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Per-plant eco-physiological responses of maize to varied nitrogen availability at low and high plant densities

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Introduction

As with many plant species, field crops routinely experience both intra- and inter-specific competition for limited resources during a growing season. Given the well-established negative relationship between inter-specific competition and plant productivity, plant-plant interaction studies in field crops have principally focused on crop-weed interactions. While a limited number of experiments has explored aspects of intra-specific competition in crops such as maize (*Zea mays* L.) and soybean [*Glycine max* (L.) Merr.] (e.g., Vega and Sadras, 2003), a majority of studies focusing on intra-specific competition in plant monocultures have been performed by ecologists using species not commonly grown in crop production systems (e.g., Weiner and Thomas, 1986). Those studies which have intensively investigated intra-specific competition in field crops have predominately focused on responses to increased plant density (e.g., Edmeades and Daynard, 1979; Maddonni and Otegui, 2004). Few investigations have considered the impacts of nitrogen (N) availability on intra-specific competition in field crops. This is particularly true in maize, which is strongly dependent upon N application for high productivity. As N fertilizer prices fluctuate upwards, environmental concerns over excessive N application increase, and recommended maize plant densities move progressively higher, it is crucial that both the crowding tolerance and N stress tolerance of current maize germplasm continue to be investigated and improved. Fundamental to these efforts is an understanding of the per-plant eco-physiological responses of modern maize to above- and below-ground intra-specific competition. By describing individual plant behavior within a community context, such an understanding can provide insight into avenues for genetic improvement not offered by more simplistic canopy-level investigations. Thus the objective of this field study was to examine the per-plant eco-physiological responses of modern maize genotypes to varied N availability at both low and high plant densities and, in so doing, to improve the ideotype employed by the maize breeding community for the enhancement of abiotic stress tolerance.

Materials and Methods

Field research during the 2006 and 2007 growing seasons was conducted at the Purdue University Agronomy Center for Research and Education (ACRE) (40°28'07" N, 87°00'25" W) near West Lafayette, Indiana. In each year, maize was grown following no-till soybean. The study was arranged as a split-split-plot design with four blocks. Hybrid (main plot), plant density (subplot), and N rate (sub-subplot) served as the three treatment factors. The Pioneer hybrids 31G68 and 31N28 were planted to achieve final plant densities of 54,000 and 104,000 plants ha⁻¹. For all plots, starter fertilizer (10-34-0) was applied at planting 5 cm to the side and 5 cm below the seed at a rate equivalent to 25 kg N ha⁻¹. Urea Ammonium Nitrate (UAN) (28-0-0) was applied via side-dressing at a rate equivalent to 165 kg N ha⁻¹ once (V3), twice (V3, V5), or not at all, depending upon each plot's prescribed N rate. All other nutrients were kept non-limiting. See Boomsma et al. (2009) for a more complete description of this experiment and mean grain yield responses to treatment combinations.

In a designated sampling area ($\approx 6 \text{ m}^2$) within each plot, extensive, non-destructive, eco-physiological measurements were taken on tagged plants from seedling emergence through physiological maturity. Discussion here is limited to the following per-plant parameters: R1 green leaf area (LA_P), R1 SPAD, anthesis-silking interval (ASI_P), grain yield (GY_P), R6 aboveground total biomass (TB_P), and harvest index (HI_P). At R1 in both years, LA_P was determined using a modified procedure from Valentinuz and Tollenaar (2006). Per-plant SPAD measurements at R1 were taken on each plant's uppermost earleaf. For determination of ASI_P ,

anthesis and silking were defined according to Borrás et al. (2007). In each year, GY_P was corrected to 0% moisture content. For each plant, $R6\ TB_P$ was calculated as the sum of each plant's GY_P and $R6$ vegetative biomass (VB_P). In both years, $R6\ VB_P$ was determined using a modification of the allometric model-based procedure employed by Maddonni and Otegui (2004). For each plant, HI_P was calculated as the quotient of GY_P and $R6\ TB_P$. Plant-to-plant variability for each of these six parameters was calculated on a plot-level basis using the coefficient of variation (CV) or standard deviation (SD). To examine plant hierarchy responses, plants were ranked in ascending order by GY_P within each plot. The cumulative frequency was calculated for each plant based upon its respective rank. A plant was classified as dominated, intermediate, or dominant when its GY_P rank position was in the lowermost 25%, middle 50%, or uppermost 25% of the plot-level population of plants, respectively. Each plant was thus assigned to a single plant group based solely upon its GY_P .

For all analyses of variance (ANOVA), hybrid was treated as a random effect. For ANOVA on plant hierarchy responses, the study was analyzed as a split-split-plot design with plant density (main plot), side-dress N rate (subplot), and plant group (sub-subplot) serving as the three treatment factors. For ANOVA on plant-to-plant variability responses, the study was analyzed as a split-plot design with plant density (main plot) and side-dress N rate (subplot) serving as the two treatment factors. In all instances, ANOVA was performed using SAS PROC MIXED. When treatment effects were significant at $P = 0.05$, least-squares mean (LS-mean) separation tests were performed for appropriate fixed effects.

Results

As indicated in Tables 1 and 2, the application of $165\ kg\ ha^{-1}$ of side-dress N often increased each set of mean values (i.e., overall, dominated, intermediate, and dominant) for $R1\ LA_P$, $R1\ SPAD$, GY_P , $R6\ TB_P$, and HI_P and additionally decreased these mean values for ASI_P at both the low and high plant densities for each year. For either plant density in both years, a second side-dress N application often had a minimal effect on each set of means. Depending upon the parameter, the $104,000\ plants\ ha^{-1}; 0\ kg\ N\ ha^{-1}$ treatment combination often exhibited either the lowest or highest values for the overall, dominated, intermediate, and dominant means in both years. Regardless of year or treatment combination, values for each parameter (except ASI_P) were nearly always lower for the dominated relative to intermediate and dominant plant group(s). For all parameters but ASI_P , the application of either 165 or $330\ kg\ N\ ha^{-1}$ often decreased the dominant group/dominated group mean ratio in both years for either plant density. In both years, increasing plant density produced the opposite effect for these parameters regardless of N rate. For these same parameters, the highly crowded, low-N treatment combination often exhibited the numerically greatest dominant group/dominated group mean ratio in both years.

As evident in Table 3, an initial application of $165\ kg\ N\ ha^{-1}$ at either plant density resulted in a decrease in plant-to-plant variability for some parameters in 2006 and/or 2007. Regardless of year or plant density, a second side-dress N application rarely impacted plant-to-plant variability for all parameters. The highly crowded, low-N environment exhibited the highest plant-to-plant variability for $R1\ SPAD$ and ASI_P in 2006 and for GY_P and HI_P in both 2006 and 2007.

As shown in Figure 1A-D, the high plant density, low-N environment displayed a greater frequency of barrenness and a higher frequency of low-yielding plants than the low plant density, high-N environment in both years. For the highly crowded, low-N environment, low-yielding plants displayed markedly high ASI_P values in both years (Figure 1B,D).

As displayed in Figure 2A-D, the high plant density, low-N environment displayed a higher frequency of poorly productive plants than the low plant density, high-N environment in both years. In the high plant density, low-N environment, HI_P pronouncedly declined with decreasing R6 TB_P in both years (Figure 2B,D). Contrarily, in the low plant density, high-N environment, HI_P was relatively stable across R6 TB_P values in both years (Figure 2A,C).

Table 1. Plant density and nitrogen (N) rate effects on maize R1 per-plant green leaf area (LA_P), R1 per-plant SPAD, and per-plant anthesis-silking interval (ASI_P) for 2006 and 2007. Within each data cell for each parameter, the top number indicates the overall mean for all plants for that treatment combination while the lower set of numbers indicates the means (from left to right) for the dominated, intermediate, and dominant plant groups for that treatment combination.

Year	Plant density	N rate	R1 LA_P	R1 SPAD	ASI_P		
	plants ha^{-1}	kg N ha^{-1}	$cm^2 plant^{-1}$		days		
2006	54,000	0	5176a ¹	44a	0.5a		
		165	4763aA ² /5231aB/5537aC	41aA/45aB/47aC	1.0aA/0.4aB/0.0aB		
		330	6495bA/7222bB/7472bC	55bA/59bB/61bC	0.5aA/0.1aB/0.0aB		
		104,000	0	3522a³	36a	2.8a	
		165	3047aA/3547aB/3974aC	32aA/36aB/39aC	4.6aA/2.7aB/1.3aC		
		330	6664bA/7313bB/7581bC	57bA/60bB/61bB	0.7aA/0.1aB/0.0aB		
	2007	54,000	0	5166a	44a	0.2a	
			165	4555aA/5227aB/5715aC	39aA/44aB/48aC	1.0aA/-0.0aB/-0.4aB	
			330	6184bA/6829bB/7245bC	55bA/57bB/60bC	0.1bA/-0.4aB/-0.6aB	
			104,000	0	2891a	36a	3.0a
			165	2470aA/2941aB/3262aC	33aA/36aB/39aC	4.7aA/3.0aB/1.4aC	
			330	6123bA/7151bB/7345bB	54bA/58bB/59bB	0.2abA/-0.5aB/-0.5aB	
104,000		0	2891a	36a	3.0a		
		165	4957b	50b	1.2b		
		330	4337bA/5022bB/5513bC	45bA/51bB/54bC	2.3bA/1.1bB/0.1bC		
		104,000	0	2891a	36a	3.0a	
		165	4957b	50b	1.2b		
		330	5095b	51b	1.3b		
			4444bA/5153bB/5687bC	47bA/52bB/55bC	2.8bA/1.0bB/0.2bC		

¹ For a given type of mean within column, year, and plant density, means with different lowercase letters indicate statistically significant differences at $P \leq 0.05$.

² Within column, year, plant density, and N rate, means with different uppercase letters indicate statistically significant differences between plant groups at $P \leq 0.05$.

³ For a given type of mean, a bolded value indicates that the 104,000 plants ha^{-1} ; 0 kg N ha^{-1} treatment combination exhibits the lowest or highest value for that parameter in that year.

Discussion

As evidenced by pronouncedly low LA_P and SPAD values at R1, severe intra-specific competition for N in the highly crowded, low-N environment before and during flowering resulted in reductions in per-plant source activity around silking. As indicated by high ASI_P values for this treatment combination, such decreases in C assimilation severely reduced C partitioning to the developing ear at silking, particularly among dominated plants (Borrás et al., 2007). Exceptionally low GY_P , R6 TB_P , and HI_P values among plants in this treatment

combination suggest that C partitioning to the developing grain was further limited during the grain-filling period, especially among dominated plants. Thus, as suggested by (i) high dominant group/dominated group mean ratios for most parameters; (ii) high CV values for R1 SPAD, ASI_P, GY_P, and HI_P; and (iii) high frequencies of barren, low-yielding, poorly productive plants; severe intra-specific competition in the highly crowded, low-N environment led to the formation of plant hierarchies composed of dominated individuals with a diminished amount of source activity and a drastically decreased ability to partition C to developing grain (Maddonni and Otegui, 2004; Pagano and Maddonni, 2007). Overall, such results suggest that adequate N availability is critical for high grain production in crowded maize stands (Boomsma et al., 2009) since it reduces plant-to-plant variability for key eco-physiological traits and limits the formation of plant hierarchies. Maize genetic improvement efforts in abiotic stress tolerance should focus on (and potentially select for) enhanced by-plant uniformity under stress conditions. Improved uniformity requires (i) greater C partitioning to the developing grain among dominated plants and/or (ii) improved compensatory grain production among dominant individuals.

Table 2. Plant density and nitrogen (N) rate effects on maize per-plant grain yield (GY_P), R6 per-plant aboveground total biomass (TB_P), and per-plant harvest index (HI_P) for 2006 and 2007. Within each data cell for each parameter, the top number indicates the overall mean for all plants for that treatment combination while the lower set of numbers indicates the means (from left to right) for the dominated, intermediate, and dominant plant groups for that treatment combination.

Year	Plant density	N rate	GY _P	R6 TB _P	HI _P
	plants ha ⁻¹	kg N ha ⁻¹	g plant ⁻¹	g plant ⁻¹	g g ⁻¹
2006	54,000	0	118a ¹	234a	0.49a
		165	85aA ² /120aB/148aC	186aA/236aB/280aC	0.44aA/0.51aB/0.53aB
		330	140bA/195bB/225bC	265bA/347bB/399bC	0.51bA/0.56bB/0.56aB
		104,000	155cA/204bB/230bC	285cA/366bB/413bC	0.51bA/0.56bB/0.56aB
		0	52a³	127a	0.36a
		165	19aA/54aB/82aC	85aA/127aB/168aC	0.19aA/0.42aB/0.48aC
	104,000	165	102b	190b	0.51b
		330	61bA/109bB/136bC	131bA/199bB/241bC	0.42bA/0.55bB/0.56bB
		0	110b	209b	0.50b
		165	67bA/116bB/148bC	147bA/215bB/264cC	0.41bA/0.54bB/0.56bB
		330	80aA/120aB/157aC	176aA/244aB/311aC	0.42aA/0.49aB/0.50aB
		104,000	148bA/186bB/218bC	259bA/346bB/407bC	0.51bA/0.54bB/0.54bB
2007	54,000	0	119a	244a	0.47a
		165	80aA/120aB/157aC	176aA/244aB/311aC	0.42aA/0.49aB/0.50aB
		330	137bA/186bB/218bC	259bA/346bB/407bC	0.51bA/0.54bB/0.54bB
		104,000	148bA/194bB/224bC	277bA/358bB/414bC	0.52bA/0.54bA/0.54bA
		0	56a	129a	0.40a
		165	28aA/58aB/83aC	89aA/130aB/168aC	0.28aA/0.44aB/0.49aC
	104,000	165	96b	187b	0.49b
		330	56bA/101bB/132bC	122bA/193bB/248bC	0.41bA/0.52bB/0.53bB
		0	103b	197b	0.50b
		165	59bA/108bB/141bC	127bA/204bB/260bC	0.42bA/0.53bB/0.54bB
		330	103b	197b	0.50b
		104,000	59bA/108bB/141bC	127bA/204bB/260bC	0.42bA/0.53bB/0.54bB

¹ For a given type of mean within column, year, and plant density, means with different lowercase letters indicate statistically significant differences at $P \leq 0.05$.

² Within column, year, plant density, and N rate, means with different uppercase letters indicate statistically significant differences between plant groups at $P \leq 0.05$.

³ For a given type of mean, a bolded value indicates that the 104,000 plants ha⁻¹; 0 kg N ha⁻¹ treatment combination exhibits the lowest or highest value for that parameter in that year.

Table 3. Plant density and nitrogen (N) rate effects on maize plant-to-plant variability for R1 green leaf area (R1 LA_{CV}), R1 SPAD (R1 SPAD_{CV}), anthesis-silking interval (ASI_{SD}), grain yield (GY_{CV}), R6 aboveground total biomass (R6 TB_P), and harvest index (HI_P) for 2006 and 2007.

Year	Plant density plants ha ⁻¹	N rate kg N ha ⁻¹	R1 LA _{CV} ¹	R1 SPAD _{CV}	ASI _{SD} ²	GY _{CV}	R6 TB _{CV}	HI _{CV}
			%		Days	%		
2006	54,000	0	9.2a ³	9.7a	1.0a	22.3a	16.4a	9.5a
		165	8.9a	8.3a	0.8a	20.6a	17.1a	9.1a
		330	10.4a	9.2a	0.9a	18.2a	16.5a	9.3a
	104,000	0	15.3a	13.9a⁴	1.9a	51.5a	27.2a	39.7a
		165	12.8ab	9.9b	1.2b	31.3b	23.7ab	20.7b
		330	11.5b	8.5b	1.2b	30.2b	22.9b	19.1b
2007	54,000	0	12.6a	12.2a	1.3a	27.2a	23.1a	13.5a
		165	10.4a	8.0b	1.0a	20.1b	19.2ab	7.8a
		330	13.5a	9.0b	1.1a	17.6b	17.0b	7.0a
	104,000	0	15.9a	11.3a	2.0a	40.2a	24.5a	26.3a
		165	14.5a	10.7a	1.7a	32.5b	27.7a	19.0b
		330	13.8a	10.2a	1.7a	32.5b	27.5a	18.6b

¹ CV, coefficient of variation.

² SD, standard deviation.

³ Within column, year, and plant density, means with different lowercase letters indicate statistically significant differences at $P \leq 0.05$.

⁴ A bolded value indicates that the 104,000 plants ha⁻¹; 0 kg N ha⁻¹ treatment combination exhibits the lowest or highest value for that parameter in that year.

Figure 1. Frequency distributions for per-plant grain yield (GY_P) and scatter plots for per-plant anthesis-silking interval (ASI_P) values for the 54,000 plants ha⁻¹; 330 kg N ha⁻¹ (A,C) and 104,000 plants ha⁻¹; 0 kg N ha⁻¹ (B,D) treatment combinations in 2006 (A,B) and 2007 (C,D). Bars with diagonal lines indicate the frequency of barren (GY_P ≤ 25 g) plants.

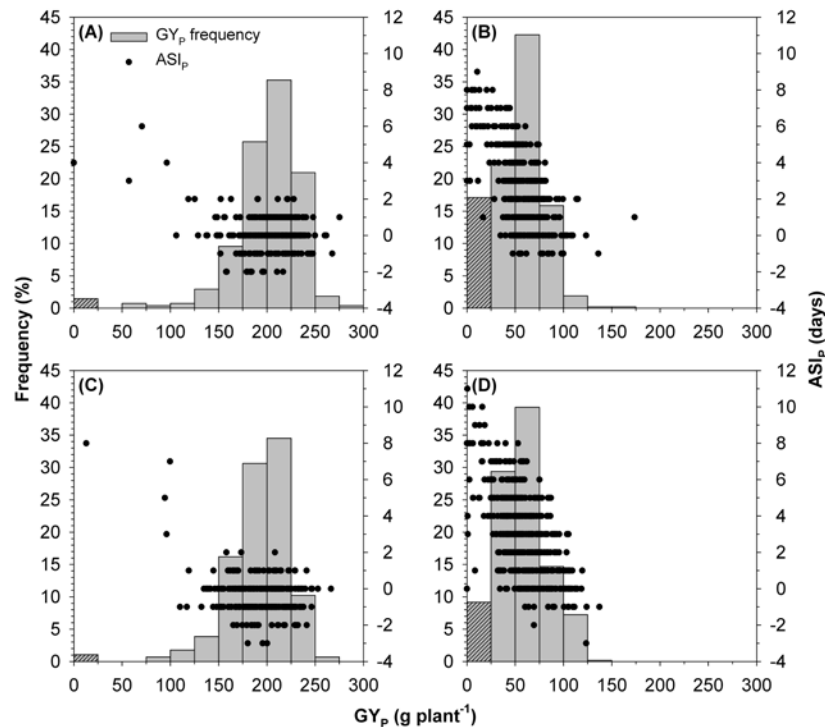
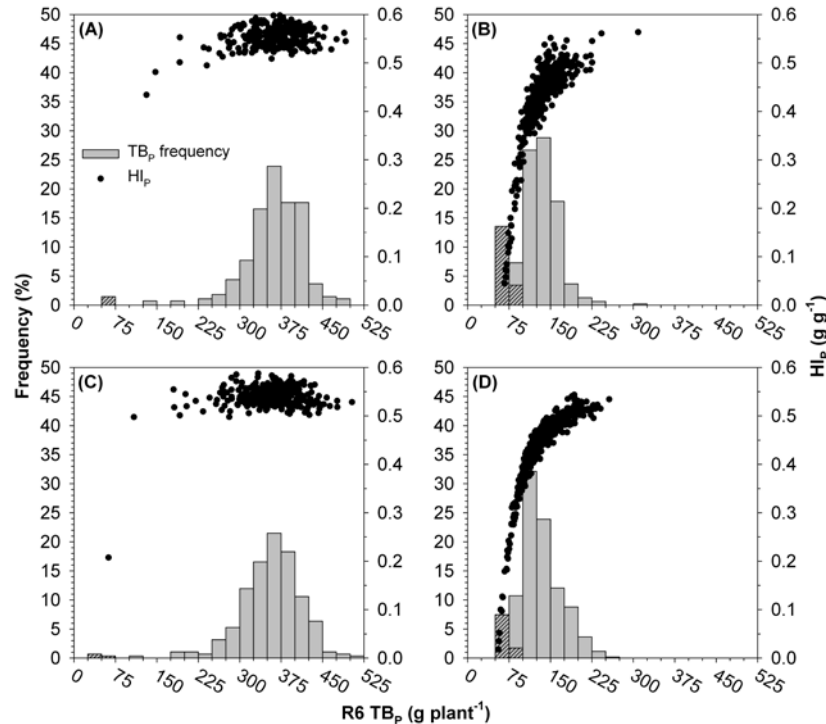


Figure 2. Frequency distributions for R6 per-plant aboveground total biomass (TB_P) and scatter plots for per-plant harvest index (HI_P) (non-zero) values for the 54,000 plants ha^{-1} ; 330 kg N ha^{-1} (A,C) and 104,000 plants ha^{-1} ; 0 kg N ha^{-1} (B,D) treatment combinations in 2006 (A,B) and 2007 (C,D). Bars with diagonal lines indicate the TB_P and frequency of barren ($GY_P \leq 25$ g) plants.



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