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Variation in nitrogen use efficiency among soft red winter wheat genotypes*

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Summary. Nitrogen use efficiency (NUE), defined as grain dry weight or grain nitrogen as a function of N supply, was evaluated in 25 soft red winter wheat genotypes for two years at one location. Significant genotypic variation was observed for NUE, nitrogen harvest index, and grain yield. Genotype × environment interaction for these traits was not significant. Several variables including N uptake efficiency (total plant N as a function of N supply), grain harvest index, and N concentration at maturity were evaluated for their role in determining differences in NUE. Nitrogen uptake efficiency accounted for 54% of the genotypic variation in NUE for yield and 72% of the genotypic variation in NUE for protein. A path coefficient analysis revealed that the direct effect of uptake efficiency on NUE was high relative to indirect effects.

Key words: *Triticum aestivum*, L. – Nitrogen use efficiency – Path coefficients

Introduction

Nitrogen use efficiency (NUE) has been defined as grain production per unit of available N (Novoa and Loomis 1981; Moll et al. 1982). Genetic variation in NUE has been demonstrated in maize (Moll et al. 1982; Kamprath et al. 1982). Widespread interest in maximizing wheat (*Triticum aestivum* L.) yields, in part through increased levels of nitrogen fertilizer, suggests that evaluation of NUE may be useful in identifying responsive genotypes.

Considerable research has been done with wheat evaluating nitrogen uptake prior to and during the grain filling period. Seth et al. (1960) detected no varietal differences in N uptake at anthesis. McNeal et al. (1966) found differences among five spring wheat varieties in leaf nitrogen at anthesis, but no differences in stem nitrogen were detected. Austin et al. (1977), in an evaluation of 47 winter wheat genotypes, showed little variation for N accumulation at anthesis, while Cox et al. (1985) reported genetic variation in pre-anthesis N uptake in spring wheat. Several authors have reported continued uptake of nitrogen during grain fill (McNeal et al. 1966; Spiertz and Ellen 1978; Gregory et al. 1981) and genetic differences have been reported (Austin et al. 1977, Cox et al. 1985). Nitrogen uptake has been associated with grain yield in several studies (Austin et al. 1977; Desai and Bhatia 1978; Cox et al. 1985; Loeffler et al. 1985), yet the absence of this relationship has also been reported (Dubois and Fossati 1981). The proportion of nitrogen taken up that was translocated to the developing grains has been estimated in several studies (McNeal et al. 1968; McNeal et al. 1972; Blacklow and Incoll 1981; Campbell et al. 1983). In soft red winter (SRW) wheat, however, nitrogen metabolism has not been widely studied. Specifically, the importance of N uptake versus N use within the plant in determining differences in nitrogen use efficiency has not been evaluated in the SRW germplasm.

The objectives of this study were (1) to evaluate nitrogen use efficiency in a set of adapted soft red winter wheat genotypes, (2) to determine the relative importance of N uptake versus intra-plant use in determining variation in NUE and grain protein levels, and (3) to quantify genotype × environment interaction in several measures of N utilization.

Materials and methods

The 25 SRW genotypes evaluated in 1983 and 1984 are listed in Table 1. Seed was planted at a rate of 100 kg/ha in

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Table 1. Two year genotype means for grain yield, protein and components of nitrogen metabolism

Genotype	NUEY (GDW/NS)[a]	NUEP (TGN/NS)	HI (GDW/TDW)	(TDW/TN)	(TN/NS)	(TGN/TDW)	Yield ($g \cdot m^{-2}$)	NHI (TGN/TN)	Grain protein (%)
'Feland'	68.3	1.27	0.47	75.5	1.84	0.0097	677	0.73	11.6
'Saluda'	67.6	1.05	0.48	91.4	1.46	0.0083	669	0.75	9.7
'JS 222'	63.8	1.22	0.47	75.7	1.58	0.0101	632	0.76	12.1
'FLA 302'	59.1	0.99	0.44	84.9	1.52	0.0081	586	0.67	10.2
'Wheeler'	58.2	1.05	0.46	85.1	1.48	0.0089	577	0.74	10.9
'Auburn'	58.1	1.11	0.46	77.7	1.49	0.0098	576	0.76	12.1
'Arthur'	55.6	1.13	0.45	80.3	1.46	0.0094	550	0.75	11.9
'Beau'	55.0	1.03	0.48	73.1	1.39	0.0108	545	0.79	12.9
'2550'	53.0	1.00	0.46	80.3	1.62	0.0089	525	0.69	10.8
'Scotty'	53.0	0.91	0.42	88.4	1.35	0.0082	525	0.70	10.8
'Caldwell'	52.9	0.91	0.46	85.1	1.32	0.0087	524	0.72	10.6
'Massey'	52.7	0.88	0.42	79.4	1.24	0.0087	522	0.68	11.8
'S-76'	51.0	0.79	0.43	82.8	1.32	0.0084	506	0.69	11.0
'Abe'	50.0	0.88	0.43	70.4	1.30	0.0099	496	0.70	13.1
'Tyler'	49.6	0.87	0.42	87.1	1.33	0.0076	492	0.64	10.0
'Fillmore'	49.2	1.04	0.41	86.2	1.52	0.0081	487	0.69	11.0
'Sullivan'	49.0	0.93	0.42	81.7	1.31	0.0090	486	0.71	11.9
'McNair 1003'	48.6	0.91	0.45	71.8	1.34	0.0096	482	0.69	12.1
'Coker 916'	47.1	0.86	0.45	66.5	1.26	0.0102	466	0.68	12.8
'Pike'	46.6	0.95	0.44	79.6	1.47	0.0092	462	0.72	11.7
'Coker 747'	45.4	0.84	0.45	75.4	1.35	0.0095	449	0.71	11.9
'Hart'	44.2	0.85	0.38	83.2	1.21	0.0082	438	0.66	11.9
'Hunter'	43.7	0.83	0.45	71.8	1.28	0.0090	432	0.64	11.5
'Doublecrop'	42.8	0.94	0.44	66.5	1.37	0.0110	424	0.71	13.8
'Arthur 71'	42.5	0.78	0.43	84.7	1.06	0.0090	421	0.76	11.7
SE[b]	9.65	0.21	0.04	7.97	0.30	0.0009	95	0.05	0.9

[a] GDW = grain dry weight (g); NS = nitrogen supplied to the plant (g); GN = grain nitrogen (mg); TDW = total plant dry weight (g); TN = total plant nitrogen (mg)

[b] Standard error of a genotype mean

conventional six row yield plots in rows 17.8 cm apart. The experimental design was a randomized complete block with two replications. Planting dates were 15 October 1982 and 28 October 1983 and the location each year was the Spindletop Research Farm near Lexington, KY. The soil type was a Maury silt loam, Typic Paleudalf.

Nitrogen was applied as ammonium nitrate at the rate of 54 kg/ha N at growth stage 5 and 27 kg/ha N at growth stage 9 in 1983 and 18 kg/ha N at growth stage 3, 54 kg/ha N at growth stage 6 and 27 kg/ha N at growth stage 9 in 1984 (Large 1954). The reason for the early application of N at growth stage 3 in 1984 was that the severe winter had reduced plant stands and early spring tiller initiation was desired. Temperatures remained cool and the rate of plant growth was slow, so that a second application of N was not called for until growth stage 6.

At harvest maturity, a 1 m segment of an interior row was harvested from each plot with a hand sickle. The samples were divided into vegetative and grain portions, dried for 48 H at 45 C and weighed. Samples were ground with a UDY cyclone mill using a 1 mm screen. Total nitrogen was determined by a micro-Kjeldahl method (Bradstreet 1965).

Statistical analysis

Individual analyses of variance were conducted for the 1983 and 1984 data as well as a combined analysis over years. Characters measured included grain dry weight, vegetative dry weight, total grain N and total vegetative N at maturity. From these measurements, estimates of harvest index (HI), nitrogen harvest index (NHI), and grain protein, (total grain N×5.65; Tkachuk 1969) were also computed and analyzed.

Variation in NUE among genotype means was evaluated according to the method of Moll et al. (1982). Two measures of NUE were considered: (1) nitrogen use efficiency for yield (NUEY) and (2) nitrogen use efficiency for protein (NUEP). The two variables were defined as follows:

$$\text{NUEY} = (\text{GDW}/\text{NS})$$
$$\text{NUEP} = (\text{TGN}/\text{NS})$$

where GDW/NS = grain dry weight/fertilizer nitrogen supplied to the crop, and
TGN/NS = total grain nitrogen/fertilizer nitrogen supplied to the crop.

The analysis of NUEY and NUEP makes use of the fact that as ratios, these two variables can be expressed as products of ratios. Thus,

$$\text{NUEY} = \text{GDW}/\text{NS} = (\text{GDW}/\text{TDW})\,(\text{TDW}/\text{TN})\,(\text{TN}/\text{NS})$$

and

$$\text{NUEP} = \text{TGN}/\text{NS} = (\text{TGN}/\text{TDW})\,(\text{TDW}/\text{TN})\,(\text{TN}/\text{NS}),$$

where TDW = total above ground dry weight
TN = total plant nitrogen

and other variables are as defined previously. Thus, NUEY is expressed as a product of nitrogen uptake efficiency (TN/NS), biomass production efficiency (TDW/TN) and harvest index (GDW/TDW). Similarly NUEP can be expressed as a product of N uptake efficiency, biomass production efficiency, and the ratio of total gain N to total dry weight (TGN/TDW). Taking logarithms of these expressions yields the following identities:

$$Y_1 = X_1 + X_2 + X_3$$
$$Y_2 = X_4 + X_2 + X_3$$

in which $Y_1 = \log$ (NUEY), $Y_2 = \log$ (NUEP), $X_1 = \log$ (GDW/TDW), $X_2 = \log$ (TDW/TN), $X_3 = \log$ (TN/NS), $X_4 = \log$ (TGN/TDW).

The contributions of each X_i term to sums of squares of Y_1 and Y_2 were estimated according to the method of Moll et al. (1982). As those authors noted, both sums of squares due to an X_i term itself as well as sums of cross products between the X_i terms and other X_i terms in the expression are reflected in these estimates. In order to assess the magnitude of direct versus indirect effects of the X_i terms on Y_1 and Y_2, a path analysis of these identities, according to the method of Wright (1921) and Li (1975) was conducted.

Table 2. Mean squares for NUEY, NUEP, NHI and grain protein from the combined analysis, 1983–84

Source	df	Mean square			
		NUEY	NUEP	NHI	Grain protein
Year	1	1,402.9	1.8341*	1.1876*	33.3200*
Rep/Year	2	136.4	0.0604	0.0215**	0.7233
Genotype	24	199.9*	0.0801*	0.0058**	3.7984**
Year × Genotype	24	152.3	0.0653	0.0030	0.7262
Error	45	93.25	0.0438	0.0025	0.7752

* $P \leqq 0.05$
** $P \leqq 0.01$

Table 3. Relative contributions to the sums of squares for NUEY and NUEP of components in each identity

Trait	Log	1983 $\Sigma xy/y^2$	1984 $\Sigma xy/y^2$	1983–84 $\Sigma xy/y^2$
NUEY (GDW/NS)	Y_1	–	–	–
HI (GDW/TDW)	X_1	0.24	0.04	0.26
TDW/TN	X_2	0.16	0.15	0.20
TN/NS	X_3	0.60	0.81	0.54
NUEP (GN/NS)	Y_2	–	–	–
TDW/TN	X_2	−0.06	−0.02	−0.14
TN/NS	X_3	0.80	0.80	0.72
TGN/TDW	X_4	0.26	0.22	0.42

Results and discussion

Two year genotypic means for several traits are shown in Table 1, and the analyses of variance of NUEY, NUEP, NHI and grain protein presented in Table 2. Genotype means ranged from 42.5 to 68.3 for NUEY and from 0.78 to 1.27 for NUEP. Significant genotypic variation was observed for both characters. The correlation between NUEY and NUEP was high (r = 0.89), which agrees with reports from the literature indicating similar patterns of assimilation for carbon and N in the developing wheat kernel (Simpson et al. 1983). Genotypic variation in assimilation patterns of photosynthate and nitrogen has been reported however (Borghi et al. 1983). In the present study, for example, Fillmore demonstrated low NUEY yet high NUEP (Table 1). The range in genotypic means for HI was quite narrow (0.38–0.48, Table 1) and significant variation attributable to genotypes was not observed. Significant genotypic variation was detected for the other three components of nitrogen use efficiency: (TDW/TN), (TN/NS), and (TGN/TDW) (Table 1) and also for grain yield, grain protein concentration, and NHI (Table 1). Significant genotype × year interaction was not detected for any character studied (Table 2).

The analysis of nitrogen use efficiency is presented in Table 3. It is not possible in this analysis to resolve the term $\Sigma\, xy/y^2$ into individual versus joint contributions to the variance of the Y term in the model. Thus, the interpretation that an individual X term is responsible for a certain proportion of the variation in Y must be made with caution. Nitrogen uptake efficiency (X_3) was associated with a large proportion of the sums of squares of NUEY (Y_1): 60% in 1983, 81% in 1984 and 54% in the two year analysis. Biomass production efficiency (X_2) accounted for a smaller proportion of the variation in NUEY (Y_1): 16% in 1983, 15% in 1984, 20% over both years. The contribution of harvest index (X_1) to the sums of squares of NUEY varied widely over the two years: 24% in 1983 and 4% in 1984. The average contribution of X_1 over both years was 26%.

Determination of the sums of squares of NUEP (Y_2) followed a pattern similar to that observed for Y_1, in that uptake efficiency (X_3) played a major role (72% over two years), while the other components of Y_2, X_2 and X_4, were associated with much less of the variation in Y_2. The contribution of X_2 to the sums of squares of Y_2 was, in fact, negative (−14% in the combined analysis). Negative contributions to sums of squares derive from negative correlations between the components in the identity. In the case of X_2, the negative contribution stemmed from the negative correlation between X_2 and Y_2 (Table 4).

Correlations between the components of nitrogen use efficiency, NHI, and grain protein are presented in Table 4. The highly significant positive correlations between N uptake (X_3) and Y_1 (r = 0.70) and X_3 and Y_2 (r = 0.89) are in agreement with the results shown in Table 3. Harvest index (X_1) was significantly correlated with Y_1 (r = 0.61), although it contributed much less to the variation in NUEY than did N uptake efficiency (Table 3). Interestingly, although NUEP (Y_2) and N uptake efficiency (X_3) were highly correlated (r = 0.89),

Table 4. Correlations between two year means for grain protein, NHI and components of nitrogen use efficiency

	Grain protein	NHI	X_1	X_2	X_3	Y_1	X_4	Y_2
Grain protein	1.00	0.19	−0.07	−0.85**	0.23	−0.39	0.81**	0.24
NHI		1.00	0.64**	0.04	0.20	0.46*	0.54**	0.61**
X_1			1.00	−0.13	0.36	0.61**	0.51**	0.59**
X_2				1.00	−0.33	0.31	−0.81**	−0.22
X_3					1.00	0.70**	0.40*	0.89**
Y_1						1.00	0.01	0.79**
X_4							1.00	0.55**
Y_2								1.00

* $P \leqq 0.05$; ** $P \leqq 0.01$

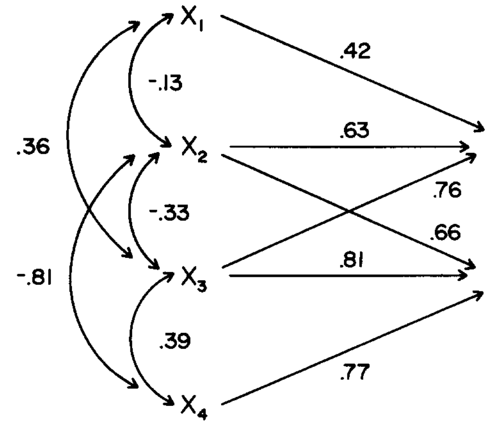

Fig. 1. Path diagram of nitrogen use efficiency for yield (Y_1) and protein (Y_2) as determined by harvest index (X_1), biomass production efficiency (X_2), N uptake efficiency (X_3), and protein production efficiency (X_4)

neither X_3 nor Y_2 was significantly correlated with grain protein (Table 4). In 1984, N uptake and grain protein were correlated (r = 0.42), but in 1983 and in the combined analysis, the association was not significant. While the concentration of protein in the grain may not be independent of total N uptake, the association between the two is at best weak and subject to environmental influences which may affect partitioning of photosynthate to the grain. The ratio of total grain N to total dry weight (X_4) was significantly correlated with NUEP (r = 0.55).

Path coefficients are presented in Fig. 1. The objective of the path analysis was to uncover relationships between variables not revealed in either the correlation or the log analyses. For N uptake efficiency (X_3) it appears that the direct effects of X_3 on both Y_1 and Y_2 are of much greater magnitude than the indirect effects in either case (0.76 versus −0.05 for Y_1; 0.81 versus 0.08 for Y_2). Biomass production efficiency, X_2, had a strong positive direct effect on Y_1 ($p_{21} = 0.63$) and on Y_2 ($p_{22} = 0.66$). This effect was diminished considerably, however, by the negative correlations between X_2 and X_1, X_3 and X_4. Thus the indirect effects of X_2 on Y_1 and Y_2 were negative, a fact which is evident in the negative contribution of X_2 to the sums of squares of Y_2 (Table 3). Similarly, the positive direct effect of X_4 on Y_2 ($p_{42} = 0.77$) was opposed by the strong negative correlation between X_4 and X_2.

It appears from this study that nitrogen uptake efficiency was associated with a significant proportion of the genotypic variation in nitrogen use efficiency for yield and protein. This agrees with the results of Moll et al. (1982) in which NUE in maize was determined largely by N uptake efficiency under a high N regime. Under low N conditions, however, uptake efficiency played a smaller role in determining NUE. Cox et al. (1985) reported a significant association between total N assimilation and grain yield in spring wheat in both low and high N environments. Uptake efficiency per se was not measured. Our data suggest that under non-limiting N conditions there will be a strong association between N uptake and grain yield and protein per unit area.

Interestingly, nitrogen concentration in the biomass at maturity did not explain a significant amount of variation in NUEY. This is in contrast to Stanford and Hunter (1973) and Van Keulen (1977). The review by Novoa and Loomis (1981), citing these two studies, suggests that a level of 1.4 to 1.6% N in the biomass at maturity is necessary for high wheat yields. In the present study, N concentration, (TN/TDW), the reciprocal of X_2 (TDW/TN), ranged from 1.09% to 1.50% and averaged 1.26%. The contribution of nitrogen concentration (TN/TDW) to variation in Y_1 or Y_2 can be estimated from an analysis of logarithms. If the model (GDW/NS) = (GDW/TN) (TN/TDW) (TDW/NS) is considered, for example, it can be shown that the contribution of log (TN/TDW) to the sums of squares of Y_1 is −20%. Thus, in the two year analysis N concentration in the tissue made a negative contribution to the sums of squares of NUEY (−20%) and a small positive contribution to the sums of squares of NUEP (14%). These results correspond to the observations of Austin et al. (1977), who found that high yielding wheat genotypes which took up the most nitrogen were generally the largest plants, and that variation in tissue N concentration at harvest was of little consequence. Similarly, in the present study the correlation between total dry weight and nitrogen uptake was highly significant ($r=0.71$). It can be shown, in fact, that the contribution of (TDW/NS) to the sums of squares of NUEY was 74% (Table 3).

Soft red winter wheat cultivars are selected for low grain protein in accordance with industry standards. There is concern that in high N environments, grain protein may be elevated to excessive levels. Thus, it was of interest in the present study to evaluate nitrogen use in terms of protein production as well as grain production. In a recent review of the genetics of nitrogen metabolism, Cregan and Van Berkum (1984) suggested that one might select for NHI in developing genotypes which use N efficiently in protein production. In the present study, NHI was significantly correlated with HI, NUEY, NUEP, and remobilization efficiency (X_4) (Table 4). Using the values obtained from the analysis of logs (Table 3), it can be shown that, in the two year analysis, NHI contributed 28% of the sums of squares of NUEP versus the 72% associated with uptake efficiency (TN/NS). Additionally, in a path analysis involving only uptake efficiency and NHI as determinants of NUEP, the direct effect of uptake on NUEP ($p_{12}=0.81$) is significantly greater ($P<0.05$) than that of NHI ($p_{22}=0.45$). In this group of genotypes there are examples of cultivars with high NHI and low NUEP ('Arthur 71') or low NHI and high NUEP ('FLA 302') (Table 1). Based on the genotypes in this study, under high N conditions, nitrogen uptake would be a better criterion than NHI for identifying genotypes which use nitrogen most efficiently in producing protein.

It is apparent that in a high N environment, N uptake is associated with the capacity of the plant to produce grain and protein. Plant breeders generally evaluate physiological characters in the hope that there will be a trait which can be measured more efficiently than grain yield. Nitrogen concentration in the flag leaf, for example, would be such a trait. In the present study, however, N concentration was not related to NUE. Nitrogen uptake efficiency, which explained a substantial portion of the variation in NUE in this study, was estimated by measuring total plant N at harvest. While this trait is not measured more efficiently than yield in mature plants, it is possible that efficient seedling or in vitro screening procedures could be devised.

In order to assess the overall importance of N uptake efficiency, the genotypes in the present study must be evaluated in a low N environment. In maize, N uptake efficiency played a much smaller role in determining genotypic variation in NUE in a low N environment than in a high N environment (Moll et al. 1982). Genotypes which are efficient under one nutritional regime may thus be inefficient in a different nutritional environment. The next step to be taken in this area is the characterization of genetic variation in SRW wheat populations in both low N and high N environments.

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