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CORN

Agronomic Responses of Corn Hybrids from Different Eras to Deficit and Adequate Levels of Water and Nitrogen

Patrick M. O'Neill, John F. Shanahan,* James S. Schepers, and Bob Caldwell

ABSTRACT

Maintaining current high yields of corn (*Zea mays* L.) grown in the USA poses an environmental threat due to continued overuse of water and N inputs. To reduce overreliance on inputs, future corn breeding efforts should focus on improving tolerance of corn to water and N stresses, utilizing appropriate tolerance mechanisms. The objective of this study was to identify appropriate mechanisms by characterizing agronomic responses of 12 hybrids from three different eras ('B73 × Mo17' from 1970s and three early 1990s and eight late 1990s Pioneer brand hybrids) to varying water and N supply. This was done by growing the hybrids under deficit and adequate levels of water (one-half and full evapotranspiration) and N (0 and 200 kg ha⁻¹) in a field study and measuring yield and other agronomic variables. While hybrid eras didn't differ in response to varying water or N, individual hybrids varied in ability to maintain yield under water or N stress. For example, under deficit water, '3417' produced 27% more yield than '3162' while they yielded similarly under adequate water. Likewise, under deficit N, '34R07' produced 42% more grain yield than '33G27' while they yielded similarly under adequate N. Agronomic variables such as kernel number per unit area were highly correlated with grain yield ($r = 0.98$), indicating hybrid ability to maximize kernel number under varying water and N supply was critical to maximizing yield. Determining physiological mechanisms associated with ability to maintain kernel number under stress should be a high priority of breeding programs.

CORN GROWN UNDER the semiarid conditions of the Great Plains region of the USA requires supplemental irrigation to attain maximum yields (Musick and Dusek, 1980). While irrigation increases corn yields, it depletes groundwater supplies (Clark et al., 2002) and is expensive, with fully irrigated corn requiring 500 to 600 mm of irrigation water and pumping costs reaching over \$0.20 mm⁻¹ ha⁻¹ in some regions (Norwood and Dumler, 2002). Nitrogen availability represents another major factor limiting corn yields in the Great Plains, requiring the addition of large quantities of N fertilizers to achieve current high yields (Marschner, 1995). Recent statistics (USDA-NASS, 2003) show for example that corn grown in the USA receives around 5 million tons of N annually, over 2.5 times the amount applied to wheat

(*Triticum aestivum* L.). These high application levels result in low N use efficiency (NUE), with estimates of NUE for world cereal grain production systems at only 33% (Raun and Johnson, 1999). This represents a \$15.9 billion annual loss of fertilizer N. In addition to economic losses, N overapplication results in environmental contamination through nitrate N runoff or leaching, making nitrate N the most common contaminant found in the surface and ground waters of the Corn Belt (CAST, 1999). Thus, while average corn yields have quadrupled over the last 50 yr from the combined use of improved irrigation practices, greater N fertilizer use, and other technological innovations (Christensen, 2002), maintaining current high yields of corn grown in the Great Plains of the USA poses an environmental threat due to continued overuse of these inputs.

To minimize input costs and environmental damage, farmers will likely have to resort to producing corn with less irrigation water and N fertilizer in the future. This will lead to increased levels of water and N stress imposed on the crop. To reduce overreliance on these inputs, future corn breeding efforts should focus on improving tolerance of corn to water and N stresses, utilizing appropriate stress tolerance mechanisms. Characterizing the agronomic and physiological responses of differing corn hybrids to water and N stresses could help identify appropriate stress tolerance mechanisms for future corn breeding efforts.

Corn is relatively insensitive to water stress imposed during early vegetative growth stages because water demand is relatively low and plants can adapt to water stress to reduce the impact of subsequent periods of water stress (Shaw, 1977). However, corn grain yield is sensitive to water stress from just before silking through grain fill (Shaw, 1977; Hall et al., 1981; Westgate and Boyer, 1986), with the greatest degree of sensitivity occurring during the period of kernel number determination (Andrade et al., 1999). Hall et al. (1981) indicated that kernel number was most sensitive to stress between tasseling and just after silking.

Nitrogen stress reduces grain yield by delaying plant growth and development (Uhart and Andrade, 1995a) and reducing leaf area index, leaf area duration, and photosynthetic rate (Novoa and Loomis, 1981; Lemcoff and Loomis, 1986; Sinclair and Horie, 1989; Connor et al., 1993). Uhart and Andrade (1995b) also showed that grain yield and kernel number were reduced by N stress. These results from the literature imply that measurement of agronomic variables like yield components may provide an indication or characterization of hybrid response to stresses.

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Abbreviations: NUE, nitrogen use efficiency.

The role corn breeding efforts have played in increasing average grain yields in the USA over the past 70 yr has been significant, with 60% of the historic increase attributed to genetic improvement (Duvick, 1992). The genetic improvement has been more specifically ascribed to increased stress tolerance (Duvick, 1992; Tollenaar et al., 1994). A genotype \times environment interaction for grain yield is usually observed when comparing older vs. more recently introduced corn hybrids under multiple environments (Tollenaar and Wu, 1999). For example, a previous study by Tollenaar (1989) showed that a newer hybrid was more tolerant of water and N stress than an older hybrid. Thus, it was hypothesized that more recently developed hybrids would be more tolerant to these stresses than older hybrids. The objective of this study was to identify appropriate stress tolerance mechanisms by characterizing the agronomic responses of hybrids of different eras to varying water and N supply.

MATERIALS AND METHODS

Experimental Treatments and Field Design

This experiment was conducted near Shelton, NE (40°45'01" N, 98°46'01" W; elevation 620 m above mean sea level), during the growing seasons of 1999 through 2002. The soil at the site is a Hord silt loam (fine-silty, mixed mesic Pachic Haplustolls). The crop was grown under conventional tillage practices following corn with a linear-move sprinkler irrigation system. Climatological data (Fig. 1) were recorded for all growing seasons through the use of an automated weather station (High Plains Climate Center Network, University of Nebraska) located on the research site. Phenology data according to Ritchie et al. (1997) were recorded weekly from the first of June through mid-August.

Treatments consisted of a factorial combination of two water levels (deficit and adequate irrigation), two N levels (0 and 200 kg N ha⁻¹), and 12 corn hybrids (11 Pioneer hybrids—'3394', '33H67', '3162', '33R87', '33G27', '34K77', '34G82', '34D34', '34R07', '33A14', and '3417'—and the older check hybrid 'B73 \times Mo17'). Hybrids were selected because of their differences in era of release, maturity, and canopy architecture (upright architecture for 3394 vs. planophile orientation for the other hybrids). The hybrid B73 \times Mo17 was included as the older check in this study because it was a popular and widely grown hybrid in Corn Belt region during the 1970s (Troyer, 1999). The experimental design was a strip-split plot design, with water levels as whole plots, N levels as split plots, and corn hybrids as strip plots with three replications. The same experimental design, regarding plot randomization for all experimental units, was used in each year of the study to minimize water and N treatment carryover effects from one year to the next. Hybrid characteristics are given in Table 1. Individual plot dimensions were 30.5 m long by 3.7 m wide, consisting of four rows spaced at 0.925 m, a row spacing commonly used in this region. Each hybrid was seeded at a density of 81 500 plants ha⁻¹. Liquid starter fertilizer (10–34–0) was applied at the rate of 94 L ha⁻¹ in the furrow at planting, providing approximately 18 kg ha⁻¹ of P. Weed control was accomplished through a combination of cultivation and herbicide application. Pests were controlled with pesticide applications as needed. At V6 growth stage, 200 kg ha⁻¹ of N was sidedressed as anhydrous ammonia on the adequate N plots.

Water treatments (deficit and adequate irrigation) were initiated during late vegetative growth stage (around V9).

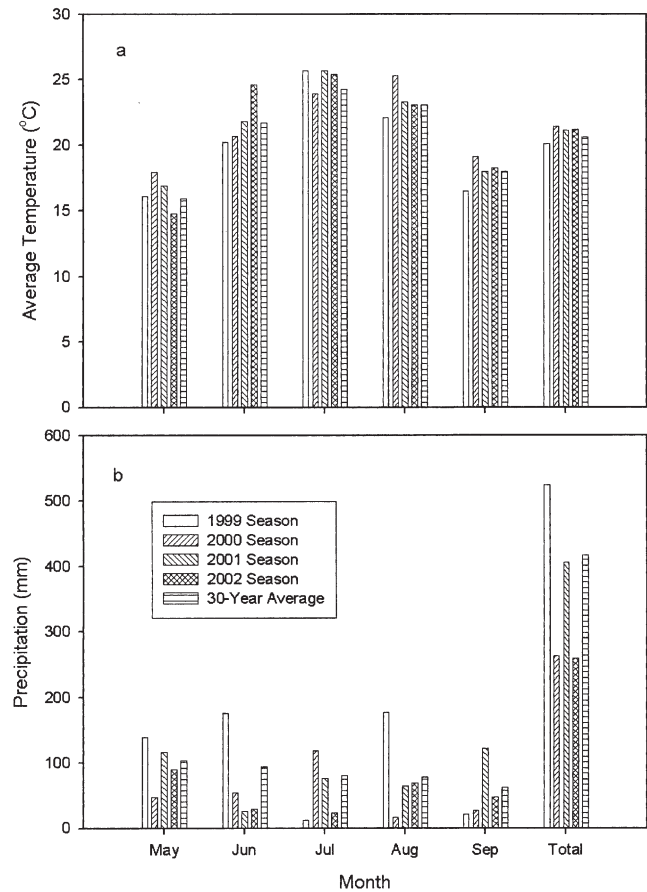


Fig. 1. Monthly average (a) temperature and (b) precipitation for the 1999–2002 growing seasons calculated from measurements gathered by an automated weather station (High Plains Climate Center Network, University of Nebraska) located at Shelton, NE. For comparison purposes, 30-yr averages of (a) temperature and (b) precipitation of the surrounding area are also presented.

Beginning on these dates, water was applied at weekly intervals based on the amount of evapotranspiration for the previous week as determined by the on-site weather station using a modified version of the Penman equation (Kincaid and Heerman, 1974). The adequate irrigation treatment received the amount of water required to fully replace the previous week evapotranspiration while the deficit treatment received approximately one-half this amount. This was continued throughout the remainder of the growing season.

Table 1. Era and year of introduction and growing days until harvest (CRM) for 12 corn hybrids grown during the 1999–2002 growing seasons at Shelton, NE.

Hybrid	Era and year of introduction	CRM
B73 \times MO17	1970s	118
Pioneer brand hybrids	Early 1990s	
3162	1989	118
3417	1990	109
3394	1991	110
	Late 1990s	
33A14	1997	113
33H67	1998	112
33G27	1999	113
33R87	1999	113
34G82	1999	106
34K77	1999	108
34D34	1999	110
34R07	1999	110

Harvest Procedures and Statistical Analysis

At physiological maturity, plants from a 3.1-m section of row within the center two rows of each plot were harvested to determine total biomass yield. The ears were removed from the plants and the stalks chopped and weighed. A subsample of stover biomass was collected and oven-dried for 48 h at 40°C to adjust stover biomass yields to 0 g kg⁻¹ water. The harvested ears were oven-dried for 48 h at 40°C and weighed to determine ear mass at 0 g kg⁻¹ water. Total plot biomass was calculated from the sum of stover and ear weights. Ears were shelled and total grain weight determined. A subsample of 100 kernels was used to determine mass per kernel. After plot biomass sampling, the center two rows of the entire length (30.5 m) of each plot were machine-harvested. A subsample of machine-harvested grain was collected and moisture content determined using a Burrows digital moisture meter (model 700, Seedburrow Equipment Co., Chicago, IL), and yield adjusted to 0 g kg⁻¹ water. Total grain yield for each plot was determined by summing hand- and machine-harvested grain samples. Kernel numbers per unit area for each plot were determined by calculation using plot grain yield per unit area and kernel weight estimates from hand-harvest samples.

To determine N concentrations of grain and stover, grain and stover subsamples were first processed with a Stein mill and then a Wiley mill (20-mesh sieve). A subsample of approximately 0.3 g of the processed stover and 1.5 g of the processed grain was further ground on a roller mill as per Arnold and Schepers (2004). Approximately 5.5 mg of the roller-milled stover and grain subsamples were used to determine N concentration using a Carlo Erba flash combustion N analyzer, Model 1500 Series 2 (Carlo Erba Instruments, Milan, Italy). The analyzer was calibrated periodically using standards with known N concentration. Total N uptake per plot was determined by multiplying N concentration for the stover and grain samples times their respective weights and summing the two values.

Yield response to applied N was calculated for each unique hybrid and water treatment combination as:

$$\text{N response (\%)} = \frac{\text{Adequate N yield} - \text{Deficit N yield}}{\text{Deficit N yield}} \times 100\%$$

Yield response to adequate water was calculated in a similar fashion. Fertilizer use efficiency (FUE) was calculated as:

$$\text{FUE (\%)} =$$

$$\frac{(\text{N uptake under } 200 \text{ kg N ha}^{-1}) - (\text{N uptake under } 0 \text{ kg N}^{-1})}{200 \text{ kg N ha}^{-1}} \times 100\%$$

Grain NUE was calculated as:

$$\text{NUE} = \frac{\text{Mg dry grain ha}^{-1}}{\text{Mg N uptake ha}^{-1}}$$

Analyses of variance for the various agronomic variables were performed using SAS PROC MIXED (Littel et al., 1996) with the Kenward–Roger degrees-of-freedom method. This method uses an adjusted estimator of the covariance matrix to reduce small sample bias (Kenward and Roger, 1997). Water, N, and hybrid were treated as fixed effects and year and replication as random effects. One ANOVA was calculated with corn hybrids grouped by era of introduction (Table 2), and a second ANOVA was calculated without era grouping of hybrids (Table 3). Treatment means were compared by LSD and calculated using SAS PROC GLM. Associations between grain yield and the other agronomic variables were determined with genotypic correlations, using hybrid treatment means for each year.

RESULTS AND DISCUSSION

Climatological Conditions

Climatological measurements for the four growing seasons are shown in Fig. 1. While fluctuations in monthly temperatures were observed from year to year, average seasonal temperatures for each of the 4 yr were comparable and similar to the long-term average for this location. On the other hand, seasonal precipitation was slightly more variable among the 4 yr, with the 1999 season receiving 25% more precipitation than the long-term average while the other 3 yr received either average or below-average precipitation.

Water and Nitrogen Effects on Grain Yields

Although seasonal precipitation varied slightly among the 4 yr, there was a consistent effect of the water treatment on grain yields (Table 2), with an average yield increase of around 23% associated with adequate vs. deficit water levels (Fig. 2). Likewise, N application affected grain yields as well, with an average yield increase of around 100% associated with adequate vs. deficit N

Table 2. Analysis of variance for grain yield, total dry matter (DM), kernel weight (KW), kernels per hectare (KN), total N uptake per hectare (NUP), N use efficiency (NUE), and fertilizer use efficiency (FUE) from 12 corn hybrids representing three eras of introduction exposed to two water levels (deficit and adequate) and two N levels (0 and 200 kg N ha⁻¹) during the 1999–2002 growing seasons at Shelton, NE.

Source of variation	df	Agronomic variables						
		Yield	DM	KW	KN	NUP	NUE	FUE
Water (W)	1	**	*	NS†	**	NS	‡	‡
N	1	**	**	‡	**	**	**	**
Hybrid era (E)	2	NS	NS	NS	NS	**	NS	*
W × N	1	‡	NS	NS	NS	NS	NS	‡
W × E	2	NS	NS	NS	‡	NS	NS	‡
N × E	2	*	NS	NS	*	**	NS	
W × N × E	2	NS	NS	NS	NS	NS	NS	

* Significant at the 0.05 probability level.

** Significant at the 0.01 probability level.

† NS, nonsignificant.

‡ Significant at the 0.10 probability level.

Table 3. Analysis of variance for grain yield, total dry matter (DM), kernel weight (KW), kernels per hectare (KN), total N uptake per hectare (NUP), N use efficiency (NUE), and fertilizer use efficiency (FUE) from 12 corn hybrids exposed to two water levels (deficit and adequate) and two N levels (0 and 200 kg N ha⁻¹) during the 1999–2002 growing seasons at Shelton, NE.

Source of variation	df	Agronomic variables						
		Yield	DM	KW	KN	NUP	NUE	FUE
Water (W)	1	**	*	NS†	**	‡	‡	‡
N	1	**	**	‡	**	**	**	**
Hybrid (H)	11	**	**	**	**	**	**	**
W × N	1	‡	NS	NS	NS	NS	NS	NS
W × H	11	**	‡	‡	**	**	**	**
N × H	11	**	**	**	**	**	**	**
W × N × H	11	NS	NS	NS	NS	NS	NS	NS

* Significant at the 0.05 probability level.

** Significant at the 0.01 probability level.

† NS, nonsignificant.

‡ Significant at the 0.10 probability level.

levels. The water × N interaction term was also significant and was due to a greater yield response for N application under adequate water conditions vs. lower yield response to N under deficit water conditions (Fig. 2). These results are consistent with previous work (Pandey et al., 2000) and illustrate the additive effect that water and N inputs have on maximizing corn productivity. In summary, the imposed water and N treatments used in this study provided consistent differences in crop water and N status across years to successfully address the study objective of evaluating hybrid agronomic responses to varying water and N levels.

Hybrid Response to Varying Water and Nitrogen Levels

To evaluate hybrid responses to varying water and N levels, the ANOVA was done first (Table 2) with hybrids grouped into three eras of introduction (Table 1) and then with the hybrids considered individually (Table 3). To test the hypothesis of whether newer hybrids are more tolerant than older hybrids to water or N stress, the interaction terms of era × water and era × N were considered the main criterion for determining whether there was a differential era response to varying water or N supply. Additionally, other interaction terms involving era were also evaluated in an attempt to better understand era responses. The water × N × era interaction term was not significant, indicating that era response to water and N was independent of the other treatment factor. Thus, evaluation of the era responses to water and N independently was considered to be a valid means for expressing the differential era response to varying water or N supply.

Comparing the era × water and era × N interaction terms (Table 2), it is clear that eras responded differently only to varying N levels and not to varying water levels. This is further illustrated by comparing average yields for the three eras grown under both deficit and adequate levels of water and N (Table 4), with the three hybrid eras producing comparable yields under deficit and adequate water. While the three eras produced similar yields under deficit N, the early- and late-1990s hybrids yielded more than the 1970s hybrid under adequate N conditions, indicating a greater yield response to N application. For example, the 1970s hybrid exhib-

ited a 73% increase in yield in response to N application while the early- and late-1990s hybrids produced 102 and 111% increases, respectively (Table 4). These results imply that the differential era response to N was not due to era differences in N stress tolerance but rather to era differences in ability to respond to N application, with newer hybrids exhibiting greater yield responses than older hybrids. Collectively, these results do not support our initial hypothesis regarding increased tolerance to water and N stresses for newer vs. older hybrids and are contrary to the results of Tollenaar and Wu (1999), who suggested that newer hybrids possess greater stress tolerance than older hybrids. However, it should be noted that the range in age of hybrid eras used in our work was only around 20 yr compared with around 30 yr for the hybrids studied by Tollenaar and Wu (1999). Hence, the work by the previous authors likely represents a better estimate of progress in genetic gain in stress tolerance associated with corn breeding efforts over time.

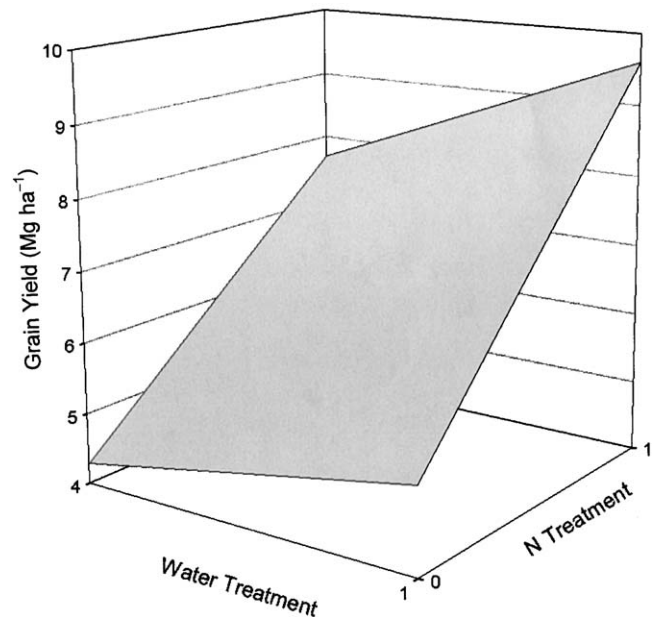


Fig. 2. Mean grain yield for 12 hybrids under a factorial combination of two water treatments (0 = deficit and 1 = adequate) and two N treatments (0 = deficit and 1 = adequate) averaged over 4 yr (1999–2002) at Shelton, NE.

Table 4. Mean grain yield and yield response to water and N for 12 corn hybrids representing three eras of introduction. Means represent averages across four growing seasons (1999–2002) at Shelton, NE.

Hybrid	Era	Water treatment			N treatment		
		Deficit	Adequate	Response	Deficit	Adequate	Response
		Mg ha ⁻¹		%	Mg ha ⁻¹		%
B73 × Mo17	1970s	6.10 a†	7.20 a	24 a	5.02 a	8.23 c	73 b
3162	early 1990s	5.30	7.61	50	4.33	8.67	123
3394		5.61	6.73	23	4.44	7.90	86
3417		6.75	7.93	21	5.09	9.58	97
	era average	5.90 a	7.45 a	31 a	4.62 a	8.72 b	102 a
33A14	late 1990s	6.19	8.09	35	5.10	9.18	90
33G27		5.77	6.98	21	3.93	8.82	150
33H67		5.98	7.63	29	4.46	9.15	120
33R87		6.25	7.93	28	4.49	9.69	126
34D34		6.32	7.64	24	4.55	9.41	123
34G82		5.76	6.98	21	4.15	8.59	117
34K77		6.31	7.68	25	4.86	9.13	95
34R07		6.52	8.18	29	5.60	9.10	66
	era average	6.14 a	7.62 a	27 a	4.64 a	9.13 a	111 a
	hybrid LSD	0.57	0.56	16	0.58	0.56	21

† Era means within a column and having the same letter are not significantly different (0.05).

Even though hybrid eras in our study did not respond differently to varying water levels, individual hybrids did, as shown by the significant water × hybrid interaction (Table 3). This is best illustrated by comparing yields of hybrids 3162 and 3417 under deficit and adequate water (Table 4). Under deficit water, 3417 produced 27% more grain yield than 3162, with the other hybrids yielding between these two extremes, while under adequate water, the same two yielded similarly. This resulted in hybrid 3162 exhibiting a more pronounced yield response than 3417 to additional water, with the former showing a 50% increase, the latter only a 21% increase, and the other hybrids ranging between these two extremes. Individual hybrids also responded differently to varying N levels (Table 3), as seen by the significant N × hybrid interaction (Table 3). This is best demonstrated by comparing the yields of hybrids 34R07 and 33G27 under deficit and adequate N (Table 4). Under deficit N, 34R07 produced 42% more grain yield than the lowest-yielding hybrid 33G27, with the other hybrids yielding between these two extremes (Table 4). With adequate N, these same two hybrids produced similar yields. This resulted in hybrid 33G27 exhibiting a greater yield response to additional N than 34R07, with the former

showing a 150% increase and the latter only a 66% increase. The ANOVA for fertilizer use efficiency values for the hybrids also revealed that hybrids responded differently to additional N fertilizer (Table 3), with newer hybrids producing more grain per unit of additional N fertilizer (Table 5), and this was especially true under adequate water conditions.

While the hybrids grouped by era of introduction did not vary in their ability to tolerate water or N stress, the individual hybrids did vary in their ability to maintain yields under these stresses. Likewise, they varied in their ability to respond to adequate water and N conditions, maximizing yields. To determine the associations between hybrid performance under deficit and adequate levels of water and N (Table 6), linear correlation analysis was conducted using mean yields of the hybrids grown under both levels of water and N (Table 5). This analysis revealed that hybrid yield variation was more highly associated for the deficit water vs. deficit N levels ($r = 0.72$, $P \leq 0.01$) than for deficit water vs. adequate water levels ($r = 0.65$, $P \leq 0.05$). Similarly, hybrid yield variation was more highly associated for adequate N vs. adequate water levels ($r = 0.78$, $P \leq 0.01$) than for adequate vs. deficit N levels ($r = 0.24$, NS). Thus, variation in

Table 5. Mean fertilizer use efficiency (FUE) and grain N use efficiency (NUE) for 12 corn hybrids representing three eras of introduction. Means represent averages across four growing seasons (1999–2002) at Shelton, NE.

Hybrid	Era	FUE		NUE			
		Deficit water	Adequate water	Deficit water	Adequate water	Deficit N	Adequate N
		Mg Mg ⁻¹		Mg Mg ⁻¹			
B73 × Mo17	1970s	41 b†	44 c	55 a	57 a	62 a	50 a
3162	early 1990s	44	56	49	54	55	48
3394		39	49	53	57	61	49
3417		47	54	60	62	68	54
	average	43 b	53 b	54 a	58 a	61 a	50 a
33A14	late 1990s	47	55	57	60	66	51
33G27		54	70	46	49	52	44
33H67		48	60	50	60	60	50
33R87		60	65	52	56	59	48
34D34		60	63	51	54	58	47
34G82		52	61	52	53	58	47
34K77		52	63	56	57	65	48
34R07		44	53	55	63	68	50
	average	52 a	61 a	52 a	57 a	61 a	48 b
	hybrid LSD	11	10	3	3	3	3

† Era means within a column and having the same letter are not significantly different (0.05).

Table 6. Genotypic correlations of hybrid mean yields grown under deficit and adequate water and N conditions.

	Deficit water	Adequate water	Deficit N	Adequate N
Deficit water	1.000			
Adequate water	0.655*	1.000		
Deficit N	0.715**	0.679*	1.000	
Adequate N	0.676*	0.789**	0.242	1.000

* Significant at the 0.05 probability level.

** Significant at the 0.01 probability level.

hybrid performance under deficit water was better predicted by hybrid performance under deficit N than under adequate water conditions, which is consistent with observations of Bänziger et al. (2002), who observed a low correlation between corn genotype performance under deficit and well-fertilized N conditions. The likely explanation for these observations is that the water and N stresses imposed on the hybrids produced similar adverse effects on key physiological processes, as suggested by Andrade et al. (2002), with both stresses having similar negative impacts on grain yield. For example, Bänziger et al. (2002) found that genotypes selected for drought tolerance also possessed physiological mechanisms conferring tolerance to N stress, with tolerant genotypes maintaining yields under both stresses relative to susceptible genotypes. It should also be noted that while the stress tolerant hybrids like 3417 and 34R07 maintained yields under water or N stress relative to more susceptible hybrids, they also produced yields similar to the highest-yielding hybrid 3162 under adequate levels of both inputs (Table 4). Thus, physiological mechanisms conferring water and N stress tolerance, apparently possessed by 3417 and 34R07, did not limit yields under optimal conditions. These results suggest that combining stress tolerance along with high yield potential should be feasible for future corn breeding efforts.

Associations between Grain Yield and other Agronomic Variables

Corn grain yield is closely linked with kernel number at maturity, with kernel number being determined by the physiological status of the crop around flowering (Kiniry and Ritchie, 1985; Otegui and Andrade, 2000). The importance of kernel number to grain yield was also noted in this study, as seen by the strong association between treatment (water, N, and hybrids)-induced variability in grain yield and kernel number per unit area (Table 7). Thus, hybrids' possessing physiological mech-

Table 7. Genotypic correlation values for associations among grain yield, total dry matter (DM), kernel weight (KW), number of kernels per hectare (KN), N uptake (NUP), and N use efficiency (NUE) collected from 12 corn hybrids grown under two water levels and two N levels during the 1999–2002 growing seasons at Shelton, NE.

	Yield	DM	KW	KN	NUP	NUE
Yield	1.000					
DM	0.975**	1.000				
KW	0.833**	0.813**	1.000			
KN	0.985**	0.958**	0.730**	1.000		
NUP	0.966**	0.956**	0.807**	0.955**	1.000	
NUE	-0.548**	-0.581**	-0.460*	-0.545**	-0.733**	1.000

* Significant at the 0.05 probability level.

** Significant at the 0.01 probability level.

anisms conferring the ability to maximize kernel number under deficit and adequate levels of both water and N was critical to their ability to maximize grain yields. According to Andrade et al. (2002) and Bänziger et al. (2002), crop stresses imposed during flowering, regardless of whether induced by water, N or light, have similar adverse effects on the physiological status of the crop through diminished photosynthetic rates, assimilate supplies, and plant growth rates. This in turn adversely affects the capacity of the corn plant to set kernels during critical reproductive growth stages, with kernel number and ultimately grain yield being negatively impacted by these stresses. Corn is thought to be more susceptible to stresses at flowering than many crops because of the large distance between male and female organs, exposing pollen and fragile stigmatic tissue to desiccating conditions during pollination (Bänziger et al., 2000). Finally, silk growth and kernel number determination are extremely sensitive to the availability of photosynthetic products during flowering (Schussler and Westgate, 1995). Studies comparing the response of stress-tolerant hybrids with sensitive hybrids have found different relationships between kernel number and crop physiological status (Tollenaar et al., 1992), with stress-tolerant hybrids setting more grains than susceptible hybrids under similar levels of crop stress.

As previously stated, the ability to maintain photosynthesis and assimilate supply under water and N stresses during flowering is crucial for maintaining seed number and grain yield. The role crop N status plays in maintaining photosynthesis has been well documented (Wolfe et al., 1988; Uhart and Andrade, 1995b; Settini and Maranville, 1998), with previous research showing about 50% of all leaf N being directly involved in photosynthesis either as enzymes or as chlorophyll. Because of the physiological link between crop N status and photosynthesis, N uptake, crop biomass production, kernel number, and grain yield are all typically strongly correlated, as was confirmed in our work (Table 7). Thus, the ability of hybrids to maximize N uptake under deficit and adequate levels of N was critical to their ability to maximize kernel number, as seen by the strong association between N uptake and kernel number (Table 7), and consequently grain yields were maximized. According to Bänziger et al. (2000), maintenance of grain yield under N stress is obtained by maximizing both N uptake and NUE. They observed NUE values of 30 to 70 kg grain per kg N at low levels of N availability, which is similar to the values observed in this study for the 12 hybrids grown under deficit N (Table 5). Under adequate N levels, NUE decreased by an average of 12% for the 12 hybrids relative to deficit N conditions (Table 5), indicating N assimilated into the plant was used less efficiently under increasing N availability. These results are consistent with the observations of Bänziger et al. (2000). The association between hybrid variation in grain yield and NUE can be further understood by examining the correlation between hybrid values for NUE and grain yield under all levels of water and N where it was observed to be negatively correlated (Table 7). However, when the correlation analysis was done (data

not shown) using hybrid values for only deficit N treatments, then the correlation was positive ($r = 0.79$, $P \leq 0.01$). Thus, across a wide range of available N, hybrid variability in NUE and grain yield appears to be negatively associated while under low-N conditions, the association is positive. These results suggest that selection of potential new hybrids should occur under limited soil N, if the goal is to develop hybrids with increased NUE and ability to maintain grain yield under N stress, which agrees with the recommendation of Bänziger et al. (2000).

SUMMARY AND CONCLUSIONS

Twelve corn hybrids from three eras of release (1970s and early 1990s and late 1990s) were grown under deficit and adequate levels of water and N to characterize their agronomic responses to varying water and N supply. While hybrid eras did not differ, individual hybrids varied in their ability to maintain yields under water or N stress. Likewise, they varied in their ability to respond to adequate water and N conditions, maximizing yields. Some hybrids were observed to yield relatively well under both deficit and adequate conditions of water or N, suggesting that it should be feasible to combine stress tolerance along with high yield potential in future elite germplasm.

Kernel number was highly associated with grain yield ($r = 0.98$), indicating that possessing physiological mechanisms conferring ability to maximize kernel number under deficit and adequate levels of both water and N was critical for hybrids to maximize grain yields. Thus, determining physiological mechanisms associated with ability to maintain kernel number under water and N stress should be a high priority of corn improvement programs. Previous research has shown that kernel number is strongly linked to assimilate supply during the critical period around flowering, which is in turn determined by ability to maintain photosynthetic rate under stress during this time. Perhaps measurements of leaf photosynthetic rates of differing genotypes grown under water or N stress during this critical time period could provide additional insights regarding stress tolerance mechanisms.

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