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^{13}C discrimination in corn grain can be used to separate and quantify yield losses due to water and nitrogen stresses

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It is difficult to quantify the mechanism(s) responsible for competition-induced yield loss using traditional experimental techniques. A technique using yield and ^{13}C discrimination (Δ) for wheat, a C_3 plant, has been developed to separate total yield loss (TYL) into yield loss due to N (YLNS) and water (YLWS) stresses. The objective of this research was to determine whether the Δ approach could be used in corn, a C_4 plant, to separate TYL into YLNS and yield loss due to a combination of water and light stresses (YLWLS). The field study had a factorial design using five corn densities and five N rates and was conducted in western Nebraska in 1999 and 2000. Relationships for YLNS and YLWLS with TYL were derived from only a portion of the yield and Δ data collected in 1999 and validated based on the remaining data collected in 1999 and 2000. In 1999, 20 to 40% of TYL was due to YLWLS, whereas in 2000, a dry year, YLWLS accounted for 60 to 80% of the TYL. Results from using the Δ-based approach were consistent with analysis of variance results. For example, calculated YLWLS values were related to measured YLWLS by the equation: calculated YLWLS = 19 + 0.91 (measured YLWLS) ($r^2 = 0.95$; $P < 0.01$). The Δ approach, based on a plant's physiological response to the environment, can be used to separate and quantify competition-induced YLNS and YLWLS in corn.

Nomenclature: Corn, *Zea mays* L.; wheat, *Triticum aestivum* L.

Key words: Modeling yield loss, nitrogen stress, water stress.

In dryland agriculture, water and N are often the most limiting resources for crop growth, and ultimately, yield (Arnon 1975; Smika 1970). Competitive mechanisms must be identified and quantified to help develop effective management solutions to lessen yield loss. For example, if competition between plants is primarily for N and not water, then applying N may reduce yield loss. This phenomena is possibly the reason that the addition of N or specific N placement has been reported to alleviate yield loss caused by low to moderate weed pressure (Blackshaw et al. 2002; Tollenaar et al. 1994). However, if competition between plants is primarily for water, then applying N may not increase yield even if weeds are not present (Clay et al. 2001b). Management solutions that minimize plant competition are often based on trial and error rather than understanding the importance of each competitive mechanism.

At present, techniques to separate yield loss due to water, nutrients, and other factors require either a very large number of treatments or a modeling effort where the results are not easily validated. A ^{13}C discrimination (Δ)–based approach has been proposed (Clay et al. 2001a, 2001b) to mechanistically evaluate competition. The approach is based on the development of independent equations that are solved simultaneously to develop a unique solution to a plant growth equation based on yield and Δ. Yield and Δ provide seasonally adjusted values that are the net result of plant competition for water and N (Clay et al. 2001b; Paz et al. 2003; Smeltekop et al. 2002).

Theoretical Basis for Δ to Evaluate Plant Competition

In a simplistic sense, the Δ value provides an index concerning the relative amount of Δ that might occur from a variety of different events and is an indirect measure of a plant's physiological response to stress. A Δ value of 0 indicates that ^{13}C discrimination did not occur, whereas positive values indicate that ^{13}C discrimination occurred relative to the atmospheric concentration of ^{13}C (1.1%). Different chemical and biological processes have different degrees of discrimination associated with them. The effects of water stress on Δ occurring during photosynthesis of C_3 and C_4 plants are summarized below.

When water is not limiting, stomata are open and CO_2 diffuses freely in and out of the leaf. When water stress occurs, plants reduce water loss by closing stomata that slows or stops CO_2 exchange between the leaf interior and the atmosphere. These events influence Δ because ribulose bisphosphate carboxylase (RuBisCo), an important enzyme involved in photosynthesis, discriminates against $^{13}CO_2$. When gas exchange through a stoma is not impeded, the amount of ^{13}C fixed in sugar of C_3 plants is very low and Δ is high, whereas when CO_2 diffusion into the leaf decreases, the C_3 plant is forced to use $^{13}CO_2$ in photosynthesis with a concomitant decrease in Δ. The bundle sheath cells of C_4 plants are leaky and more $^{13}CO_2$ is fixed than in C_3 plants, and when stomata close, the Δ value increases. The mathematical solutions to solve for Δ in C_3 and C_4

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plants are presented in Farquhar and Lloyd (1993) and O'Leary (1993). The equations are based on diffusion of $^{13}CO_2$ into stomata and fractionation of carboxylation of ^{13}C by RuBisCo. In addition, the equation for C_4 plants accounts for the amount of discrimination that occurs during the formation of HCO_3, the rate of CO_2 leakage from the bundle sheath cells relative to the rate of phosphoenolpyruvate (PEP) carboxylation, and the fractionation that occurs during this process.

Measured Δ values for C_3 plants (soybean [*Glycine max* (L.) Merr.] and wheat) and C_4 plant (corn) grown under well-watered, non–N stressed conditions are about 18 and 3, respectively (Clay et al. 2001a, 2001b; Paz et al. 2003; Smeltekop et al. 2002). Under water-limiting conditions, the Δ value for soybean decreases, whereas in corn, the Δ value increases.

The Δ value of a plant was proposed as a direct index of water-use efficiency; however, this use has not been totally successful because other factors, including N, affect Δ (Carelli et al. 1999; Clay et al. 2001a). Clay et al. (2001b) showed that water and N stresses in wheat had opposite effects on Δ: N stress increased Δ, whereas water stress decreased Δ. Consequently, plants undergoing both N and water stresses had identical Δ values as plants that were well watered and well fertilized. An explanation of this result is that N stress decreases the plant's photosynthetic capacity, which, in turn, reduces not only the total CO_2 fixed but also the amount of $^{13}CO_2$ fixed and results in a relatively high Δ value. Therefore, Δ should not be used to directly assess water stress without first evaluating the influence of N on Δ. However, these effects can be separated when a few selected treatments are included in field experiments.

Basis for Using Yield and Δ to Quantify N and Water Stresses

Yield can be defined as a function of many variables as follows:

$$\text{Yield} = f(\text{water, nutrients, light, energy, diseases, insects, other}) \quad [1]$$

This equation includes all factors and interactions that influence yield. Of course, because of its complexity, the function is impossible to solve. Therefore, experiments attempt to control or eliminate (or both) factors seen as extraneous to the study. Water and N are the focal points of many experiments (Blumenthal et al. 2003; Clay et al. 2001b; Farahani et al. 1998; Kolberg et al. 1996; McGee et al. 1997; Norwood 2001) because of their importance in dryland agriculture. The generalized yield loss equation for experiments with N and water treatments can be simplified to:

$$\text{Optimum yield} - \text{measured yield} = f(\text{yield loss due to N and water stresses}) \quad [2]$$

In this equation, yield loss is a function of N and water stresses resulting from the imposed treatment(s). In this form, factors not specifically influenced by the treatments are optimized so that the number of main effects and interactions are simplified. Even in a simplified experiment, the N and water stresses can be confounded by other factors, such as shading from surrounding plants as density or plant size increase, and difficult to experimentally separate. The approach to separate these factors requires: (1) the transformation of Equation 2 into a mathematical expression, (2) the development of independent equations for each unknown in the new equation, and (3) simultaneously solving the equations for the unknowns. One set of equations for defining water and N stresses on wheat yield was based on yield and another set of equations was based on Δ, both of which provide seasonally adjusted values influenced by soil and climatic factors (Clay et al. 2001b).

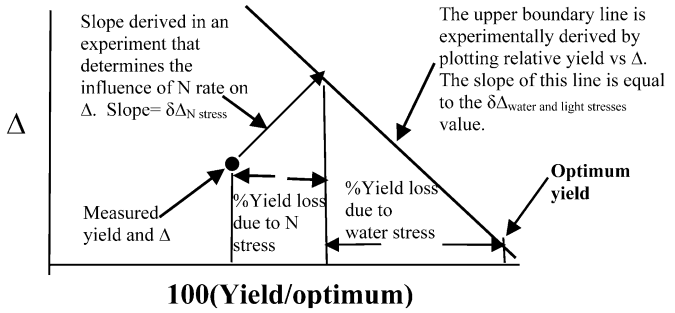


FIGURE 1. A diagram showing how yield loss due to nitrogen stress and yield loss due to a combination of water and light stresses were calculated for corn, a C_4 plant.

Research suggests that Equation 2 can be transformed into the equation:

$$\text{TYL} = \text{YLWS} + \text{YLNS} \quad [3]$$

(Clay et al. 2001a, 2001b). This equation indicates that yield loss is primarily the result of water and N stresses and that an additive model can be used to describe yield loss. In the authors' unpublished studies (D. E. Clay, unpublished data), interactions between water and N treatments have not been significant and are not included in Equation 3. Equation 3 contains two unknowns, and at least two independent equations are needed to solve this equation. On the basis of on analysis of variance (ANOVA) analysis of Δ data, the second equation was:

$$\delta\Delta = \text{YLWS}(\delta\Delta_{\text{water stress}}) + \text{YLNS}(\delta\Delta_{\text{N stress}}) \quad [4]$$

where δΔ was the total change in Δ resulting from the imposed treatment, $\delta\Delta_{\text{water stress}}$ was the change in Δ for each percentage of yield lost to water stress, $\delta\Delta_{\text{N stress}}$ was the change in Δ for each percentage of yield lost due to N stress (Clay et al. 2001a, 2001b). The $\delta\Delta_{\text{water stress}}$ value is defined as the slope of the upper boundary line relating yield and Δ when N is not limiting (Figure 1). Yields to the left of the line are limited by one or several other factors (Webb 1972). The upper boundary approach has been used in numerous studies to evaluate biological and ecological systems (Kitchen et al. 2003; Schmidt et al. 2000; Webb 1972). The $\delta\Delta_{\text{N stress}}$ value is the first-order derivative of the line relating Δ and relative yield [100(yield/optimum yield)] of the fertilized and unfertilized plants (Figure 1).

The Δ approach provides a powerful tool to separate losses due to stress into different components in C_3 plants, adds value to competition studies, gives insight into designing management solutions to reduce yield loss, and reduces the number of treatments needed to evaluate certain aspects of competition. The objective of this study was to determine

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whether ^{13}C discrimination could be used to evaluate intraspecies competition for N and water in corn, a C_4 plant, using several plant population densities and N rates.

Materials and Methods

Field Information and Sample Collection

Research was conducted near Sidney, NE, in 1999 (lat 41.231°N, long 103.020°W) and 2000 (lat 41.235°N, long 103.017°W). The study was a randomized block design with five replicates. Factorial treatments were five corn populations and five N rates. Individual plot size was 3 by 9.1 m.

Soils at the sites in 1999 and 2000 were a Duroc loam (Pachic Halplustoll) and Keith silt loam (Aridic Argiustoll), respectively. Soil samples (10 cores per site) from two depths (0 to 20 cm and 20 to 120 cm) were collected from each site in the spring before planting. Soil samples were analyzed for gravimetric water (0 to 120 cm), organic matter (0 to 20 cm), Bray-P (0 to 20 cm), and NO_3-N (0 to 120 cm). Initial gravimetric water in the surface 120 cm was 0.175 and 0.177 g g^{-1} in 1999 and 2000, respectively. Organic matter contents in the surface 20 cm in 1999 and 2000 were 31.6 and 22.4 g kg^{-1}, respectively. Nitrate-N concentrations in the surface 120 cm in 1999 and 2000 were 5.4 and 5.5 mg kg^{-1} and Bray-P in 1999 and 2000 in the surface 20 cm was 7.2 and 27.8 mg kg^{-1}. Total rainfall amounts during 1999 and 2000 growing seasons were 270 and 111 mm, respectively.

Corn 'Pioneer 3893' was no-till seeded in 76-cm rows at a rate of 103,000 seeds ha^{-1}. About 3 wk after emergence, plants were thinned to 17,300, 27,200, 37,100, 46,900, and 56,800 plants ha^{-1}. Ammonium nitrate was surface applied after corn planting but before emergence at rates of 0, 34, 67, 101, and 134 kg N ha^{-1}.

Grain was harvested mechanically from the middle two rows of each four-row plot. The total harvest area was 13.6 m^2, and the numbers of ears harvested ranged from 24 (low-density plots) to 77 (high-density plots). Grain from each plot was bagged individually, dried at 65 C to constant weight, and weighed. Weights were adjusted to 150 g kg^{-1} moisture content and reported on a per plant basis. Additional experimental details, such as weed management and detailed soil properties, are available in Blumenthal et al. (2003).

Isotope Ratio Calculations

A subsample (10 to 15 g) of grain from each plot was ground to a fine flour texture in a cyclone-type mill. About 2.5 mg of subsample of the corn flour was analyzed for total N, δ^{15} N, total C, and $\delta^{13}C$ on an isotope-ratio mass spectrometer.[1] Samples were run in duplicate with at least 30% standards for calibration purposes.

The ratio between C^{13} and C^{12} is the *R* value (O'Leary 1993). The *R* value is used in the following equation to calculate $\delta^{13}C$:

$$\delta^{13}C = [R(\text{sample})/R(\text{standard}) - 1] \times 1{,}000‰ \quad [5]$$

where, *R*(sample) is the $^{13}C/^{12}C$ ratio of the sample and *R*(standard) is the $^{13}C/^{12}C$ ratio of PDB, a limestone from the Pee Dee formation in South Carolina (Farquhar and Lloyd 1993; O'Leary 1993). Typically, $\delta^{13}C$ values for air, C3, and C4 plants are −8, −27, and −13‰, respectively. A negative sign indicates that the sample has a lower $^{13}C/^{12}C$ ratio than PDB. In many cases it is convenient to report ^{13}C discrimination (Δ) that is calculated using the equation:

$$\Delta = (\delta^{13}C_a - \delta^{13}C_p)/(1 + \delta^{13}C_p/1{,}000) \quad [6]$$

where $\delta^{13}C_a$ is the $\delta^{13}C$ value of air (−8‰) and $\delta^{13}C_p$ is measured value of the plant.

The $\delta^{15}N$ values were calculated with the following equation:

$$\delta^{15}N = \left\{\left[\frac{(^{15}N/^{14}N_{\text{sample}} - {}^{15}N/^{14}N_{\text{standard}})}{(^{15}N/^{14}N_{\text{standard}})}\right] \times 1{,}000\right\}‰ \quad [7]$$

where $^{15}N/^{14}N_{\text{sample}}$ was the isotopic ratio of nitrogen in a sample. $^{15}N/^{14}N_{\text{standard}}$ was the isotopic ratio of the standard, air (0.0036765).

Data Analyses

ANOVA (SAS 1998) (PROC GLM) was used to determine treatment differences. Regression analysis was used to assess relationships among variables.

As density increased, it would be reasonable to expect that shading among plants occurred and yield losses under non–N limiting conditions may have been due to both light and water stresses (Hashemi-Dezfouli and Herbert 1992). Equations 3 and 4 were modified because light stress was not specifically measured in this study and were rewritten in the forms:

$$\text{Optimum yield} - \text{measured yield} = \text{YLWLS} + \text{YLNS} \quad [8]$$

$$\delta\Delta = \text{YLWLS}(\delta\Delta_{\text{water and light stress}}) + \text{YLNS}(\delta\Delta_{\text{N stress}}) \quad [9]$$

where YLWLS is the yield loss due to the combined stresses of water and light and $\delta\Delta_{\text{water and light stresses}}$ is the change in Δ due to the combination of water and light stresses. To calculate the YLWLS and yield loss due to N stress (YLNS) values defined in Equations 8 and 9, values for $\delta\Delta_{\text{water and light stresses}}$ and $\delta\Delta_{\text{N stress}}$ are needed. In previous studies, population density had been fixed and the upper boundary line of the plot related yield and Δ to calculate the $\delta\Delta_{\text{water stress}}$ value (Clay et al. 2001b; Smeltekop et al. 2002). Given that the experiment did not include control treatments where light and water effects could be quantitatively separated, Equations 8 and 9 were used to calculate $\delta\Delta_{\text{water and light stresses}}$ by choosing two yield data points along the upper line and determining the Δ values (Figures 1 and 2). The slope of the boundary line for $\delta\Delta_{\text{water and light stresses}}$ was −0.014‰ (%YLWLS)$^{-1}$. For example, a −0.7‰ change in Δ occurred as yield decreased from 8,000 to 4,000 kg ha^{-1}; therefore, the slope of the upper boundary line was equal to −0.014‰ [−0.7‰/{(8,000 − 4,000 kg ha^{-1})/8,000 kg ha}100]. The slope of the line was similar to the value of −0.012‰ (% yield loss due to water stress [YLWS])$^{-1}$ reported in South Dakota (Clay et al. 2001a) and used by Smeltekop et al. (2002).

The $\delta\Delta_{\text{N stress}}$ value was calculated using the N rates in the 17,300 plants ha^{-1} treatment in 1999. This technique minimized secondary effects of N on YLWLS. Based on re-

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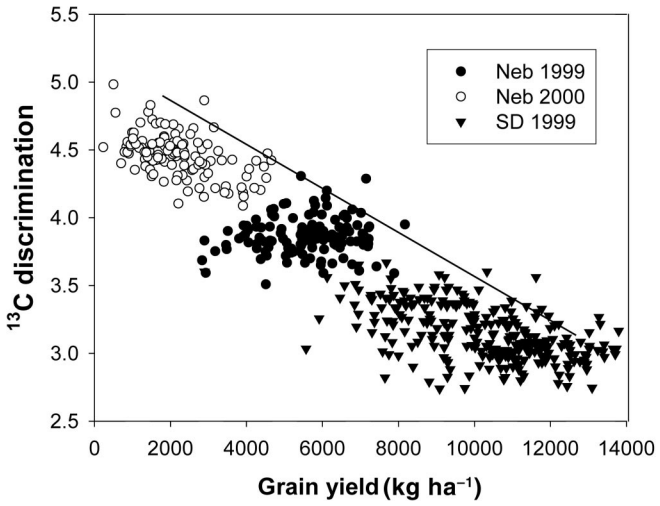


FIGURE 2. A comparison between yield and Δ for data collected in Nebraska and South Dakota. The $\delta\Delta_{\text{water and light stresses}}$ value was determined by plotting yield vs. Δ and empirically fitting a linear regression to the upper boundary of the data (Webb 1972). The South Dakota data (reported in Smeltekop et al. 2002) are included for comparative purposes.

gression analysis, $\delta\Delta_{\text{N stress}}$ was calculated to be 0.00883‰. This value was similar to the value of 0.0091‰ reported at Aurora, SD, by Smeltekop et al. (2002). Figure 2 shows the relationship between Δ and yield data collected in South Dakota and Nebraska.

Validation Procedures

Data used in model development were a subset of the data collected in this study and were not used in validation. Two approaches were used to validate the method. First, calculated YLNS in the 0 N treatments were compared with plant available N (Figure 3a). Plant available N is defined as the amount contained in the grain at harvest in the 0 N treatments plus the N contained in the soil at planting. The comparison showed that the predicted plant response to N followed expectations, yields increased with higher available N.

Second, calculated and measured yield losses in 1999 and 2000 due to the combined effect of water and light stress were compared (Figure 3b). Treatments included in the validation in 1999 were the 100 and 134 kg N ha^{-1} N rates applied to the 17,300 and 27,200 plant ha^{-1} populations. In 2000, data included in the validation were from the 134 kg N ha^{-1} at all population levels. These treatments were selected because yields were maximized. Calculated yield losses were determined by subtracting the measured yield from 370 g plant^{-1} (the highest yield measured in a single plot [low plant density and high N] in 1999). In well-fertilized corn, yield per plant decreased as plant population increased and was attributed to YLWLS. A linear line related measured yield loss to predicted yield loss (r^2 = 0.95, P < 0.01; slope = 0.91, 95% CI = 0.10).

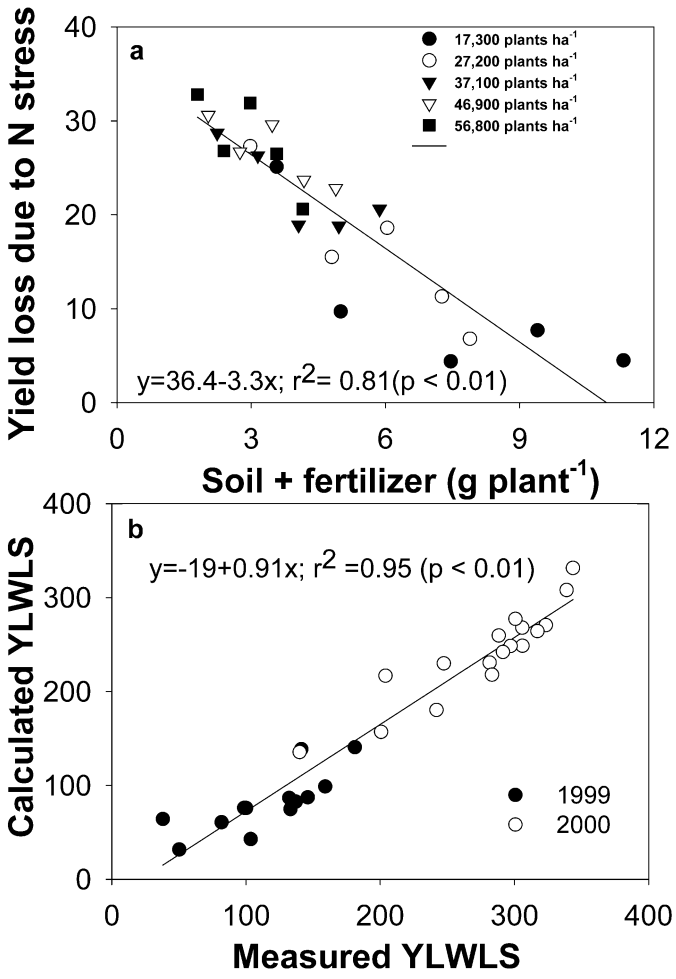


FIGURE 3. Validation of Δ approach: a comparison between yield loss due to (a) N stress vs. plant available N in 1999 and (b) measured and calculated yield losses due to a combination of water and light stresses in 1999 and 2000.

Results and Discussion

Nitrogen Rate and Population Density Effects on Plant Yield

The discussion is limited to main effects because two-way interactions between N rate and population density were not significant for yield, %N, Δ, δ^{15}N, and N removal. Yield per plant in 1999 ranged from an average of 118 to 240 g plant^{-1} at 56,800 and 17,300 plants ha^{-1}, respectively (Table 1). Adding N increased yield per plant, Δ, and N removal but reduced δ^{15}N in 1999 (Table 1). These results were expected and indicated that the site was responsive to N fertilizer. The δ^{15}N values decreased as the N rate increased because the percentage of N derived from fertilizer increased (Clay 1997). N removal and yield decreased as plant population increased, indicating N stress occurred at high populations. The Δ values when averaged across N rates were not influenced by plant population (Table 1).

Yield per plant in 2000 was 60% lower than in 1999 because of a 40% reduction in rainfall (Table 2). The highest average yields of 131 and 83.2 g plant^{-1} were in the 17,300 plants ha^{-1} and 34 kg N ha^{-1} treatments, respectively. The Δ value was not influenced by N rate and increased with increasing population. N removal was at a maximum in the 34 kg N ha^{-1} treatment and decreased as population increased. The relationship between δ^{15}N values and N rate was similar to that observed in 1999, δ^{15}N values decreased as N was added but were not influenced by population.

The yield data presented above were used to define opti-

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TABLE 1. The influence of N rate plant competition on grain yield, Δ, total N content, $\delta^{15}N$, YLNS, and YLWLS in 1999.[a]

Plant density	N rate	Yield	Δ	N removal	$\delta^{15}N$	YLNS	YLWLS
plant ha^{-1}	kg ha^{-1}	g plant^{-1}	‰	g plant^{-1}	‰	% loss	
Main effects							
Density							
17,300		240	3.85	3.57	−0.49	10.3	19.5
27,200		192	3.87	2.99	−0.50	15.3	26.6
37,100		148	3.85	2.33	−0.40	22.7	32.7
46,900		132	3.88	2.05	−0.20	26.6	33.4
56,800		118	3.86	1.81	−0.17	27.7	36.8
$LSD_{(0.05)}$		13	ns	0.24	0.30	2.83	2.77
N rate							
	0	148	3.80	2.19	−0.03	28.3	28.3
	34	161	3.84	2.43	−0.09	20.9	29.9
	67	168	3.84	2.57	−0.22	20.7	28.5
	101	174	3.88	2.65	−0.50	17.6	30.1
	134	178	3.96	2.81	−0.66	15.1	30.1
$LSD_{(0.05)}$		13	0.07	0.24	0.30	2.83	ns
Density by N rate							
17,300	0	201	3.78	2.85	−0.05	25.1	20.5
	34	228	3.85	3.47	−0.35	9.7	21.3
	67	257	3.89	2.79	−0.45	4.4	18.5
	101	251	3.81	3.71	−0.66	7.7	16.9
	134	262	3.91	4.05	−0.92	4.5	20.0
27,200	0	160	3.80	2.47	0.23	24.3	27.1
	34	180	3.91	2.76	−0.17	15.5	29.8
	67	190	3.79	2.95	−0.15	18.6	23.6
	101	205	3.90	3.27	−0.57	11.3	26.4
	134	225	3.95	3.52	−0.60	6.8	26.2
37,100	0	136	3.80	1.95	−0.08	28.7	29.9
	34	147	3.73	2.16	−0.21	26.3	27.4
	67	150	3.90	2.47	−0.42	18.9	35.9
	101	156	3.90	2.20	−0.53	18.8	35.9
	134	150	3.95	2.39	−0.74	20.6	34.7
46,900	0	126	3.87	1.92	−0.19	30.6	31.7
	34	126	3.93	1.91	−0.05	26.7	35.2
	67	130	3.80	1.91	0.03	29.6	30.0
	101	137	3.90	2.23	−0.47	23.7	34.3
	134	141	3.91	2.27	−0.30	22.8	34.3
56,800	0	120	3.75	1.77	−0.07	32.8	32.3
	34	124	3.79	1.86	0.34	26.8	36.6
	67	114	3.82	1.73	−0.12	31.9	36.6
	101	122	3.90	1.86	−0.27	26.5	36.6
	134	112	4.07	1.82	−0.75	20.6	45.2

[a] Abbreviations: YLNS, yield loss due to nitrogen stress; YLWLS, yield loss due to a combination of water and light stresses; ns, not significant.

mum N rates, population levels, and economics of a system (Blumenthal et al. 2003). However, this economic analysis did not quantify intraspecific competition for N and water.

Separating Yield Loss by Stress Factors

The Δ approach was used to separate total yield loss (TYL) into the component parts of stress, YLWLS, and YLNS. YLNS was reduced at higher N rates and increased at higher plant densities because of competition (Tables 1 and 2). YLWLS increased at higher plant densities and remained relatively stable over N rate (Tables 1 and 2). These results were expected because less water is available to an individual plant at higher population densities. Grain yield was highly correlated to YLWLS and YLNS in 1999 and 2000 (Figure 4). These relationships showed that these stresses influenced yield and the results were consistent with the ANOVA of yield data. Adding N increased yield, and high plant density decreased yield.

YLWLS and YLNS were similar in magnitude in 1999, and each accounted for about 50% of the loss (Figure 4). In 2000, YLWLS accounted for almost 80% of the TYL. YLNS decreased slightly with increasing N rate and increased as plant population increased. These findings were consistent with the ANOVA of the $\delta\Delta_{\text{water and light stresses}}$ and $\delta\Delta_{\text{N stress}}$ values. The observed relationship between yield, YLNS, and YLWLS may occur if N influenced water (precipitation)-use efficiency. Evidence supporting this hypothesis includes that in 1999 adding N fertilizer increased yields, reduced YLNS, and did not influence YLWLS, whereas in 2000, only increasing the N rate from 0 to 34 kg N ha^{-1} increased yield and reduced YLNS.

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TABLE 2. The influence of N rate plant competition on grain yield, Δ, total N content, $\delta^{15}N$, YLNS, and YLWLS in 2000.[a]

Plant density	N rate	Yield	Δ	N removal	$\delta^{15}N$	YLNS	YLWLS
plant ha^{-1}	kg ha^{-1}	g plant^{-1}	‰	g plant^{-1}	‰	% loss	
Main effects							
Density							
17,300		131.0	4.38	2.10	0.80	4.10	57.2
27,200		89.6	4.44	1.51	0.89	9.06	64.7
37,100		63.4	4.67	1.08	0.86	11.9	68.9
46,900		45.1	4.48	0.70	0.91	14.8	71.4
56,800		30.2	4.54	0.51	0.87	14.9	76.0
$LSD_{0.05}$		16.1	0.08	0.24	0.27	2.98	5.0
N Rate							
	0	66.4	4.43	1.03	1.01	13.39	66.9
	34	83.2	4.43	1.34	1.01	10.55	64.7
	67	68.3	4.49	1.16	0.88	10.48	69.6
	101	67.6	4.47	1.10	0.81	10.90	68.7
	134	73.9	4.48	1.26	0.63	9.52	68.3
$LSD_{0.05}$		16.1	0.08	0.24	0.27	2.98	ns
Density by N rate							
17,300	0	116	4.36	1.79	0.97	6.8	58.0
	34	158	4.37	2.56	0.92	1.7	52.9
	67	129	4.34	2.02	0.50	6.3	55.5
	101	120	4.44	1.94	0.84	3.3	61.0
	134	132	4.41	2.20	0.80	2.6	58.2
27,200	0	86.8	4.51	1.38	1.01	7.6	68.0
	34	92.8	4.35	1.46	1.09	11.9	59.9
	67	83.0	4.54	1.51	0.91	7.9	69.7
	101	83.6	4.43	1.33	0.86	9.7	64.5
	134	102	4.39	1.4	0.59	8.2	60.8
37,100	0	44.8	4.45	0.80	1.04	16.1	70.4
	34	67.0	4.53	1.14	1.02	8.5	71.2
	67	52.2	4.51	0.93	0.88	12.1	72.1
	101	66.0	4.44	1.11	0.87	12.9	67.2
	134	87.2	4.41	1.41	0.50	9.9	63.7
46,900	0	54.4	4.39	0.74	1.20	16.6	66.9
	34	58.8	4.32	0.86	1.17	19.3	62.9
	67	48.0	4.57	0.81	0.82	10.1	75.3
	101	33.2	4.55	0.55	0.78	13.7	76.2
	134	31.2	4.52	0.54	0.60	14.5	75.9
56,800	0	29.6	4.43	0.45	0.84	19.9	71.1
	34	39.6	4.58	0.68	0.85	11.4	76.7
	67	29.2	4.52	0.52	0.96	15.9	75.3
	101	35.2	4.51	0.56	1.04	15.2	74.2
	134	17.6	4.65	0.32	0.68	12.3	82.6

[a] Abbreviations: YLNS, yield loss due to nitrogen stress; YLWLS, yield loss due to a combination of water and light stresses.

Understanding the mechanism(s) responsible for competition-induced yield loss is critical in developing management systems that can optimize yield within the environmental constraints of a site. Plant responses to abiotic and biotic factors must be recognized to quantify and predict the end result of plant competition. Field experiments and mechanistic and empirical models are used to evaluate the influence of different factors on plant growth and development. Field experiments designed to identify competition mechanisms require many treatments, and separation of causal factors is difficult. The modeling approach, however, assumes that the correct model was selected, properly validated, and accurately reflects the natural system. Uncertainty in where a given model should and should not be used has led to reluctance in scientists, consultants, and producers to fully integrate them into their recommendation and decision processes. To solve this problem, models must be stringently tested and validated under a wide range of conditions. Nonmodeling approaches to quantify competition mechanisms are needed to assist in these activities.

The Δ-based approach for corn produced results that were consistent with a population by N rate factorial experiment and separated yield loss into component parts. It appears that this approach can be used to define yield loss in both C_3 (Clay et al. 2001b) and C_4 crops although their photosynthetic mechanisms differ, which greatly influence their Δ values.

The approach can be easily integrated into the experimental design of competition studies by including unfertilized and fertilized, well-watered control plots. The approach represents an alternative approach from relying on ANOVA and multiple regression to a technique where yield and Δ are used to develop independent equations that are solved

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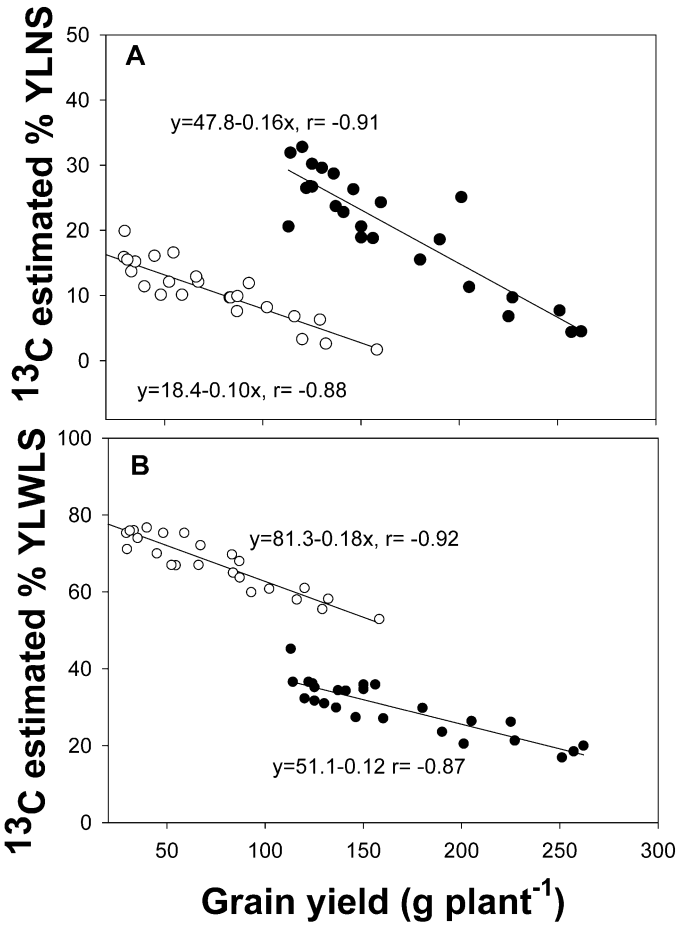


FIGURE 4. Relationship between yield loss due to (a) N stress and (b) a combination of water and light stresses in 1999 and 2000.

simultaneously to develop a unique solution to plant growth equations. These data can be used to define management strategies. For example, in this study, it was shown that when yield loss in 2000 was due primarily to water stress, there was only a limited response to adding N. This would suggest that if the season starts off dry, split fertilizer applications may be warranted, with more fertilizer applied when more water is available. These data also could be used to unify the yield and competition discrepancies observed in regional data sets, such as those presented in Lindquist et al. (1996, 1999), to determine and compare the magnitude of N and water stresses at each site.

Additional research is needed to further assess the Δ technique. Studies are needed to determine the treatments required to separate the combined effect of water and light stresses, if competition from weed species within a crop has similar effects on Δ, and if the approach is valid under a wide range of climatic conditions.

Sources of Materials

[1] Europa 20-20 ratio mass spectrometer, SerCon, Wistaston Road, Crewe, Cheshire, U.K. CW2 7RP.

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