PLANT AND N IMPACTS ON CORN (*Zea mays*) GROWTH: WHATS CONTROLLING YIELD?

D.E. Clay, S.A. Clay, and G. Reicks

Plant Science Department
South Dakota State University, Brookings, SD and

D. Horvath,

USDA-ARS
Fargo, ND

ABSTRACT

Studies were conducted in South Dakota to assess mechanisms of intraspecific competition between corn (*Zea mays*) plants. Treatments were two plant populations (74,500 and 149,000 plants ha^{-1}), three levels of shade (0, 40, and 60%) on the low plant population, two water treatments (natural precipitation and natural + irrigation), and two N rates (0 and 228 kg N ha^{-1}). In-season leaf chlorophyll content was measured. At harvest, grain and stover yields were quantified with grain ^{13}C-discrimination (Δ) and N percent determined. Soil samples at harvest were collected and analyzed for soil water and inorganic N. Grain yield per plant decreased when shaded or when planted at high population. If similar mechanisms reduced yield in shade and high population treatments, then we expected that plant and soil responses would be similar. However, differences in several key measurements were noted and suggest that factors responsible for yield reductions in these treatments differed. These differences included 1) grain N% was minimally impacted at high population, whereas N% increased in shade treatments; 2) chlorophyll levels in plants grown in high N/irrigated treatments with or without shade either increased or were not impacted by treatment whereas chlorophyll levels in plants grown in high populations decreased compared with levels measured in plants in low population; 3) grain from plants grown in high N/irrigated treatments with shade had increased Δ (0.27‰), whereas Δ was not impacted by population level; and 4) population level did not impact the amount of available water or inorganic N remaining in the surface 60 cm of soil at harvest. The mechanism responsible for the yield reduction in shade treatments was attributed to reduced light availability, whereas at high population, reduced yield was attributed to reduced growth of plants.

Keywords: precision farming, genomics, microarray, stable isotopes, shade

INTRODUCTION

Corn has been bred to grow at high populations with yields per field gradually increasing as population increases to an optimum value (Nafziger, 2006). Associated with the per unit area yield increase are reduced per plant yields. The mechanisms responsible for the decreased yield per plant are not well understood. It is difficult to implement precision plant populations without understanding how plants compete.

The ability of corn to respond to competition is influenced by the plant growth stage, population, and plant plasticity. Plasticity generally decreases with increasing growth stage and increases with decreasing plant population (Nafziger, 2006; Sarlangue et al., 2007). Plants may detect potential competition by detecting changes in the amount of far-red light sorbed by leaves. Corn in closely spaced conditions receive more reflected far-red and higher far-red/red ratios, and crowded seedlings typically have longer, narrower leaves, longer stems, and less massive root systems (Kasperbauer and Karlen, 1994). Kasperbauer and Karlen (1994) also reported that corn morphological responses to far-red/red ratios were not dependent on the cause of the altered ratio.

Competition occurs between plants of the same species (intraspecfic) as well as plants of different species (interspecific) (Doerge et al., 2002; Al Kaisi aand Yin, 2003; Heshermi, et al., 2005; Nafziger, 2006; Saulangue et al., 2007). Plant response to competition may be to 1) modify growth characteristics to aggressively compete, 2) fail to compete, or 3) have little or no response.

Measurable outcomes for aggressive competition might be enhanced shoot growth (i.e. taller plants), and up-regulation of auxin and photosynthetic capability (shade avoidance) (Smith and Whitelam, 1997; Ballaré and Casal, 2000; Rajcay et al., 2004; Horvath et al., 2007). In addition, plants may aggressively compete for resources, observed in soil samples with reduced available water (Norwood, 2001) or nutrients.

Measurable outcomes if a plant does not compete well with neighboring plants may be down regulation of photosynthetic capacity (Horvath et al., 2006) and yield loss on a per plant basis. The shade avoidance response has been shown to undergo adaptive evolution (Schmitt, 1997). The domestication process may have selected for corn plants with low shade avoidance mechanisms and this may partially explain why relatively uniform corn yields are observed even when planted at very high densities (Pierik et al., 2004). By better understanding corn response to competition, it is likely that weed control and plant density decisions can be improved.

The objective of this research was to assess the mechanisms responsible for intraspecific competition in corn. In this study, grain ^{13}C isotopic discrimination (Δ)
was used in conjunction with yield and N status at harvest and in-season chlorophyll content to assess plant stress. The grain Δ values were quantified because they provide additional information about how environmental stress impacts plant growth and development (Clay et al., 2001).

MATERIALS AND METHODS

Experiment 1: Shade impact on yield and grain Δ

A 2-yr (2005-2006) study was conducted at Aurora, SD to measure shade impact on corn yield and grain Δ. The longitude and latitude at the site was 96° 40’ west and 44° 18’ north, respectively. The soil parent materials were loess over glacial outwash, and the soil series was a Brandt silty clay loam (fine-silty, mixed, superactive, frigid Calcic Hapludolls). The surface horizon contained approximately 110 g sand, 580 g silt, and 310 g clay kg^{-1}. Total nitrogen in the 0-15 and 15-60 cm depths were approximately 5.1 and 10.2 Mg N ha^{-1}, respectively. Total C in the 0-15 and 15-60 cm depths were approximately 44.6 and 78.5 Mg C ha^{-1}, respectively. Additional information about the site is available in Clay et al. (1994) and Clay et al. (1995).

Corn was seeded in 76 cm rows at a rate to achieve a population of 74,500 plants ha^{-1}. Treatments were three shade treatments (0, 40, and 60% shade), two water rates [natural rainfall (dryland) and natural plus supplemental (irrigated)], and two N rates (0 and 228 kg N ha^{-1}). Shade cloths were applied at V5 and enclosed a 2 m^2 area. A spectral radiometer was used to determine the efficiency of the shade cloths.

Precipitation in 2005 was 57.2 cm and an additional 9.5 cm was applied in the irrigated treatment (66.7 cm total water). In 2006, total growing season water was 32 cm and an additional 22 cm (54 cm) was added in the irrigated treatment. Mass balance calculations at the sites between 2002 and 2004 indicated that irrigation water supplied about 15 kg N (ha year)$^{-1}$ (Kim et al., 2008).

Soil samples were collected in the spring and fall each year from the 0-15, 15-30, 30-45, 45-60, and 60-75 cm soil depths. Soil samples were analyzed for gravimetric soil moisture and inorganic N. For inorganic N analysis, soil samples were air-dried (35 ^{o}C), ground (2 mm), extracted with 1.0 M KCl, and analyzed for ammonia and nitrate-N using the phenate and Cd reduction methods, respectively (Maynard and Kalra, 1993). In 2005, preseason inorganic N was 105 kg (NH_4 + NO_3-N) ha^{-1} with 60% in the nitrate form. In 2006, preseason inorganic N was 153 kg (NH_4 + NO_3-N) ha^{-1} with 32% of the N in the nitrate form.

Chlorophyll was measured on the most recently expanded leaf using a SPAD chlorophyll meter. Measurements were taken on 5 July, 19 July, and 23 August in 2005, and on 12 July 2006. In 2005, readings were taken and averaged from 5 plants located near the center of each plot, whereas in 2006 meter readings were the average of 10 plants per plot.

Corn ears and stover were harvested at physiological maturity. Grain yield was quantified after drying, removing grain from the cob, and adjusting to 15% moisture. Grain and stover samples were analyzed for total N, δ^{15}N, total C, and ^{13}C discrimination (Δ) (Farquar and Lloyd, 1993; Clay et al., 2003).

The experimental design was a split-block split-plot with water as the main block, fertilizer as a subplot, and shade level as a sub-subplot. All treatments were replicated 4 times each year. ANOVA was used to determine treatment differences.

Experiment 2: Intraspecific Competition for Resources

The experiment described above included additional treatments where corn was planted at a population of 149,000 plants ha^{-1}. This density was achieved by planting corn into interrow areas, so that row spacing was 38 cm. The high corn population was grown in two soil moisture regimes (moderate and high) and fertilized at two N rates (0 and 228 kg N ha^{-1}). Preseason and post season soil samples were collected and analyzed for soil water and inorganic N. Corn grain and stover yield were measured as described above. Grain and stover samples were analyzed for total N, δ^{15}N, total C, and Δ. The Δ values were used to calculate yield losses due to water and N stress (Clay et al., 2005). Four replications were placed into the above experiment. ANOVA was used to determine treatment differences.

RESULTS AND DISCUSSION

Experiment 1: Shade Impacts on Plant Characteristics

Higher yields were measured in 2005 compared with 2006 due to the drier conditions in 2006. The three-way interaction of shade/fertilizer/water averaged over years was significant for yield on an area and per plant basis, above ground biomass, % N in grain, and relative chlorophyll (Table 1). Shade, low N, and dryland conditions

Table 1. The influence of shade, N rate, and water regime on grain yields, above ground biomass production, ^{13}C discrimination (Δ), grain N percentage, and relative chlorophyll (normalized by dividing the obtained value by the highest obtained value each year).

Shade	N rate	Water regime	Grain yield	Grain yield	Above ground biomass	Δ	Grain N Percent	Relative chloro.	Inorganic N Harvest	Soil water Harvest
%	kg/ha		kg/ha	g/plant	kg/ha	‰	%		kg/ha	cm
0	0	Dryland	10,330	139	19,560	3.33	1.33	0.82	105	22
0	228	Dryland	12,330	167	21,960	3.35	1.47	0.92	155	25
0	0	Irrigated	12,040	162	21,800	3.27	1.36	0.84	100	23
0	228	Irrigated	12,770	172	22,620	3.30	1.42	0.87	174	26
40	0	Dryland	8,980	121	15,300	3.36	1.40	0.90	96	23
40	228	Dryland	8,970	120	15,700	3.37	1.45	0.91	231	22
40	0	Irrigated	9,280	125	16,330	3.31	1.39	0.90	113	23
40	228	Irrigated	9,030	121	15,760	3.43	1.48	0.93	183	23
60	0	Dryland	6,410	86	11,890	3.67	1.55	0.90	126	23
60	228	Dryland	6,140	82	10,930	3.69	1.56	0.91	119	23
60	0	Irrigated	6,520	88	12,800	3.51	1.50	0.88	171	23
60	228	Irrigated	6,100	82	11,200	3.58	1.54	0.90	193	23
P			0.006	0.006	0.015	0.806	0.067	0.024	0.238	0.55
Main	effects									
Shade										
0			11,870	160	21,500	3.31	1.40	0.86	133	24
40			9,060	122	15,800	3.37	1.42	0.91	156	23
60			6,290	85	11,700	3.61	1.54	0.90	152	23
P			0.0001	0.001	0.0001	0.0001	0.0001	0.0001	0.01	0.05
Water		dryland	8,860		15820	3.46	1.46	0.89	150	23
		irrigated	9,290		16800	3.40	1.45	0.89	149	24
P			0.270		0.080	0.30	0.685	0.855	0.95	0.14

N rate	0	8,925		16210	3.41	1.42	0.87	118	23
	228	9,220		16400	3.45	1.48	0.91	176	24
P		0.141		0.0588	0.041	0.0001	0.0001	0.001	0.04
Year									
2005		9,750	131	17,290	3.30	1.47	0.89	174	23
2006		8,399	113	15,330	3.56	1.44	0.89	124	23
P		0.009	0.009	0.067	0.003	0.376	0.70	0.021	NS

reduced corn yield on an area and per plant basis from 45 to 60% compared with unshaded, well fertilized, irrigated plants. These reductions were directly attributable to reduced available light. Corn under shade actually had higher relative chlorophyll content, but was not influenced by N or water. Under full sun, chlorophyll was higher in high N treatment in both dryland and irrigated treatments.

The Δ value of grain was influenced by the main effects of shade and nitrogen but not by water (Table 1). Shade and fertilizer addition increased Δ in both years. The impact of shade on Δ was greatest in the 60% treatment. Previous research has shown that Δ is influenced by N and water stress (Clay et al., 2005). The impact of water stress on Δ values das been attributed to: 1) closure of the stomata resulting from water stress; 2) ^{13}C depletion of gaseous CO_2 in the stomata resulting from the ^{13}C enrichment and fixation of H_2CO_3; and 3) increased ^{13}C fixation of ^{13}C depleted CO_2 following stomatal closure. The measured effect of shade on Δ would be consistent with equation 1 if shade increased CO_2 leakage from the bundle sheath cells.

Experiment 2: Intraspecific Competition for Resources

Yield on a per area basis was increased by N fertilizer and population but not both (Table 2). The per plant yield was reduced in high population vs low population and low vs high N rate. In low plant populations, N and water application impacted per plant yield. The amount of water contained in the soil was influenced by population level at harvest and averaged 24 and 22 cm of water contained in the 0-75 cm depth in the 74,500 and 149,000 population levels, respectively. Similar results were observed on 10 July 2006, where 12.5 and 12.1 cm of water were contained in the surface 60 cm of soil in the 74,500 and 149,000 plants ha^{-1} treatment, respectively.

Increasing the plant population from 74,000 to 149,000 plants ha^{-1} resulted in a slightly higher grain yield per ha (kg ha^{-1}) and reduced yields per plant (Table 3). The grain yields per plant in the 149,000 plants per ha treatment were similar to the yields in the 60% shade treatments. Based on only yield information, yield similarities would seem to indicate that yield reductions were the direct result of plant competition for light.

If similar mechanisms reduced the yields in the shade and 149,000 plant per ha treatment, similar plant responses should be measured. However, for several key measurements this was not the case. Grain N percent was minimally impacted by population level, whereas in the shade experiment N% increased with shade. The higher N% in the shade plots were attributed to luxury N uptake and not N deficiencies.

Shade and plant population had different impacts on chlorophyll content. In the shade plots, chlorophyll increased in shade while in the population study, chlorophyll decreased with increasing population. Based on the grain N percentages this decrease was not attributed to higher N deficiencies. In addition, plants growing in the high population were more efficient at using soil and fertilizer N, which resulted in lower amount of residual N remaining in the soil at harvest.

Shade and population level also had different impacts on Δ. In the shade experiment, Δ increased with shade, whereas in the population study Δ was not impacted by population. Differences in key plant measurements suggest that the plants responses to shade and high population densities were different.

Table 2. The influence of plant population, N rate, soil moisture regime on yield, above ground biomass, ^{13}C discrimination, N percentage, chlorophyll, yield loss to N stress (YLNS), and yield loss to water stress (YLWS).

Plant Population	N	Water regime	Grain Yield	Grain Yield	Above ground biomass	Δ	Grain N%	Relative Chlor.	YLNS	YLWS	Soil water	Inorganic N-harvest
Plants/ha	kg/ha		kg/ha	g/plant	kg/ha	‰			kg/ha	kg/ha	100*g/g	kg/ha
74,500	0	Dryland	10330	139	19160	3.33	1.33	0.86	2,187	2046	21.7	103
74,500	228	Dryland	12330	167	22000	3.35	1.47	0.96	1,270	1167	25.2	178
74,500	0	Irrigated	12090	162	21800	3.27	1.36	0.89	1,601	919	23.1	101
74,500	228	Irrigated	12770	172	22900	3.30	1.42	0.92	1,254	349	26.5	212
149,000	0	Dryland	12410	83	22700	3.20	1.29	0.80	1,611	736	20.5	101
149,000	228	Dryland	13200	89	24500	3.28	1.39	0.86	1,465	896	22.4	105
149,000	0	Irrigated	13570	91	24300	3.12	1.34	0.76	1098	444	22.9	132
149,000	228	Irrigated	13470	91	24900	3.23	1.33	0.85	968	372	22.7	159
p			0.283	0.06	0.81	0.289	0.657	0.13	0.25		0.276	0.004
Population												
74,500			11870	160	21450	3.31	1.39	0.91	1566	1120	24.13	149
149,000			13160	88	24100	3.20	1.34	0.82	1285	612	22.14	124
			0.0002	0.0001	0.0001	0.0001	0.08	0.0001	0.088		0.03	0.03
N rate												
	0		12090	119.3	21970	3.23	1.33	0.82	1629	1211	22.1	109
	228		12986	128.9	23600	3.29	1.40	0.90	1238	521	24.2	163
p			0.011	0.005	0.007	0.015	0.03	0.001	0.026		0.02	0.0001
Water												
		Dryland	12070	119	22210	3.28	1.37	0.87	1630	1211	22.4	122
		Irrigated	13000	129	23470	3.23	1.36	0.86	1230	521	23.8	151
p			0.1949	0.165	0.214	0.459	0.91	0.36	0.1		0.144	0.077
Year												
2005			13270	132	24290	3.09	1.37	0.88	1520		23.35	173
2006			11762	115	21270	3.42	1.36	0.84	1343		22.92	100
p			0.0528	0.037	0.077	0.004	0.75	0.116	0.44		0.64	0.002

Understanding Competition

Based on the measured Δ values and calculated yield losses due to water and N stress in the population study, the differences between the well fertilized and irrigated plots in the full sun and shaded plots, could not be directly attributable to light, N, or water stress. This is based on the observations: 1) that if light stress reduced yields, then Δ should be higher in the 149,000 plants ha^{-1} treatment than the 74,500 plants ha^{-1} treatment; 2) if water stress reduced yields, then Δ should be higher in the 149,000 plants ha^{-1} treatment than the 74,500 plants ha^{-1} treatment and soil water levels should be lower in the high population treatment; and 3) if N stress reduced yields then Δ and grain N percentages should be lower in the 149,000 plants ha^{-1} fertilized treatments than the 74,500 plants ha^{-1} treatment.

The chlorophyll data may provide a clue as to the plants response to high population. Corn grown in the 149,000 plants ha^{-1} treatment had lower chlorophyll measurements than corn grown in the 74,500 plants ha^{-1} treatment. Lower chlorophyll contents were not attributed to higher N stress because corn in both populations had similar grain N percentages and the field contained a substantial amount of inorganic N at harvest (over 100 kg N ha^{-1} in well fertilized and irrigated plots at harvest in 2005 and 2006). For example, in the well fertilized and irrigated plots, chlorophyll meter readings averaged 54 and 49 in the 74,500 and 149,000 plants ha^{-1} treatments, respectively.

Different results were observed in the shade plots, where corn grown under shade had similar chlorophyll contents as the full sunlight treatment. These results suggest corn in 149,000 plants ha treatment reduces its' chlorophyll content, while this response was not observed in corn grown under shade. The differences between the shade and population treatment most likely are related to different mechanism controlling yield in the shade and high population treatments.

Differences between the shade and population rates studies may be related to light quality. Weinig (2000) evaluated competition between corn and velvetleaf (*Abutilon theophrasti*). They exposed corn and corn + velvetleaf to different shade treatments at different growth stages. Weinig (2000) concluded that, "reliable environmental cues enable individuals to facultatively adopt highly elongated, costly phenotypes in crowded patches while avoiding the cost of that phenotype in less crowded microsites." Rajcan et al. (2004) reported that corn responds to competition even though competition did not occur. They and others hypothesized that the stimuli inducing shade avoidance mechanisms was the far-red to red ratio (Kasperbauer and Karlen, 1994). Kassperbauer and Karlen (1994) concluded that early morphological responses of corn seedlings are not dependent on the cause of the altered ratio. In the shade treatment the plant would not detect changes in the ratio while they would in the high population treatment

Plant response to perceived and actual competition for resources may be more extensive than stem elongation and reduced root growth. Horvath et al. (2006) used the microarray approach to assess the impact of velvetleaf (*Abutilon theophrasti*) on the responses of corn to competition in plots adjacent to those discussed in this paper in 2005. Plant samples were collected at the V11 growth stage. At this growth stage, corn and velvetleaf were approximately 1.5 and 0.5 m tall, respectively. It was found that velvetleaf competition with corn resulted in the down regulation of 240 and up-regulation of 13 genes in corn. Down regulated genes in corn were glutamate dehydrogenase, PEP carboxylase, ribulose 1,5-bisphosphate carboxylase/oxygenase, and NADP dehydrogenase, nitrate reductase, aspargine synthetase, and glutamate binding. The down regulated genes suggests that in response to crowding, corn reduced its' C fixing potential (PEP carboxylase and ribulose 1,5-bisphosphate carboxylase/oxygenase were both down regulated). Differential C fixing capacity in the shade and population study discussed above could explain the measured differences in Δ and chlorophyll values.

Based on these results we attributed the per plant yield reduction in the shade and high population study to different mechanisms. In the shade experiment, light limitation reduced yields whereas in the high population treatment lower yields were the result of corn implementing its' shade avoidance mechanisms. In this case the shade avoidance mechanism was down-regulation of the plants photosynthetic capacity.

The process of selecting plants that grow well at high population may impact the plants responses to competition. Recent work reported by Horvath et al. (2007) showed that velvetleaf in competition with corn and velvetleaf grown alone resulted in the opposite impacts, i.e. velvetleaf in corn up-regulated many genes involved in photosynthesis. In summary, differences between the shade and population studies suggest that the factors responsible for the per plant yield reduction in corn were different. The mechanisms responsible for the yield reduction in the shade plots were attributed to reduced light availability, whereas reduced yield per plant in the high populations were attributed to reduced growth on a per plant basis.

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