Analysis and Interpretation of Factors Which Contribute to Efficiency of Nitrogen Utilization[1]

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ABSTRACT

Differences in N response among corn (*Zea mays* L.) genotypes reflect variation in numerous processes involved in N use efficiency. In order to facilitate the study of such variation, we develop and demonstrate a concept for evaluating the contribution of N uptake and utilization processes to variation in N use efficiency. Eight hybrids were grown in a replicated field experiment at two levels of N fertilizer on a Dothan loamy sand (Typic Plinthic Paleudult). Differences among the hybrids for components of N use efficiency were evaluated from measurements of grain yield, N accumulation in the plant at silking, and N accumulation in the grain and stover at harvest. Significant differences were found among hybrids and between N levels for all traits. Interactions among hybrids and N levels were significant for all traits except grain yield. At low N supply, differences among hybrids for N use efficiency were due largely to variation in utilization of accumulated N, but with high N they were due largely to variation in uptake efficiency. Variation in proportion of N translocated to grain was also important at the low N supply. Variation in N accumulated after silking was not important at either level of N supply. Variation in N remobilization from vegetative tissue to grain was moderately important at the low N supply. Hybrids with similar levels of N use efficiency showed marked differences in component traits which contribute to efficiency.

Additional index words: **N uptake, N translocation, *Zea mays* L.**

The effectiveness with which N is used by corn (*Zea mays* L.) and other non-legume crop plants has become increasingly important because of increased costs of manufacture and distribution of N fertilizer. Differences in N utilization among corn genotypes have been demonstrated, not only in differential responses to N fertilizer (Smith, 1934; Stringfield and Salter, 1934), but also in differences in absorption and in utilization of absorbed N (Beauchamp et al., 1976; Chevalier and Schrader, 1977; Moll and Kamprath, 1977; Pollmer et al., 1979; Reed et al., 1980). Thus, the potential for developing superior, N-efficient hybrids appears to exist.

Efficiency in uptake and utilization of N in the production of grain requires that those processes associated with absorption, translocation, assimilation, and redistribution of N operate effectively. The relative contribution of these processes to genotypic differences in N use efficiency is unknown and may vary among genetic populations and among environments, including N supply. It therefore is important to characterize efficiency of N use in terms related to variation in the major processes involved. However, a severe constraint in doing so is that direct measurements are not feasible in large field studies involving both genotypic and fertilizer variables because of high costs in terms of land, labor, and time. As a consequence, most studies to date have been limited to estimates of N accumulation in certain plant parts at certain stages of growth. We contend herein that judicious use of such data can afford appreciable insight about genotypic variation in response to N supply.

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Our objective is to develop and to demonstrate a concept for using data on N accumulation to evaluate the relative contribution of various N acquisition and distribution processes to variation in overall efficiency of N use.

THEORY

We define N use efficiency as grain production per unit of N available in the soil. Nitrogen use efficiency is Gw/Ns in which Gw is grain weight and Ns is N supply expressed in the same units (e.g., g/plant). There are two primary components of N use efficiency: (1) the efficiency of absorption (uptake), and (2) the efficiency with which the N absorbed is utilized to produce grain. These are expressed as follows: uptake efficiency = Nt/Ns, and utilization efficiency = Gw/Nt, where Nt is total N in the plant at maturity.

It follows that:

$$Gw/Ns \equiv (Nt/Ns)(Gw/Nt).$$

We let $Y = \log Gw/Ns$, $X_1 = \log Nt/Ns$, and $X_2 = \log Gw/Nt$, so that $Y_k \equiv X_{1k} + X_{2k}$ for the kth experimental unit. The sum of squares for $y = Y - \mu$ over all experimental units will be:

$$\Sigma_k Y_k^2 \equiv \Sigma_k x_{1k}^2 + \Sigma_k x_{2k}^2 + 2\Sigma_k x_{1k} x_{2k}.$$

The expression can be expanded to include additional factors. For example, N uptake during grain filling and translocation of N to grain may be important variables (Pollmer et al., 1979). Let Na represent N accumulation after silking and Ng represent N accumulated in grain at harvest. Utilization efficiency, Gw/Nt, can be expressed as:

$$Gw/Nt \equiv (Gw/Ng)(Ng/Nt), \text{ and}$$
$$Ng/Nt \equiv (Na/Nt)(Ng/Na),$$

in which

Gw/Ng = grain produced per unit of grain N
Ng/Nt = fraction of total N that is translocated to grain
Na/Nt = fraction of total N that is accumulated after silking
Ng/Na = ratio of N translocated to grain to N accumulated after silking.

Therefore: $Gw/Ns \equiv (Nt/Ns)(Gw/Ng)(Na/Nt)(Ng/Na)$.

Other expressions might be devised to evaluate different factors. As long as the expression is a multiplicative identity, the general expression in terms of logs will be:

$$Y_k \equiv \Sigma_i X_{ik},$$

in which Y_k = log of N use efficiency (Gw/Ns) for the kth experimental unit and X_{ik} = log of the ith multiplicative component.

By simple algebra, sums of squares of log N use efficiency is:

$$\Sigma_k y_k^2 \equiv \Sigma_k[\Sigma_i x_{ik}^2 + \Sigma_{i \neq j} x_{ik} x_{jk}] \equiv \Sigma_k(\Sigma_i y_k x_{ik}).$$

Therefore, the contribution of the ith component to the sum of squares of log N use efficiency is $\Sigma_k y_k x_{ik}$, which includes not only the sum of squares of the log of the ith component but also the sum of products between it and the logs of other components in the model. This is related to the direct and indirect effects of a path analysis (Wright, 1921), which becomes obvious if the above expression is substituted into

Table 1. Mean performance of eight hybrids in terms of grain production and N accumulation at two levels of N fertilizer.

Applied nitrogen (Ns)	Hybrid	Grain yield (Gw)	Nitrogen accumulation: Total (Nt)	Before silking (Nv)	After silking (Na)	Grain (Ng)
g/plant		g/plant				
2.47	1	223	5.48	2.38	3.10	3.94
	2	218	5.25	2.71	2.54	3.59
	3	185	4.63	2.42	2.21	2.99
	4	270	5.64	3.05	2.59	3.91
	5	180	5.15	2.64	2.51	3.18
	6	264	5.01	2.70	2.31	4.07
	7	297	5.05	2.18	2.87	3.88
	8	254	4.34	2.34	2.00	3.50
9.89	1	243	6.47	3.31	3.16	4.35
	2	275	7.64	2.69	4.95	4.86
	3	217	6.70	3.26	3.44	3.92
	4	310	7.15	3.72	3.43	5.07
	5	195	424	2.00	2.24	3.05
	6	319	7.48	3.70	3.78	5.76
	7	276	5.75	2.41	3.34	4.28
	8	257	5.66	4.41	1.26	4.26
Standard error		16	0.29	0.25	0.39	0.27

Table 2. Contribution of variation in efficiency components to hybrid sum of square for efficiency of N use.

Trait		Logarithm	N Applied (kg/ha)	Fraction of hybrid SS $\Sigma x_i y/\Sigma y^2$	ryx_i	Sx_i/S_y
N use efficiency	Gw/Ns	Y	–	–	–	–
Uptake efficiency	Nt/Ns	X_1	56	0.048	0.102	0.469
			224	0.829	0.719	1.153
Utilization efficiency	Gw/Nt	X_2	56	0.952	0.897	1.061
			224	0.171	0.209	0.817
Grain N/total plant N	Ng/Nt	X_3	56	0.449	0.813	0.552
			224	0.228	0.402	0.568
N uptake after silking/total	Na/Nt	X_4	56	0.070	0.143	0.487
			224	0.031	0.016	1.944
Grain N/N uptake after silk	Ng/Na	X_5	56	0.379	0.528	0.718
			224	0.197	0.088	2.242
Grain yield/grain N	Gw/Ng	X_6	56	0.503	0.814	0.618
			224	−0.058	−0.147	0.392

ryx_i = correlation coefficient between Y and X_i; Sx_i, S_y = standard derivations for X_i and Y, respectively.

the equation for the correlation coefficient, and the terms are rearranged. The proportion of the sum of squares for Y attributable to the *ith* component (X_i) will be:

$$\Sigma x_i y/\Sigma y^2 = (r_{yx_i})\, S_{x_i}/S_y,$$

in which r_{yx_i} is the correlation coefficient and S_y and S_{x_i} are the standard deviations for log N use efficiency and the *ith* component. Note that a negative correlation between a component trait and N use efficiency will result in a negative contribution to the sum of squares of Y.

The development above involves terms representing our concept of definitive parameters of N use efficiency. Some of these, such as available soil N and total plant N are difficult to measure accurately. In lieu of such measurements, the terms Ns and Nt could be substituted for N*s* and N*t* to represent fertilizer N and aboveground plant N, respectively. Therefore, we use below roman subscripts to represent experimental measurements. This does not change the algebraic development presented above, but, of course, must be taken into account in the interpretation of the analysis.

METHODS AND MATERIALS

Eight experimental hybrids were evaluated in a split plot experiment with two rates of N fertilizer, (56 and 224 kg N/ha), supplied as ammonium nitrate. The hybrids were single crosses between unselected inbred lines (> S_{18} generation) from 'Jarvis Golden Prolific' and 'Indian Chief.' The experiment was conducted with eight replications at Clayton, N.C. on a Dothan loamy sand (Typic Plinthic Paleudult) in 1978. Each subplot was a single 10-plant row of a hybrid between experimental inbred lines, with approximately 96 cm between rows and 46 cm between plants. Ends of the plots were planted with a purple marker stock to provide competition. One competitive plant per plot was harvested at silking and analyzed for total N. Six to eight competitive plants per plot were harvested at maturity. Stover was chopped and dried to determine dry weight, and a sample was analyzed for percent N. Shelled grain was weighed, and a sample analyzed for percent H_2O and percent N. Weight measurements were adjusted to a dry weight basis.

The following data, all in g/plant, serve for analysis:

Gw = grain dry weight
Nt = total aboveground plant N at maturity
Nv = total aboveground plant N at silk
Na = Nt − Nv = aboveground plant N accumulated after silk
Ng = N accumulated in the grain at harvest

Analyses of variance were computed for these five traits.

Contribution of the various components to variation among hybrids in efficiency of N use at each level of N fertilizer was determined by sums of squares and sums of products of log ratios of hybrid means as outlined in the previous section.

RESULTS AND DISCUSSION

Analyses of variance showed significant differences among hybrids and between N fertilizer rates for all five primary traits (Table 1). Interaction of hybrids and N rate was significant for all traits except grain yield. At the low rate of N fertilizer, comparison of hybrid means for N accumulation in aboveground tissue (Nt) with fertilizer N (Ns) shows that approximately half of the N accumulated in plants at maturity must have come from mineralization of soil N because Nt ≃ 2(Ns). The range among genotypes was from 43 to 55%.

Logarithms of N use efficiency (Gw/Ns), uptake efficiency (Nt/Ns) and utilization efficiency (Gw/Nt), which will be denoted as Y, X_1, and X_2, respectively, were computed from the means given in Table 1. Sums of squares for Y, and sums of products of Y with X_1 and X_2 were computed and the contribution of X_1 and X_2 to Σy^2 expressed as $(\Sigma x_1 y/\Sigma y^2)(100)$ and $(\Sigma x_2 y/\Sigma y^2)(100)$ (Table 2). The relative contribution of the two component traits, uptake and utilization, to variation in efficiency among hybrids was considerably different for the two levels of N applied. At low N supply the correlation between N use efficiency and N uptake efficiency was small, and variation in the latter was also relatively small. Therefore, variation in N uptake efficiency contributed very little to variation in N use efficiency among the hybrids. This is in sharp contrast to its substantial contribution to variation under high N.

A further breakdown in utilization efficiency indicates that variation in the fraction of N translocated to grain (Ng/Nt) was more than twice as important at low N supply than at high N (Table 2). This is due primarily to differences in magnitude of correlation between N use efficiency and Ng/Nt. Variation in the proportion of total N that was taken up after silking (Na/Nt) contributed relatively little to variation in efficiency of N use. Even though the variation for that component was relatively large under high N, it was not correlated with N use efficiency.

It has been reported that the amount of N remobilized from storage in vegetative tissues is important in utilization of N (Friedrich and Schrader, 1979; Pollmer et al., 1979). Accumulation of N in grain (Ng) is equivalent to N accumulated after silking (Na) plus net remobilization of N stored in vegetative tissues prior to silking. If Nr = remobilized N, then (Ng/Na) = (Na + Nr)/Na = 1 + (Nr/Na). Therefore, variation in Ng/Na reflects variation in Nr/Na, and the data show that Ng/Na was moderately important in contributing to variation in N use efficiency at the low N supply (Table 2). Its contribution at high N supply is almost entirely due to an unusually large standard deviation.

All of the hybrids were less efficient in N use at the high level of N supply (Table 3). Differences in N use efficiency (Gw/Ns) among hybrids appear to have been due to a number of factors. Even relatively inefficient hybrids may be above average for one or more of the component factors. Furthermore, hybrids with comparable high levels of N use efficiency may differ markedly in the way that level of efficiency is achieved. Hybrids designated by nos. 4, 6, and 7 were relatively efficient at both levels of N supply. Hybrid no. 4 was efficient in uptake (Nt/Ns), especially at the low N supply. Hybrid no. 7 was average or below in uptake efficiency, but it was highly efficient in utilizing the N taken up in grain production (Gw/Nt). Hybrid no. 7 was also above average in the fraction of total N that was translocated to grain (Ng/Nt). Hybrid no. 6 appeared to be efficient in uptake when N supply was high, and was highest in efficiency of translocating N to grain (Ng/Nt) at both N levels.

Causes of variation in N use efficient in terms of component factors appear to differ between levels of N supply and among genotypes. The importance of variation in uptake efficiency relative to variation in utilization efficiency was in sharp contrast between levels of N supply. This result may have important implications with regard to effects of genetic selection under specific levels of N fertility. From the limited data presented here we speculate that selection under high N supplies might favor genotypes which are efficient in N uptake when N is abundant; but there may be little or no selection pressure to improve efficiency of utilization of accumulated N. Such genotypes might perform poorly under limited N supplies.

In breeding for improved N use efficiency, it would seem desirable for both uptake efficiency and utilization efficiency to be improved simultaneously. This may require finding a unique fertility environment or developing a selection index based on data at several fertility levels in order to ensure equal selection pressure on the two components.

Table 3. N use efficiency and components of N efficiency for eight hybrids at two levels of N fertilizer.

Hybrid†	Gw/Ns	Nt/Ns	Gw/Nt	Ng/Nt	Na/Nt	Ng/Na	Gw/Ng
			Ns = 2.47 g/plant				
7	120.2	2.04	58.9	0.77	0.57	1.35	76.7
4	109.4	2.28	48.0	0.69	0.46	1.51	69.2
6	107.0	2.03	52.7	0.81	0.46	1.76	64.9
8	103.0	1.75	58.7	0.81	0.46	1.75	72.9
2	88.4	2.12	41.6	0.68	0.48	1.42	60.8
1	90.2	2.22	40.7	0.72	0.57	1.27	56.6
3	74.8	1.87	39.9	0.64	0.48	1.35	61.9
5	72.8	2.08	35.0	0.62	0.49	1.27	56.7
Mean	95.7	2.05	46.9	0.72	0.50	1.46	65.0
			Ns = 9.88 g/plant				
7	27.9	0.58	48.0	0.74	0.58	1.26	64.5
4	31.4	0.72	43.4	0.71	0.48	1.48	61.1
6	32.3	0.76	42.7	0.77	0.51	1.53	55.4
8	26.0	0.57	45.4	0.75	0.22	3.39	60.3
2	27.8	0.77	36.0	0.64	0.65	0.98	56.6
1	24.6	0.65	37.6	0.67	0.49	1.38	55.9
3	22.0	0.68	32.4	0.58	0.51	1.14	55.4
5	19.7	0.43	46.0	0.72	0.53	1.36	64.0
Mean	26.5	0.65	41.4	0.70	0.49	1.56	59.2

† Hybrids in rank order by Gw/Ns averaged over both N levels.
Gw/Ns = Efficiency of use
Nt/Ns = Uptake efficiency
Gw/Nt = Utilization efficiency
Ng/Nt = Grain N/Total N uptake
Na/Nt = N uptake after silking/ Total N uptake
Ng/Na = Grain N/N uptake after silking
Gw/Ng = Grain yield/Grain N

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