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Identifying nitrogen-use efficient soft red winter wheat lines in high and low nitrogen environments

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ABSTRACT

Nitrogen use efficiency (NUE) is of great interest to wheat (*Triticum aestivum* L.) breeders because it addresses the daunting prospect of feeding the burgeoning population under the constraints of limited land resources and a warming climate. In this study, we evaluated a 56 entry panel of SRW breeding lines and cultivars from the eastern US wheat region in 2014 for NUE and related traits. The 56-entry block was grown at Lexington and Princeton, KY at two N rates (0 and 112 kg ha^{-1}) in a complete factorial design. We measured normalized difference vegetative index (NDVI), biomass, harvest index, N harvest index, N uptake efficiency, N utilization efficiency, post-anthesis N uptake, N remobilization efficiency and overall NUE. Breeders usually apply high rates of N fertilizer to their plots in order to maximize genetic yield potential. Our study indicates that without screening breeding lines in low N environments concurrently, it will not be possible to identify high NUE genotypes. Post-anthesis N uptake, was highly correlated with yield ($r = 0.79$) under high N, but heritability of this trait was close to zero. Heritability of NUE, on the other hand was moderately high ($h^2 = 0.65$). Five breeding lines ranked within the top 10 for NUE in both low and high N environments. NDVI was found to be both heritable and highly correlated with yield across N environments ($R^2 = 0.78$). Genome wide association studies of NUE and related traits revealed QTL associated with NUE (chromosome 2B), uptake efficiency (chromosome1B) and utilization efficiency (chromosomes 1A and 3A). In accord with other studies, these QTL are of small effect and will likely only be useful in genomic selection as opposed to marker-assisted selection.

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1. Introduction

Feeding ten billion people in a sustainable manner has become the most daunting challenge facing agriculture. Winter wheat (*Triticuum aestivum* L.) is an important component of the national and global food supply; as population increases, worldwide demand for wheat will continue to grow. As wheat breeders acknowledge the need for increased yields on a fixed land area, one strategy frequently mentioned is breeding for nitrogen use efficiency (NUE). Beyond increasing the food supply, this approach would enhance sustainability: excess nitrogen (N) fertilizer has been shown to have adverse environmental impacts such as N_2O emissions and eutrophication of freshwater and marine ecosystems (Sieling and Kage, 2008). Without an increase in N use efficiency, however, reduced N fertilizer use could decrease crop yields and quality if the plant experiences N deficiency (Cassman et al., 2003). The idea of breeding for NUE is not new, (see e.g. Moll et al. (1982)); yet it still has not gained traction as a strategy that can be easily implemented in a breeding program. NUE has been described in several different ways (Cormier et al., 2016) but a widely accepted definition is grain yield produced per unit soil N supply (soil N and fertilizer N; Moll et al., 1982). NUE defined in this way is the product of N uptake efficiency (NUpE) and N utilization efficiency (NUtE) (Moll et al., 1982; Nyikako et al., 2014).

Many studies have shown genetic variation in NUtE and NUpE (Van Sanford and Mackown, 1986; Ortiz-Monasterio et al., 1997; Foulkes et al., 1998; Muurinen et al., 2006; Barraclough et al., 2010; Gaju et al., 2011, 2014). These studies typically report genotype × N supply interaction that affects NUE, and, by definition, NUpE and NUtE (Ortiz-Monasterio et al., 1997; Foulkes et al., 1998; Muurinen et al., 2006; Barraclough et al., 2010; Gaju et al., 2011, 2014). To ensure maximum expression of genetic potential, most wheat breeding trials are conducted in high N environments. Therefore

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breeders select genotypes that perform well under what might be considered optimal conditions. The selected lines may not perform well where N is limiting. As a result, selection in low and high N environments is likely needed to identify genotypes with the potential to perform well under optimal as well as N-limiting conditions. One issue that has hindered implementation of selection for NUE is the high cost in time and resources of measuring certain NUE traits. Yet, it is critical to determine which are the "must have" traits to accurately measure NUE under low and high N conditions (Brancourt-Hulmel et al., 2005). Total N uptake at anthesis can give insight into growth of yield-generating leaves, floret fertility, amount of stem reserves, and creation of a deep root system, yet it is very costly to measure. Total N at maturity, also arduous to measure, provides information on the remobilization efficiency of N from the biomass to the grain (Cox et al., 1986; Swain et al., 2014). It has been suggested that wheat genotypes with superior N uptake, storage, and translocation capabilities will allow for further gains in NUE, along with stay-green genotypes whose slower senescence allows for a longer grain filling period through continued N uptake and translocation (Bogard et al., 2011; Swain et al., 2014).

To mitigate the cost and difficulty of measuring such traits it has been suggested that rapid and efficient selection of high NUE genotypes may be possible through canopy spectral reflectance (CSR; Li et al., 2014). CSR devices measure the amount of light reflected/absorbed by the plant's canopy surface that is affected by genotypic variation and environmental stress. A CSR index, such as the normalized difference vegetative index (NDVI), has been shown to have high correlations with wheat grain yield, biomass and N concentration (Ma et al., 1996; Raun et al., 2001; Crain et al., 2012; Prasad et al., 2007a,b). The CSR estimates of biomass and N content can be used to estimate NUpE and NUtE. The relationship of CSR with biomass is of great interest, since biomass is related to NUE and yield (Crain et al., 2012).

Though NUE has been extensively studied, traits or selection criteria that can be used in a breeding program are lacking. Therefore the objectives this study were to: identify high NUE wheat genotypes grown under low and high N environments at multiple locations, estimate heritability of NUE and related traits, and conduct genome-wide analyses of NUE to determine whether there were useful genetic markers associated with traits that determine NUE in SRW wheat.

2. Materials and methods

2.1. 2014 Experiment

The experimental material used in this study was derived from the TCAP (http://www.triticeaecap.org/) elite eastern mapping panel, comprising 280 elite soft winter wheat breeding lines and cultivars from seven winter wheat breeding programs (Ohio, Missouri, Virginia, Kentucky, Maryland, Illinois, and New York). These lines are adapted to the wheat producing region of the U.S. that stretches from the northeast to the southern corn belt and are primarily F_4-derived from different crosses selected for a wide range of genetic backgrounds. In 2014 a subset of the larger mapping panel was grown at two locations: Spindletop Farm and the West Kentucky Research and Educational Center at Princeton (PRN), KY (37°6′7.37″ N, 87°52′13.62″W) where the soil series is a Crider silt loam [fine-silty, mixed, active, mesic, Typic Paleudalfs]. The experimental material consisted of 56 winter wheat genotypes, comprising one block of the TCAP eastern elite wheat panel. This block of entries from the original TCAP panel was chosen because it contained breeding lines from the University of Kentucky (UK), University of Illinois and Purdue breeding programs that represented a sample of the diversity contained within the UK wheat breeding program. The experimental material was planted on 14 Oct. 2013 at Princeton and 24 Oct. 2013 at Lexington in a randomized complete block design under fertilizer regimes of 0 kg ha^{-1} and 112 kg ha^{-1} actual N. Each genotype/N level treatment was replicated twice at each location. The experimental unit was a single 6-row yield plot 3.3 m in length, 1.2 m wide. In the 112 kg ha^{-1} treatment, N was applied in a 34 kg ha^{-1} and 78 kg ha^{-1} split, 13 March and 9 April 2014 at Princeton and 21 March and 17 April 2014 at Lexington.

2.2. Field sampling and data collection

At each location, 20 pre-N application soil samples were taken per treatment per rep at a depth of 30.5 cm using a soil probe, mixed by hand and air dried. Monthly soil samples were taken using the same sampling protocol following N application in the spring.

Prior to N application, vegetative material was harvested from 10 genotypes that were known to differ in agronomic traits such as heading date and height. Nitrogen status of each genotype within each N environment at both locations was measured at Feekes 10 (Zadoks 45; boot stage) using the hand held CSR device, Crop Circle®. The device was held approximately 56 cm above the plot and walked along the length of the plot at a steady pace in order to generate NDVI values for each plot. Heading date (50% of spikes emerged from flag leaf sheath) and anthesis date (50% of spikes with anthers extruded) were measured in each plot. Plot length and height were measured at the soft dough stage. At both locations a 30.5 cm length of row was harvested from each plot at anthesis (Feekes 10.51; Zadoks 60) and at harvest maturity for whole plant N analysis. Harvest maturity was determined when grain was hard and could not be split by a thumbnail (Feekes 11.4; Zadoks 92). At anthesis, all biomass was ground in bulk for N analysis. At harvest maturity, biomass was separated into grain and non-grain (stems, leaves and chaff) for N analysis. Plots were harvested with a small plot combine at Princeton and Lexington on 24 June and 2 July 2014, respectively. Harvested grain from each plot at both locations was collected in harvest bags to measure yield, moisture content, and test weight.

2.3. Data processing and analysis

Soil samples collected within each treatment and location were extracted for ammonia and nitrate using the KCl method (Crutchfield and Grove, 2011). Prior to N application, soil N was estimated to be 42.1 kg ha^{-1} at PRN and 40.6 kg ha^{-1} at LEX in the low N environment. The total N supply after N application (112 kg ha^{-1}) in the high N environment was 154.6 kg ha^{-1} at PRN and 152.6 kg ha^{-1} at LEX.

Biomass sampled prior to N application was air dried in the greenhouse, ground to a fine powder using a UDY cyclone grinder, and analyzed by the FlashEA 1112 combustion analyzer to measure N concentration. The vegetative samples collected from each plot at anthesis and maturity were treated similarly, but protein concentration was determined with a Near-Infrared Reflectance (NIR; Perten instrument DA7200) instrument. Whole grain sub-samples from each plot and location were run through the NIR instrument to measure grain protein. Grain protein concentration was divided by 5.7 to convert to grain N concentration. Total plant N uptake was determined by summing: grain N content (yield * % N) plus mature biomass N content (biomass * % N). Post-anthesis N uptake (PANU) was calculated by subtracting above-ground N content at anthesis from above-ground total plant N at maturity. Nitrogen remobilization efficiency (NRE) was defined as (biomass N at anthesis – biomass N at maturity/biomass N at anthesis (Barbottin et al., 2005; Gaju et al., 2011)). Nitrogen-use efficiency (NUE) and NUE components (nitrogen uptake efficiency (NUpE) and nitrogen uti-

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