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Divergent selection for grain protein affects nitrogen use in maize hybrids

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Abstract

The Illinois high (IHP), low (ILP), and corresponding reverse (IRHP, and IRLP) protein–strains of maize represent genetic extremes for differences in grain protein concentration. The objective of this study was to determine how divergent selection for grain protein affects N use in hybrid plants. Inbreds derived from the protein–strains were crossed as males to a common tester and the resultant hybrids evaluated at eight N rates in the field over 3 years. A more than two-fold difference in grain protein concentration was observed among the strain-hybrids with ILP averaging 65 g kg^{-1}, IRHP 89 g kg^{-1}, IRLP 111 g kg^{-1}, and IHP 148 g kg^{-1} of grain protein. Except for IHP at the lowest N levels, the strain-hybrids were similar in their whole shoot biomass production both pre- and post-flowering. Conversely, the strain-hybrids differed markedly in their uptake and accumulation of plant N, and these differences were already evident at flowering before a grain sink was present. Although all hybrids had the same overall N use efficiency at maturity (approximately 24 kg kg^{-1} N), they differed in their N use components with IHP and IRLP exhibiting a higher uptake efficiency, and ILP and IRHP exhibiting high utilization efficiency. The remobilization of leaf N was also more extensive for IHP and IRLP. Changes in grain protein concentration from divergent selection were directly related to changes in uptake and use of N by the plant.
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Keywords: *Zea mays*; N use efficiency; Biomass accumulation; Illinois protein strains; Maize

1. Introduction

Modern agriculture is concerned with yield, the nutritional quality of the crop and the environmental impact of crop production. Efficient use of fertilizer N is therefore critical. Because an adequate N supply is one of the main factors powering yield of cereal crops (Below, 2002), annual applications of fertilizer N are the norm. About half of the 110 kg ha^{-1} annual increase in maize yields over the last half century can be attributed to improved cultural practices, especially N fertilizer use (Duvick, 1992; Sinclair, 1995). Variation in the N supply affects all phases of maize growth, including the development, activity, and senescence of leaves, and the initiation, growth, and composition of ovules (Muchow, 1988; Uhart and Andrade, 1995a, 1995b). Thus, understanding the processes associated with the efficiency of N use (NUE), particularly N uptake and utilization, is of major importance in designing crop management strategies and in developing breeding programs for improved N use.

We use NUE here to encompass yield efficiency (the increase in grain yield per unit of applied N fertilizer) and its two components; uptake efficiency (the fraction of fertilizer applied N found in the plant at maturity), and utilization efficiency (the ratio of grain yield to plant N). The N supply can alter the relative importance of these two components, as under high N inputs, NUE is mainly determined by the plant's ability to acquire N; whereas at low N, the ability to utilize absorbed N is generally more important (Moll et al., 1982; Ma et al., 1998). Many studies show that genotype can also impact NUE (Cerrato and Blackmer, 1990; Smiciklas and Below, 1990; Eghball and Maranville, 1993; Rice et al., 1995; Normand et al., 1997; Muchow, 1998; Ma et al., 1998, 1999; Cassman et al., 2002; Gastal and Lemaire, 2002). Because most modern hybrids are selected according to their yield and N use under high rates of applied N (Castleberry et al., 1984; Bertin and Gallais, 2000), limited genetic variability may exist among commercial hybrids for N utilization, or for the remobilization of N from the stover to the grain (Purcino et al., 1998; Bertin and Gallais, 2000).

The Illinois protein strains, which are the result of long term divergent selection for grain protein concentration are unique within the maize germplasm. Illinois high protein (IHP) and

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Illinois low protein (ILP) have been continuously selected for over 100 cycles; whereas the Illinois reverse low protein (IRLP) and Illinois reverse high protein (IRHP) strains are the result of reversing selection in ILP and IHP beginning with cycle 48. Evaluations of the strains during the past 100 cycles have continually demonstrated the effectiveness of this program in altering grain protein level (Woodworth et al., 1974; Dudley et al., 1974; Dudley and Lambert, 1992; Rizzi et al., 1996), as well as a number of other plant traits. The wide variation in protein and dry matter production of these strains must have been accompanied by corresponding changes in N and C metabolism in the plant, and the Illinois protein strains have previously been shown to differ in N metabolism (Wyss et al., 1991; Lohaus et al., 1998; Below et al., 2004). This variation, and the fact that the strains share a common parental background, makes them unique experimental material for studying physiological and biochemical mechanisms associated with differences in maize productivity.

Our approach was to make hybrids of each of the strains (including the reverse strains) using inbreds derived from generation 90 crossed to a common tester, then to evaluate these materials in the field for NUE and its main components. Uribelarrea et al. (2004) showed that these hybrids had grain protein concentrations which reflected the strain parents, and that they differed in their use of N (Below et al., 2004). Our objective in this study was to understand how differences in the acquisition, utilization, and remobilization of N are associated with divergent selection for grain protein.

2. Materials and methods

2.1. Field site, cultural practices and treatment arrangements

Field experiments were conducted at the Department of Crop Sciences Research and Education Center in Champaign, Illinois during the 2001–2003 growing seasons, on plots that had previously been shown to be responsive to N fertilizer (Gentry et al., 2001). The soil type and cultural practices were as previously reported (Uribelarrea et al., 2004). Briefly, the soil was a Drummer silty clay loam with an average organic matter of 3.7% and a pH of 6.2. The field was under a maize–soybean rotation, with the location of the experimental plots alternated each year. Plots were kept weed-free with chemical control and hand cultivation, and crops were irrigated, when necessary.

Hybrids of the Illinois protein strains were produced by crossing inbreds made from generation 90 of IHP and ILP and generation 42 of IRHP and IRLP as males to FR1064 as the tester. Hybrids were over seeded on 26 April 2001, on 25 May 2002, and 22 April 2003 and thinned to a stand density of 65,000 plants ha^{-1}. The delay in planting date in 2002 was due to above average precipitation during April and May (270 mm in 2002 compared to a 30-year average of 200 mm). Each of the hybrids was grown under eight rates of fertilizer N (0–238 kg ha^{-1}) in 34 kg increments. The fertilizer was hand applied in a diffuse band down the center of the row as ammonium sulfate and incorporated between the V2 and V3 growth stages. Treatments consisted of the factorial combination of the four protein-strain hybrids and eight fertilizer rates arranged in a randomized complete block design with four replications. Each experimental unit consisted of four-row plots that were 5.3 m long × 3 m wide, with one of the central rows reserved for final yield determination and the other used for destructive plant samplings.

2.2. Crop measurements

N acquisition and partitioning were assessed using whole shoots sampled at two growth stages; R1 (i.e. beginning of anthesis and visible silks), and R6 (physiological maturity) when 50% of the plants exhibiting a visible black layer at the base of the kernels. By R6, maize plants are considered to have attained their maximum biomass (Ritchie et al., 1997), and we used shoot dry weight as a relative indicator of net canopy photosynthesis. Because of the large differences in grain composition among these hybrids, we also calculated the energy equivalent (MJ ha^{-1}) of the grain biomass using standard caloric values (Hedin et al., 1998) and the respective starch, oil and protein concentrations of the grain (Uribelarrea et al., 2004).

At each harvest, four representative plants were separated into leaf, stalk (including leaf sheaths), reproductive support tissues (tassel, husks and cob at R6, or ear-shoot at R1), and grain (only at R6 sampling). Reproductive and grain fractions were placed into a forced-draft oven (75 °C), while the fresh weight of the entire leaf and stalk sample was determined prior to shredding. An aliquot of the shredded material was weighed fresh and then oven-dried (75 °C). The dry weight of each plant fraction was calculated using the fresh weight and the moisture level. Individual plant samples were ground in a Wiley mill to pass a 20 mesh screen, and analyzed for total N concentration (g kg^{-1}) using a combustion technique (NA2000 N-Protein, Fisons Instruments). The total N content (g N plant^{-1}) was calculated by multiplying the dry weight by the N concentration.

Table 1
Significance level of the fixed effects for each of the measured variables, for the protein-strain hybrids grown at Champaign, IL, between 2001 and 2003

Measured variable	Source of variation		
	Hybrid	N rate	Hybrid × N rate
R1 biomass	NS	NS	0.0001
R1 N content	0.0088	0.0001	0.0472
R1 N uptake	0.0001	0.0001	0.0745
R6 biomass	0.0270	0.0001	0.0514
R6 N content	0.0725	0.0001	0.0001
Post-flowering N uptake	0.0518	0.0030	0.0001
Stover N remobilization	0.0001	NS	NS
Leaf N remobilization	0.0002	0.0458	NS
Stalk N remobilization	0.0001	NS	NS
NUE	NS	0.0001	NS
N uptake	0.0103	0.0003	NS
N utilization	0.0783	0.0198	NS

A threshold of 0.10 was used to determine a significant effect of the different sources of variation over the measured variables. NS means that term was not significant.

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