growth rates of corn leaf area and biomass were maximized between the V1 and V2 growth stages of corn and increased linearly with N rate but were affected to a lesser extent by weed presence. The improvement in early season corn growth with addition of N resulted in greater leaf area, biomass, and height, which improved the competitive ability of corn against weeds. Reductions in maximum corn leaf area and height due to weed interference usually began earlier and were more extensive at reduced rates of N. Partitioning of biomass to reproductive structures increased with N during reproductive stages, likely contributing to greater harvest indices at the end of the season. Results from this study indicate that the effects of N fertilization on early-season crop growth provided a competitive advantage for corn relative to weeds, thereby increasing the length of time that weeds could compete with a crop before removal was required, but further research is needed to identify mechanisms regarding improved crop tolerance to weeds.

Nomenclature: Corn, *Zea mays* L. ‘DK589RR’.

Key words: Critical time of weed removal, duration of weed interference, growth analysis, growth curves, light competition, N competition, resource acquisition.

The competitive relationship between plant species is highly dependent on many factors including the supply and availability of nutrients. Therefore, the manipulation of soil fertility is a potential tool for integrated weed management (Di Tomaso 1995). Of all nutrients, plant response to nitrogen (N) fertilizer is the most widely observed, and it is suggested that the manipulation of soil N supply offers the most promise in the short term as a means by which crop–weed competitive outcomes can be influenced (Walker and Buchanan 1982).

Competition for light has been identified as the primary cause of crop yield loss in many crop–weed associations (King and Purcell 1997; Kropff et al. 1987; Lindquist and Mortensen 1999; Munger et al. 1987). However, above-ground plant performance is often mediated by below-ground nutrient acquisition, and vice versa (Casper and Jackson 1997). Therefore, the availability of nutrients such as N can influence the timeliness and extent of early season competition from weeds (Weaver et al. 1992).

Contrasting outcomes regarding the effects of N supply and corn–weed competition have been presented in the literature. In a greenhouse study, Teyker et al. (1991) reported greater N uptake for redroot pigweed (*Amaranthus retroflexus* L.) than corn when the addition of N was elevated, suggesting that redroot pigweed interference in corn may be greater at higher levels of N. Others also have postulated that weeds may be more competitive when fertility is en-

hanced with N addition because of the superior uptake efficiency of many weed species (Di Tomaso 1995; Sibuga and Bandeen 1980). However, evidence also suggests a positive effect of N fertilization on corn competitive ability under field conditions. For example, Nieto and Staniforth (1961) reported that the reduction in corn yield because of interference from foxtails (*Setaria* spp.) was relatively greater at low vs. high N levels. Tollenaar et al. (1994) reported that interference from mixed weeds emerging shortly after corn reduced corn biomass, harvest index, and final grain yield to a greater extent at low vs. high levels of soil N. More recently, Evans et al. (2002) showed that reduced rates of N resulted in an earlier beginning of the critical period for weed control (CPWC) in corn.

To identify the mechanisms underlying crop–weed competition for N, it is important to quantify the interactive effects of weed interference and N on crop growth parameters and determine how changes in those attributes affect yield. The outcomes of weed interference that are most often associated with crop yield reductions include (1) reduced amount and duration of green leaf area (Hall et al. 1992; Knezevic et al. 1994; Van Acker et al. 1993) and (2) reduced crop height or increased height differential between the crop and weeds (Fellows and Roeth 1992; Teasdale 1998). However, little attention has been directed toward identifying causal mechanisms for those outcomes. It is likely that competitive outcomes are related to both early-season growth

efficiency (Davis and Liebman 2001) and leaf area development (Potter and Jones 1977). In addition, Rajcan and Swanton (2001) suggest that detection of neighboring weeds by the crop early in the season can induce lasting physiological changes before the onset of competition. The objective of this study was to quantify the effects of duration of weed interference on corn growth and development parameters under varying rates of N application.

Materials and Methods

Site Description

This experiment was part of a larger study designed to identify the CPWC with varying rates of N application (Evans et al. 2002). Field experiments were conducted in 1999 and 2000 at two locations in eastern Nebraska, the University of Nebraska Agricultural Research and Development Center (ARDC) near Mead, and the Haskell Agricultural Laboratory (HAL) near Concord. Experimental sites were located in different fields for the second year of the study. Soil types were a Sharpsburg silty clay loam, 0 to 2% slope, (fine, montmorillonitic, mesic Typic Argiudolls), with a mean pH of 6.6 and mean soil organic matter content of 2.8% with inclusions of a Butler silty clay loam, 0 to 2% slope (fine, montmorillonitic, mesic Abruptic Argiaquaolls) for both years at ARDC; and a Kennebec silty clay loam, 0 to 2% slope, (fine-silty, mixed, mesic Cumulic Hapludolls) mean pH of 6.5 and mean soil organic matter content of 3.9% for both years at HAL.

Naturally occurring weed populations were used in each experiment and sites were selected on the basis of the historical presence of weeds typical of corn production in eastern Nebraska. Weed species in order of dominance (dry weight basis) were velvetleaf (*Abutilon theophrasti* Medicus), common waterhemp (*Amaranthus rudis* Sauer), and green foxtail [*Setaria viridis* (L.) Beauv.] at HAL in 1999; Pennsylvania smartweed (*Polygonum pennsylvanicum* L.), velvetleaf, and common waterhemp at ARDC in 1999; velvetleaf, green foxtail, and common waterhemp at HAL in 2000; and velvetleaf, common waterhemp, and yellow foxtail [*Setaria pumila* (Poir.) Roem & Schult.] at ARDC in 2000. Total weed densities measured at corn silking averaged 168, 364, 150, and 80 plants m^{-2} for the 1999 HAL, 1999 ARDC, 2000 HAL, and 2000 ARDC sites, respectively. Observable weed emergence was noted 2 d after crop emergence at HAL in 1999, 4 d before crop emergence at the ARDC in 1999, 4 d after crop emergence at HAL in 2000, and 5 d after crop emergence at the ARDC in 2000.

Experimental Design and Field Procedures

The experiments were established using a factorial arrangement of treatments in a split-plot randomized complete block design replicated four times. The main-plot factor consisted of three N application rates. Seven durations of weed interference comprised levels of the split-plot factor. Split-plots consisted of six corn rows, 12.2 m in length with a 0.76-m row spacing. Primary tillage consisted of fall chisel plowing at the ARDC and spring disking at HAL. Fertilizer applications reflected the University of Nebraska recommendations for corn on the basis of soil samples collected from each site a few weeks before crop planting (Hergert et al.

1995). The three N application rates selected were 0, 60, and 120 kg N ha^{-1} . The 120 kg N ha^{-1} rate represented applied N that would meet or slightly exceed the recommended rate on the basis of a grain yield goal of 8 Mg ha^{-1} with adjustments for residual nitrate-N and organic matter content (Hergert et al. 1995). Triple superphosphate fertilizer was broadcast at a rate equivalent to 45 kg P_2O_5 ha^{-1} in each year at the ARDC site 2 wk before planting. Urea was uniformly broadcast within 10 d before planting using a ground-driven fertilizer spreader¹. Immediately after application, one or more secondary tillage operations were performed to incorporate fertilizer and prepare the seedbed for planting. A glyphosate-resistant corn hybrid 'Dekalb DK589RR'² was planted on May 25 and May 13 in 1999 and on May 11 and May 2 in 2000 at the HAL and ARDC sites, respectively. Final plant populations were similar between locations within a given year, averaging 60,000 plants ha^{-1} in 1999 and 52,000 plants ha^{-1} in 2000.

Increasing durations of weed interference were established by delaying weed removal time (RT) to V3, V6, V9, V15, and R1. In addition, season-long weed-free and season-long weedy controls were included to give a total of seven durations of crop-weed interference. Each RT was based on average crop growth stage according to Ritchie et al. (1997) and was assessed every 5 d in the season-long weedy controls.

For RT treatments before the V15 crop developmental stage, weed control was achieved by commercially formulated glyphosate² applied once postemergence at a rate of 1.1 kg ai ha^{-1} plus 3.2 kg ha^{-1} ammonium sulfate. Weeds not severely injured within 6 d after treatment were removed by hand. For RTs at V15 and R1, weed control was achieved by hand weeding. Regardless of the initial method of weed control, maintenance of a weed-free condition was accomplished with periodic hand weeding.

Crop Measurements

Destructive corn plant harvests were made 2 d before each RT and at crop maturity (Table 1). An additional harvest was made at HAL in both years during the grain fill period. Successive harvest areas were separated from one another by a minimum of 1 m of undisturbed vegetation. Harvests were excluded from a 2-m portion of both the front and rear of each split-plot experimental unit to minimize neighborhood effects. In 1999, all corn plants within a 1-m section of either the second or fourth row of each split-plot were cut at the soil surface and removed, providing a sample size of approximately five plants. Because of lower populations in 2000, five plants were harvested from each split-plot experimental unit regardless of the length of row. Growth stages and heights of individual corn plants were recorded at the time of each harvest. Before tassel emergence, height was measured to the tip of the newest leaf emerging from the whorl. After tassel emergence, height was measured to the top of the tassel. Individual plants were clipped at the soil surface, and divided into leaf, stem, and reproductive components (when present). Reproductive components consisted of the entire ear shoot (i.e., husks, shank, cob, kernels, and silks) and the tassel. Leaves were separated from the stem by cutting the lamina at the ligule. Newly emerged leaves were cut just above the youngest visible collar. Leaf area of leaves was measured with an area meter³ during all

TABLE 1. Dates of destructive corn harvests by average corn growth stage at the University of Nebraska Haskell Agricultural Laboratory (HAL) near Concord, NE, and the Agricultural Research and Development Center (ARDC) near Mead, NE, in 1999 and 2000. Growing degree days (GDD) accumulated from the time of crop emergence to the time of each harvest are given in parentheses.

Corn growth stage at harvest ^a	Harvest date			
	HAL		ARDC	
	1999	2000	1999 ^b	2000
V3	June 13 (144)	June 05 (113)	June 07 (150)	May 22 (117)
V6	June 25 (255)	June 20 (271)	June 16 (250)	June 06 (239)
V9	July 08 (400)	June 29 (360)	June 29 (390)	June 14 (350)
V15	July 22 (575)	July 13 (570)	July 15 (595)	July 06 (600)
R1	August 11 (830)	July 27 (730)	July 28 (800)	July 18 (775)
R4 or R5	September 07 (1,140)	August 18 (1,000)	—	—
R6+	October 07 (1,320)	September 15 (1,310)	October 05 (1,475)	September 06 (1,430)

^a Average growth stage as determined from the weed-free controls.

^b Dashed lines indicate data not collected.

harvests except those conducted after corn silking. Senescing and dead leaves comprised < 10% “green” surface area were excluded from leaf area measurements. The newest leaves of corn were left furled as they were passed through the leaf area meter. All components were bagged separately (dead and green leaves combined together) and dried at 70 C to a constant moisture content. The average height of the weed canopy also was measured.

At crop maturity, two samples were taken from each split-plot. The first subsample consisted of individual corn plants taken using the same methodology of previous harvests. Ears from this subsample were dried at 70 C to a constant moisture content and shelled by hand. The second subsample consisted of hand-harvested corn ears taken from a 4-m length of two adjacent rows within each split-plot to determine grain yield. Grain was shelled mechanically and dried at 70 C to a constant moisture content.

Growth Curves and Statistical Analyses

Functional plant growth curves (Hunt 1982) were developed using regression models fit to corn biomass and leaf area data collected at each sampling date similar to the approach of Davis and Liebman (2001). All growth curves were constructed using thermal time as the independent variable. Thermal time correlates more closely with temperature-dependent biological processes than with calendar days (Russelle et al. 1984) and was calculated in terms of air growing degree days (GDD) as suggested by Gilmore and Rogers (1958) using a base temperature of 10 C and a temperature optimum of 30 C. Regression analysis and subsequent maximization of all growth curves was achieved using PROC NLIN in SAS⁴.

Biomass growth curves were fit to at least seven data points, each being the mean of 16 to 22 plants (e.g., four to five plants per replicate times four replicates). Similarly, leaf area growth curves consisted of six data points. Values of plant biomass and leaf area were log_e-transformed to maintain homogeneity of variances between sampling dates. In constructing plant growth curves, apparent leaf area and aboveground biomass at emergence were assumed to be equal among treatments and reflected average values reported by Lindquist and Mortensen (1999).

Asymptotic crop biomass accumulation was expressed with the Gompertz equation (Hunt 1982) (Equation 1):

$$\ln(W) = \ln(W_{\max}) \exp(-q \exp[-kT]) \quad [1]$$

where $\ln(W)$ is log_e-transformed biomass (i.e., sum of leaf, stem, and reproductive tissues) per plant in units of mg plant⁻¹ (all plant weights converted to milligrams so as to ensure positive values after the log_e-transformation), $\ln(W)_{\max}$ is maximum log_e-transformed shoot biomass per plant in mg plant⁻¹, T is the time from crop emergence in GDD in units of C. The coefficients q and k are constants.

Green leaf area (A) of corn increases in a sigmoidal fashion over time, reaching a maximum near tasseling before declining (Bennett et al. 1989). The relationship is well approximated with a third-order polynomial (Equation 2):

$$\ln(A) = a + bT + cT^2 + dT^3 \quad [2]$$

where $\ln(A)$ is log_e-transformed leaf area per plant in units of cm² and T is the time from crop emergence in GDD. The coefficients a , b , c , and d are constants.

Relative growth rates of biomass (RGRW) and leaf area (RGRA) are measures of the efficiency of production. Efficiency in biomass production in itself is not a good indicator of relative competitive ability (Roush and Radosevich 1985) but can be used early in the season when plants are of relatively equal size to predict differences in absolute growth. Relative growth rate curves for biomass and leaf area are given by the first derivatives of Equations 1 and 2 with respect to T , respectively, to obtain Equations 3 and 4:

$$RGRW = abk \exp(-kT - b \exp[-kT]) \quad [3]$$

$$RGRA = b + 2cT + 3dT^2 \quad [4]$$

Maximal leaf area (A_{\max}) and relative growth rates ($RGRW_{\max}$ and $RGRA_{\max}$) as well as the time at which those values were attained (T_{\max}) were calculated for each split-plot with the maximization of Equations 1, 3, and 4, respectively. Relative maximal leaf area (RA_{\max}) was calculated by expressing A_{\max} of each experimental unit as a percent of the A_{\max} calculated for the corresponding weed-free control within the same N main plot.

Crop height throughout the growing season was described for each split-plot experimental unit with a three-parameter logistic equation (Christensen 1995) (Equation 5):

$$H = H_{\max} / (1 + \exp[q - zT]) \quad [5]$$

where H is crop height, H_{\max} is the maximum attainable height and q and z are constants. Because the logistic function

is symmetric about its point of inflection, the ratio q/z defines the point in time at which one half of the maximum height is attained (Ratkowsky 1990), serving as an indicator of the rate of height growth.

Other growth parameters, i.e., harvest index (HI) (Equation 6), partitioning coefficients of aboveground biomass (PC_o) (Equation 7), and specific leaf area (SLA) (Equation 8), were calculated as suggested by Hunt (1990), respectively:

$$HI = W_{\text{grain}}/W \quad [6]$$

$$PC_o = \Delta W_{\text{component}}/\Delta W \quad [7]$$

$$SLA = A/W_{\text{leaf}} \quad [8]$$

where W is the total dry weight of the shoot (i.e., Σ leaf, stem, reproductive), W_{grain} is the weight of grain produced, PC_o is the partitioning coefficient of the specific plant component, Δ indicates the change in a plant biomass between two successive sampling dates, A is leaf area per plant, and W_{leaf} is the weight of those leaves. In this study, the partitioning coefficients were determined for leaf (PC_{leaf}), stem (PC_{stem}), and reproductive (PC_{rep}) components but not for roots.

The effect of years, locations, N rates (N), RTs, and their interactions on the growth parameters listed above were tested for significance by analysis of variance (ANOVA) using PROC MIXED in SAS (Littell et al. 1996). If interactions involving sites or years and either of the treatment factors were significant ($P < 0.05$), data were further analyzed by site-year. If the N by RT interaction was not significant, further analysis was conducted using main effect treatment least-squares means.

When possible, linear or nonlinear least-squares regression models were used to quantify the effects of treatments on variables computed from raw data. Otherwise, least-squares treatment means were compared using paired t tests (0.05 level) at each plant sampling time. The growth parameters W_{max} , A_{max} , $RGRW_{\text{max}}$, $RGRA_{\text{max}}$, and T_{max} , were expressed as linear functions ($Y = a + bX$) of N rate using the AXUM® 5.0 data analysis package⁵. Slopes were compared with zero using a t test (0.05 level). Nonlinear regression was used to relate corn RA_{max} , HI, and H_{max} to duration of weed interference. Best-fit nonlinear models were determined by comparison of the residual mean square error (RMSE) between similar nonlinear models. The model with the lowest RMSE was chosen because it provided the best fit to the experimental data. A four-parameter logistic equation (Ratkowsky 1990) was used to quantify the decline in RA_{max} , HI, and H_{max} with increasing duration of weed interference using PROC NL MIXED in SAS (Equation 9):

$$Y = c + (m - c)/(1 + \exp[-a + bD]) \quad [9]$$

where Y is either RA_{max} , HI, or H_{max} , D is the duration of weed interference after crop emergence in GDD, c is the lower asymptote, m is the upper asymptote; and a and b are constants. The significance of N effects was evaluated by comparing model coefficients among N rates using a pairwise t test (0.05 level) (Knezevic et al. 2002).

Results and Discussion

Phenological Development

Time to 50% silking and maturity of corn were delayed by both season-long weed interference and withholding N

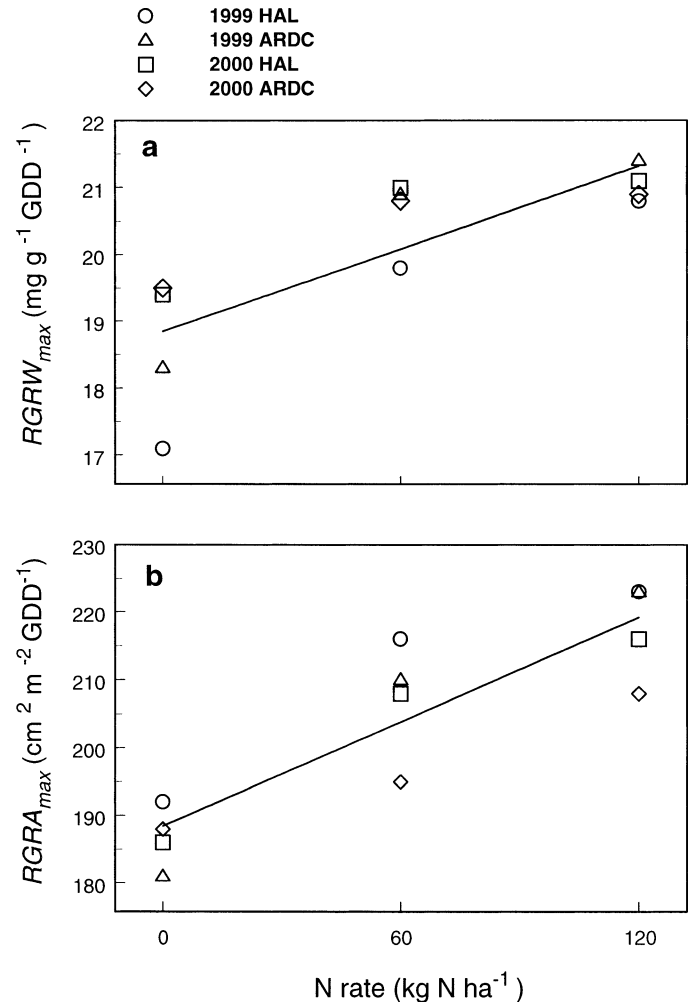


FIGURE 1. Corn maximal relative growth rate of (a) biomass ($RGRW_{\text{max}}$) and (b) leaf area ($RGRA_{\text{max}}$) as a function of N rate. Data points for each location are the N main-effect means averaged across all weed removal timings. The equations for the fitted regression equations are $RGRW_{\text{max}} = 18.85 + 0.0206N$, $n = 28$, $r^2 = 0.65$; and $RGRA_{\text{max}} = 188.46 + 0.2563N$, $n = 28$, $r^2 = 0.78$.

(data not shown). At the 0 kg N ha⁻¹ rate, lengths of time to silking and maturity were delayed an average of 2.9 and 1.8 d when compared with the average of the 60 kg N ha⁻¹ and 120 kg N ha⁻¹ rates, respectively. Season-long weed interference had a greater effect by delaying both silking and maturity by an average of 3.9 and 4.3 d, respectively, regardless of N rate when compared with the respective weed-free control. Delay in crop development is primarily attributed to reduced rates of leaf appearance (data not shown).

Relative Growth Rates

For all site-years the N by RT interactions for both $RGRW_{\text{max}}$ and $RGRA_{\text{max}}$ of corn were not significant ($P > 0.05$); therefore, only main effect means were used in the subsequent regression analysis. Both $RGRW_{\text{max}}$ and $RGRA_{\text{max}}$ increased linearly with N addition even though values differed somewhat between site years (Figure 1). For example, values of $RGRW_{\text{max}}$ ranged from 17.1 ± 0.41 to 19.5 ± 0.41 mg g⁻¹ GDD⁻¹ for the 0 kg N ha⁻¹ rate, and 20.8 ± 0.41 to 21.4 ± 0.47 mg g⁻¹ GDD⁻¹ for the 120 kg N ha⁻¹ rate (Figure 1a). Values of $RGRA_{\text{max}}$ ranged from

TABLE 2. Equations for corn maximal per plant biomass (W_{\max}) and leaf area (A_{\max}) as a function of N application rate for three durations of weed competition: season-long weed-free (wf), season-long weedy (wdy), and weedy to V9 (V9) at the University of Nebraska Haskell Agricultural Laboratory (HAL) near Concord, NE, and the Agricultural Research and Development Center (ARDC) near Mead, NE, in 1999 and 2000. P values are the probabilities that the slopes are significantly greater than zero.

Parameter	Site	Year	Competition level	Equation	P value	r^2
W_{\max}	HAL	1999	wf	$W_{\max} = 193 + 0.4500N$	0.0136	0.99
			V9	$W_{\max} = 155 + 0.4917N$	0.0170	0.97
			wdy	$W_{\max} = 100 + 0.2583N$	0.1286	0.96
	ARDC	1999	wf	$W_{\max} = 285 + 0.5417N$	0.1851	0.92
			V9	$W_{\max} = 158 + 0.8667N$	0.0564	0.99
			wdy	$W_{\max} = 112 + 0.2583N$	0.2165	0.89
	HAL	2000	wf	$W_{\max} = 289 + 0.2917N$	0.4198	0.62
			V9	$W_{\max} = 256 + 0.0333N$	0.4547	0.57
			wdy	$W_{\max} = 164 + 0.2570N$	0.2436	0.86
	ARDC	2000	wf	$W_{\max} = 235 + 0.6167N$	0.0298	0.99
			V9	$W_{\max} = 178 + 0.2643N$	0.2643	0.84
			wdy	$W_{\max} = 143 + 0.4667N$	0.1041	0.97
A_{\max}	HAL	1999	wf	$A_{\max} = 0.5588 + 0.00138N$	0.0462	0.99
			V9	$A_{\max} = 0.4240 + 0.00173N$	0.0120	0.99
			wdy	$A_{\max} = 0.3727 + 0.00114N$	0.0281	0.99
	ARDC	1999	wf	$A_{\max} = 0.6294 + 0.00073N$	0.2127	0.89
			V9	$A_{\max} = 0.3901 + 0.00119N$	0.0114	0.99
			wdy	$A_{\max} = 0.2736 + 0.00114N$	0.0136	0.97
	HAL	2000	wf	$A_{\max} = 0.6294 + 0.00044N$	0.2289	0.88
			V9	$A_{\max} = 0.4760 + 0.00085N$	0.0584	0.99
			wdy	$A_{\max} = 0.3893 + 0.00092N$	0.0264	0.97
	ARDC	2000	wf	$A_{\max} = 0.5599 + 0.00117N$	0.0456	0.99
			V9	$A_{\max} = 0.4190 + 0.00127N$	0.0455	0.94
			wdy	$A_{\max} = 0.3492 + 0.00128N$	0.0266	0.96

181 ± 3 to 192 ± 2 cm² m⁻² GDD⁻¹ for the 0 kg N ha⁻¹ rate, and 195 ± 2 to 223 ± 2 cm² m⁻² GDD⁻¹ for the 120 kg N ha⁻¹ rate (Figure 1b). For all site-years, T_{\max} , or the time of RGRW_{max} and RGRA_{max}, did not vary with either N or RT ($P > 0.05$) and occurred at approximately 35 and 40 GDD after emergence, respectively, or the V1 to V2 corn growth stages (data not shown). The presence of weeds was associated with reduced values of RGRW_{max} and RGRA_{max}, indicating that the physiology of corn changed in response to the presence of weeds even though competition for resources was likely not occurring. Rajcan and Swanton (2001) proposed that physiological changes caused by changes in light quality might be induced by neighboring weeds, regardless of whether or not those weeds are competing with the crop for resources. However, a posteriori analysis of each site-year revealed that the trend was non-significant ($P > 0.05$) for three out of four of the site-years (data not shown), indicating that N addition had a more immediate effect on early season crop growth than did the presence of weeds.

Maximum Biomass and Leaf Area

An overall ANOVA indicated significant site by N(year) ($P < 0.0001$) and site by RT(year) ($P < 0.001$) treatment interactions for both W_{\max} and A_{\max} . Therefore, data were further analyzed by site-year. Despite a positive correlation of W_{\max} and A_{\max} with N, slopes did not always differ from zero (Table 2), indicating only a slight response to N. However, within N rates, a longer duration of weed interference was associated with lower values of both W_{\max} and A_{\max} for corn. For example, at the 0 kg N ha⁻¹ rate for the HAL 1999 site, estimated values of maximal per plant biomass

were 193, 155, and 100 g plant⁻¹ for the season-long weed-free, weedy to V9, and season-long weedy treatments, respectively. Estimated maximal per plant leaf area at the same site were 0.5588, 0.4240, and 0.3727 m² plant⁻¹ for the season-long weed-free, weedy to V9 and season-long weedy treatments, respectively. Estimates of W_{\max} and A_{\max} for other N rates and site-years can be obtained from the solution of the linear regression equations.

Because of the infrequency of harvests during the grain-fill period, adequate evaluation of physical losses was not possible. Therefore, values of T_{\max} were not estimated for biomass, but generally coincided with physiological maturity for all site-years and treatments (data not shown). Nitrogen rate had little influence on T_{\max} for leaf area in 1999 at HAL ($P = 0.34$) and ARDC ($P = 0.70$) and occurred at 688 ± 4 and 674 ± 15 GDD, respectively, when averaged across RTs. Whereas T_{\max} declined from 712 ± 9 to 640 ± 9 GDD between the 0 to 120 kg N ha⁻¹ rates, respectively, at the 2000 HAL site ($P < 0.0001$), T_{\max} increased with N rate from 650 ± 5 to 688 ± 5 GDD, respectively, at the 2000 ARDC site ($P = 0.0038$). Explanation for the disparity of N effect on T_{\max} of leaf area in this study is not clear but is most likely due to environmental differences between sites. Alternatively, season-long weed interference reduced T_{\max} by an average of 20 GDD, which is equivalent to 1.3 d when the mean daily temperature is 25 C. A slight decrease in T_{\max} of leaf area in the weedy condition is probably due to an earlier onset of corn leaf senescence due to weed competition.

Eik and Hanway (1966) reported a high positive linear correlation between leaf area of corn at silking and final grain yield. The relationship between relative grain yield and

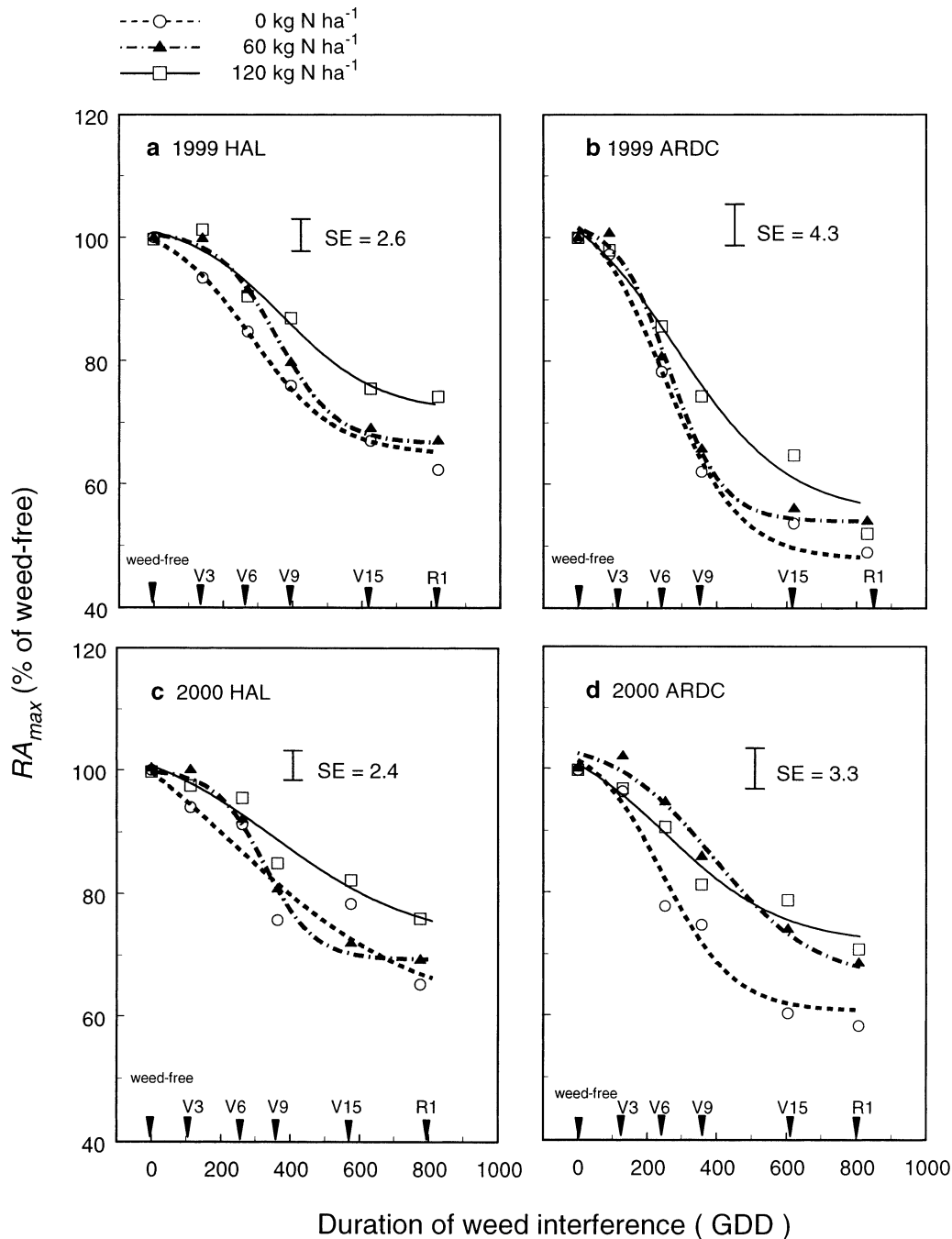


FIGURE 2. Relative maximal leaf area (RA_{max}) of corn for three N rates as a function of duration of weed interference at the University of Nebraska Haskell Agricultural Laboratory near Concord, NE, and the Agricultural Research and Development Center near Mead, NE, in 1999 and 2000. Data points are the means of four replicates. Error bars indicate \pm standard error of the treatment means for each site-year. Mean growth stages of the crop at the time of weed removal are superimposed on the x-axis. Equations for the lines are presented in Table 3.

RA_{max} in this study was not linear but was positively correlated ($r^2 = 0.90$) (data not shown). Consequently, the reduction in RA_{max} with increasing duration of weed interference might be expected to predict the pattern and extent of reduction in relative grain yield at the end of the season. The addition of N had a somewhat stabilizing effect on corn leaf area, because the extent of decline in RA_{max} with increasing duration of weed interference was least at the 120 kg N ha⁻¹ rate (34%) and greatest for the 0 kg N ha⁻¹ rate (43%) (Figure 2, Table 3). A greater reduction in green leaf area due to either accelerated rates of leaf senescence or

greater inhibition of leaf area expansion (i.e., size of individual leaves) could result in a less competitive crop and greater rates of yield reduction with increase in the duration of weed interference.

Biomass Partitioning

Biomass partitioning coefficients for corn varied somewhat between site-years but interactions between years, sites, and treatment levels were nonsignificant ($P > 0.05$) for all corn growth periods (data not shown); therefore, all

TABLE 3. Equations for relative maximal leaf area (RA_{max}) as a function of the duration of weed interference (D) by N application rate at the University of Nebraska Haskell Agricultural Laboratory (HAL) near Concord, NE, and the Agricultural Research and Development Center (ARDC) near Mead, NE, in 1999 and 2000.

Site	Year	N-rate	Equation	RMSE ^a
		kg N ha ⁻¹		
HAL	1999	0	$RA_{max} = 65 + (103 - 65)/(1 + \exp(-2.3034 + 0.00822D))$	18.13
		60	$RA_{max} = 62 + (101 - 62)/(1 + \exp(-4.1233 + 0.01162D))$	18.13
		120	$RA_{max} = 65 + (103 - 65)/(1 + \exp(-2.6464 + 0.00715D))$	18.13
ARDC	1999	0	$RA_{max} = 48 + (107 - 48)/(1 + \exp(-2.2977 + 0.00926D))$	49.51
		60	$RA_{max} = 54 + (103 - 54)/(1 + \exp(-3.4705 + 0.01316D))$	49.51
		120	$RA_{max} = 55 + (109 - 55)/(1 + \exp(-1.7606 + 0.00620D))$	49.51
HAL	2000	0	$RA_{max} = 60 + (117 - 60)/(1 + \exp(-0.8202 + 0.00365D))$	17.78
		60	$RA_{max} = 69 + (102 - 69)/(1 + \exp(-4.5543 + 0.01397D))$	17.78
		120	$RA_{max} = 72 + (106 - 72)/(1 + \exp(-1.6841 + 0.00475D))$	17.78
ARDC	2000	0	$RA_{max} = 61 + (104 - 61)/(1 + \exp(-2.4067 + 0.00980D))$	39.42
		60	$RA_{max} = 66 + (105 - 66)/(1 + \exp(-2.6830 + 0.00681D))$	39.42
		120	$RA_{max} = 72 + (107 - 72)/(1 + \exp(-1.5205 + 0.00595D))$	39.42

^a Abbreviation: RMSE, residual mean square error.

experimental data were pooled. Biomass partitioning of corn was influenced by N rate and duration of weed interference and varied with the period of crop growth (Table 4). Early in the season (V6 to V9), more biomass was partitioned to leaves when no N was applied as indicated by slightly greater values for PC_{leaf} . In competition with weeds, corn partitioned 65, 62, and 61% of new biomass to leaves ($PC_{leaf} = 0.65, 0.62, \text{ and } 0.61$) at the 0, 60, and 120 kg N ha⁻¹ rates, respectively. In the weed-free condition, corn partitioned 65, 63, and 63% of new biomass to leaves at the 0, 60, and 120 kg N ha⁻¹ rates, respectively. However, the increase in leaf partitioning was accompanied by a decline in SLA (data not shown), indicating thinner, less compact leaves at the 0 kg N ha⁻¹ rate than for either the 60 or 120 kg N ha⁻¹ rates. The presence of weeds affected biomass partitioning to a lesser extent at this time than later times, even though a wider range of values for PC_{leaf} were observed under weedy conditions (0.61 to 0.65) than under weed-free conditions (0.63 to 0.65).

During both the V9 to V15 and V15 to R1 periods of growth, partitioning of biomass to reproductive organs was

substantially greater for both the 60 and 120 kg N ha⁻¹ rates when compared with the 0 kg N ha⁻¹ rate regardless of whether or not weeds were present (Table 4). Both weed interference and withholding N resulted in greater values of PC_{stem} and leaves during the V15 to R1 growth period as indicated by lower values for PC_{rep} at the 0 kg N ha⁻¹ rate. In competition with weeds, corn partitioned 26, 38, and 37% of new biomass to reproductive structures ($PC_{rep} = 0.26, 0.38, \text{ and } 0.37$) at the 0, 60, and 120 kg N ha⁻¹ rates, respectively. In a weed-free condition, corn partitioned 42, 51, and 52% of new biomass to reproductive structures, for the 0, 60, and 120 kg N ha⁻¹ rates, respectively.

The differences in biomass partitioning quantified in this study are partially explained by the effect of treatments on the rate of crop development as discussed above. However, normalizing biomass partition coefficients to account for differences in developmental rate accounted for less than half of the variability particularly during the V15 to R1 growth period (data not shown). Moreover, quantifying biomass partitioning can be complicated by potential dry matter losses caused by premature leaf senescence (Wolfe et al.

TABLE 4. Biomass partition coefficients (PC_o) of weedy and weed-free corn (\pm SE) for three rates of N application during three periods of corn growth. Values are means of data collected at the University of Nebraska Haskell Agricultural Laboratory (HAL) near Concord, NE, and the Agricultural Research and Development Center (ARDC) near Mead, NE, in 1999 and 2000.

N rate	Corn biomass partition coefficients (PC_o) ^a								
	V6 to V9			V9 to V15			V15 to R1		
	PC_{leaf}^b	PC_{stem}^b	PC_{rep}	PC_{leaf}	PC_{stem}	PC_{rep}	PC_{leaf}	PC_{stem}	PC_{rep}
kg N ha ⁻¹									
Season-long weedy corn									
0	0.65 a	0.35 c	0.00 a	0.40 a	0.51 c	0.01 a	0.15 a	0.59 a	0.26 d
60	0.62 bc	0.39 a	0.00 a	0.33 b	0.67 b	0.02 a	0.12 ab	0.50 b	0.38 bc
120	0.61 c	0.38 ab	0.00 a	0.33 b	0.67 b	0.01 a	0.14 a	0.49 b	0.37 c
Season-long weed-free corn									
0	0.65 a	0.35 c	0.00 a	0.33 b	0.67 b	0.02 a	0.11 bc	0.47 b	0.42 b
60	0.63 b	0.37 b	0.00 a	0.30 c	0.68 ab	0.02 a	0.09 c	0.40 c	0.51 a
120	0.63 b	0.37 b	0.00 a	0.31 bc	0.69 a	0.04 b	0.09 c	0.39 c	0.52 a
SE	0.01	0.01	0.00 a	0.01	0.01	0.01	0.01	0.04	0.05

^a Means within a column followed by different letters are significantly different from one another based on a t test at the 0.05 level.

^b PC_{leaf} and PC_{rep} are the partitioning coefficients for leaf and reproductive parts, respectively.

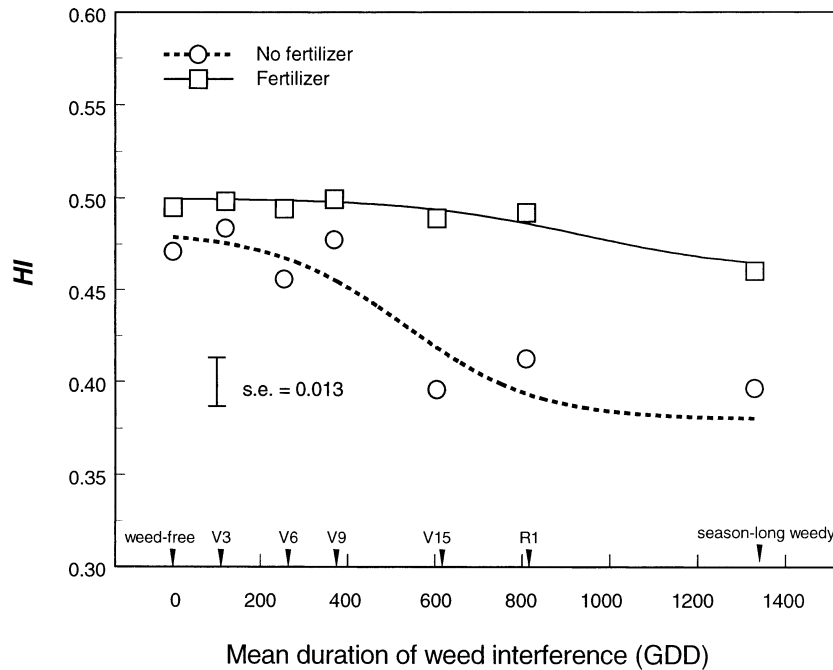


FIGURE 3. Mean harvest index (HI) as a function of the mean duration of weed interference for corn without N (0 kg N ha^{-1}) and with N (60 and 120 kg N ha^{-1}) fertilizer. Data are averages from experiments at the University of Nebraska Haskell Agricultural Laboratory near Concord, NE, and the Agricultural Research and Development Center near Mead, NE, in 1999 and 2000. Error bars indicate \pm standard error of the treatment means and mean growth stages at the time of weed removal are superimposed on the x -axis. The equations of the fitted regression lines are: $HI = 0.38 + 0.10/(1 + \exp[-3.54 + 0.0066D])$, $n = 12$, $r^2 = 0.73$ without N fertilizer; and $HI = 0.46 + 0.04/(1 + \exp[-4.76 + 0.0051D])$, $n = 24$, $r^2 = 0.89$ with N fertilizer.

1988), stem breakage, or remobilization of stored assimilates (Genter et al. 1970). The magnitude of those effects may depend on environmental factors, especially water availability. Interactions involving such factors were not investigated in this study and should be considered in future experiments.

Assuming an equal length of the grain-fill period, reduced partitioning to reproductive organs should result in a detectable reduction in the HI at crop maturity. Averaged across site-years, HI was enhanced by N addition (average of 60 and 120 kg N ha^{-1} rates) regardless of the duration of weed interference (Figure 3). Differences in HI were more substantial with increasing duration of weed interference with a maximum reduction in HI of 7.0% (of the weed-free control) when N was applied compared with 12.6% when no N was applied. These results indicate that HI was more sensitive to increasing duration of weed interference when N fertilizer was not applied, corroborating the findings reported by Tollenaar et al. (1994).

Height Growth

Maximum height (H_{\max}) of corn was influenced by N rate and duration of weed interference similarly for all site-years as indicated by nonsignificant interactions involving sites and years ($P > 0.05$) (data not shown). Therefore, data were pooled, and in all cases, differences in H_{\max} between the 60 and 120 kg N ha^{-1} rates were minor. However, corn plants were the shortest and were affected to a greater extent by weed interference when no N was applied (Figure 4). Reductions in height due to season-long weed interference were 14 ± 4 , 10 ± 4 , and $8 \pm 4\%$ of the season-long weed-free controls for the 0 , 60 , and 120 kg N ha^{-1} rates, respectively.

The application of N not only promoted greater growth in height but also hastened the rate at which H_{\max} was attained as indicated by the quotient q/z (refer to Equation 5). Depending on the site-year, the time required for the crop to reach one half of its maximum height ranged from 485 ± 6 to 549 ± 5 GDD for the 0 kg N ha^{-1} rate, and 448 ± 6 and 493 ± 5 GDD for the 120 kg N ha^{-1} rate (Table 5). A greater value of H_{\max} indicates more rapid rate of height growth and combined with greater H_{\max} predisposes a plant to be a better potential competitor with weeds.

In addition, the average height of the weed canopy approached but never exceeded that of the crop in any of the experiments (data not shown). The height differential between the crop and weeds in the season-long weedy plots was always positive and rarely differed between N rates, indicating that both weeds and corn responded to N similarly. Therefore, the differential in crop-weed height was likely not a large factor in determining the increase in corn tolerance to weeds when N was applied. However, different results may have been observed if the weed canopy was taller than the crop.

Final Grain Yields

Grain yields were variable across site-years and were likely affected by differences in amounts and periodicity of precipitation received during anthesis and the grain-fill period (Table 6). Total rainfall amounts during July and August were 6.2 , 13.5 , 8.6 , and 7.7 cm for the 1999 HAL, 1999 ARDC, 2000 HAL, and 2000 ARDC site-years, respectively. Consequently, the greatest weed-free yields were observed at the 1999 ARDC site, whereas the lowest yields were measured at the 1999 HAL site. Weed density and

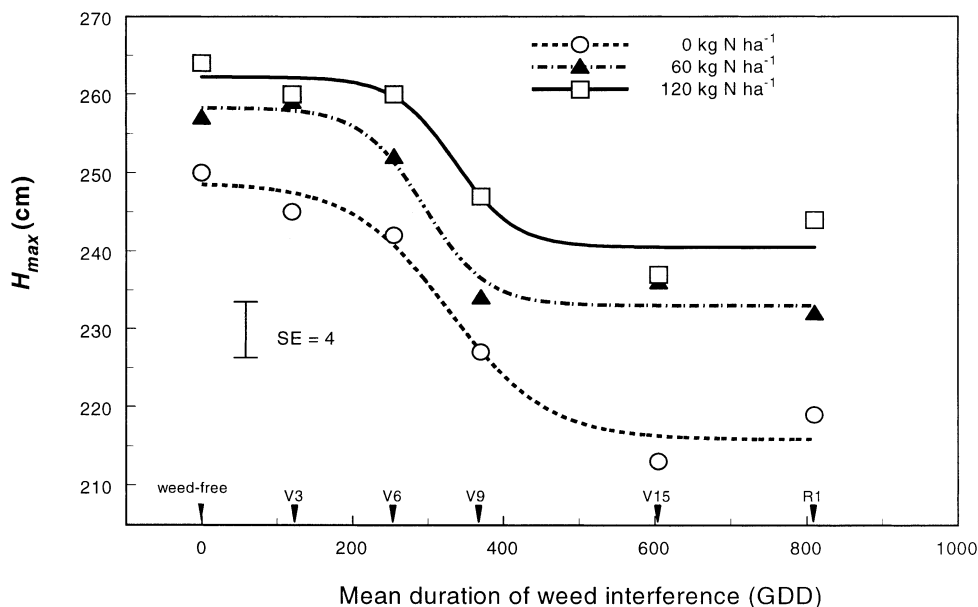


FIGURE 4. Corn maximal height (H_{max}) as a function of the mean duration of weed interference for three N rates. Data are presented as means of sites and years from experiments conducted at the University of Nebraska Haskell Agricultural Laboratory near Concord, NE, and the Agricultural Research and Development Center near Mead, NE, in 1999 and 2000. Error bars indicate \pm standard error of the treatment means and mean growth stages of corn at the time of weed removal are superimposed on the x-axis. The equations of the fitted regression lines are: $H_{max} = 214 + 35/(1 + \exp[-5.0681 + 0.0155D])$, $n = 12$, $r^2 = 0.97$ for the 0 kg N ha $^{-1}$ rate; $H_{max} = 233 + 25/(1 + \exp[-7.1184 + 0.0241D])$, $n = 12$, $r^2 = 0.98$ for the 60 kg N ha $^{-1}$ rate; and $H_{max} = 262 + 22/(1 + \exp[-8.4172 + 0.0251D])$, $n = 12$, $r^2 = 0.95$ for the 120 kg N ha $^{-1}$ rate.

timeliness of emergence determined the extent of yield reduction due to weed interference.

Despite the fact that grain yield did not always respond to N addition, the critical timing of weed removal (CTWR) or corn growth stage when weed removal resulted in no greater than a 5% yield loss, occurred earliest for the 0 kg N ha $^{-1}$ rate (V2). Addition of 60 kg N ha $^{-1}$ delayed the CTWR to the V4 growth stage, and with 120 kg N ha $^{-1}$, weed removal did not have to occur until the V6 growth stage (Table 6). Therefore, the effect of N addition on corn growth parameters ultimately conditioned a more competitive crop.

In this study, an attempt was made to improve the understanding of the effects N supply has on corn–weed interference relationships by identifying a number of corn growth parameters that are differentially affected by N level. Results suggest that addition of N improved early season corn growth, which improved the competitive ability of corn

against weeds. Practical benefit is delayed timing of weed control, which is important in farming operation.

Although this study tried to use growth analysis to identify the potential causes for differential crop losses due to weed interference, the mechanisms of crop–weed competition were not defined. We suggest that a gross investigation of aboveground physical and morphological changes linked to yield loss is likely not sufficient to identify causal competitive mechanisms for differential response to N. The supply of N likely affects other processes including the dynamics of biomass partitioning and the architecture and morphology of the root system (Durieux et al. 1994; Granato and Raper 1989; Mackay and Barber 1986), which were not investigated in this study. It is logical to hypothesize that changes in root system architecture and morphology can influence plant growth by improving the ability of a crop to acquire water and essential nutrients during periods of intense crop–weed interference or periods when yield is highly vulnerable. Enhanced resource acquisition could increase the size and longevity of green leaves, thereby increasing the size and longevity of the leaf area available for light interception (Wolfe et al. 1988).

Although early-season relative growth rates of corn due to weed interference were little affected by the presence of weeds, the findings of this study neither corroborate nor negate the theory proposed by Rajcan and Swanton (2001). However, further studies are required to verify such speculations and quantify the effects of N and weed interference at a physiological level. Information from such investigations would likely lead to an improved understanding of complex mechanisms of crop–weed interaction.

Sources of Materials

¹ Barber Engineering Ltd., 1404 N Regal Street, Spokane, WA 99202-3697.

TABLE 5. Estimated time in growing degree days (GDD) for corn to reach 50% maximum height ($T_{1/2max}$)(\pm SE) in 1999 and 2000 at the University of Nebraska Haskell Agricultural Laboratory (HAL) near Concord, NE, and the Agricultural Research and Development Center (ARDC) near Mead, NE.

N rate	Time to 50% maximum height ($T_{1/2max}$)			
	HAL		ARDC	
	1999	2000	1999	2000
kg N ha $^{-1}$	GDD			
0	549	492	485	501
60	505	465	453	469
120	493	468	448	470
SE	5	4	6	4

TABLE 6. Grain yields for corn (dry weights) grown in weed-free (wf) and weedy (wdy) conditions for three N application rates along with the average critical timing of weed removal (CTWR^a) at the University of Nebraska Haskell Agricultural Laboratory (HAL) near Concord, NE, and the Agricultural Research and Development Center (ARDC) near Mead, NE, in 1999 and 2000.

N rate	Corn grain yields ^b								CTWR
	HAL				ARDC				
	1999		2000		1999		2000		
	wf	wdy	wf	wdy	wf	wdy	wf	wdy	
kg N ha ⁻¹	Mg ha ⁻¹								
0	5.24 a	2.10 a	6.44 a	3.20 a	8.72 a	2.36 a	6.23 a	2.25 a	V2
60	5.59 a	2.34 a	6.93 a	3.85 ab	10.83 b	3.87 ab	7.47 b	4.00 b	V4
120	5.77 a	3.70 b	6.71 a	4.36 b	10.85 b	3.89 b	8.07 b	4.38 b	V6
SE	0.32	0.32	0.33	0.33	0.62	0.62	0.42	0.42	

^a The CTWR is defined as the growth stage of corn at which time weed removal is required to avoid a loss in yield of >5% of the weed-free control.
^b Means within a column followed by a different letter are significantly different from one another based on a *t* test at the 0.05 level.

² Monsanto Inc., 800 North Lindbergh Boulevard, St. Louis, MO 63167.

³ LI-3100, LI-COR, Inc., 4421 Superior Street, Lincoln, NE 68504.

⁴ SAS version 8.0, Statistical Analysis Systems Institute, SAS Campus Drive, Cary, NC 27512.

⁵ AXUM version 5.0, Technical graphics and data analysis, Math Soft Engineering and Education, Inc., 101 Main Street Cambridge, MA 02142-1521.

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