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Genetic variation in the critical specific leaf nitrogen maximising yield among modern maize hybrids

Raziel A. Ordoñez^a, Roxana Savin^{a,*}, Gustavo A. Slafer^{a,b}

^a Department of Crop and Forest Sciences and AGROTECNIO (Center for Research in Agrotechnology), University of Lleida, Av. Rovira Roure 191, 25198 Lleida, Spain

^b ICREA, Catalonian Institution for Research and Advanced Studies, Spain

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ABSTRACT

A major aim in breeding programs is to improve nitrogen use efficiency (NUE). The critical level of specific leaf nitrogen (SLNc) maximising growth and yield is a relevant trait influencing NUE. The relationship between growth or yield and SLN is hyperbolic indicating that levels of SLN higher than the critical would tend to decrease NUE. It has been recently proposed that maize breeding may profit of this relationship by phenotyping SLN and selecting for genotypes with SLN = SLNc (SLN < SLNc would result in low yields, SLN > SLNc would bring about high yields but at the expense of low NUE); being the SLNc = 1.5 gN m⁻². For this proposal to be realistic, genotypic variation in SLNc should be negligible. We aimed to determine the degree of genetic variation in SLNc in a range of modern maize hybrids. For this purpose, we carried out four field experiments with 11 contrasting maize hybrids grown under fertilized (200 kgN ha⁻¹) or unfertilized conditions in each of the four experiments. At silking, leaf area and N concentration of leaves were determined and at maturity, yield and biomass were measured. Analysing the whole dataset together (n = 88) we found a very large range of all variables measured and calculated: yield varied between c. 6 and c. 18 Mg ha⁻¹ and SLN from c. 0.7 to c. slightly more than 2.5 gN m⁻². Within that context we found a significant bi-linear regression between yield and SLN (p < 0.001). Analyzing each hybrid individually we did find substantial variation among hybrids in SLNc, ranging between c.1.0 and c.s1.93 gN m⁻². The variation was also substantial calculating SLNc with an alternative methodology and if leaf N content instead of SLN were used as independent variable. Genotypic differences in SLNc were positively related to N uptake but unrelated to other traits for which hybrids varied, including yield potential. Additionally, genotypes with low SLNc show a tendency for a better NUtE. We concluded that it does not seem appropriate to phenotype for a particular value of SLNc as any particular threshold might bring about selected lines with either a yield potential lower than possible and/or with a relatively lower than possible NUE. © 2014 Published by Elsevier B.V.

1. Introduction

Further increasing yield has always been a major aim in breeding programs of grain crops. Large genetic gains in potential yield have been achieved in most major crops during the last century, though recent gains seem to proceed at a substantially slower pace than that required to match expected growing demands (Fischer et al., 2014; Ray et al., 2013). In maize, genetic gains in yield were mostly associated with increases in radiation use efficiency (RUE) (Fischer and Edmeades, 2010) and in tolerance to stresses, particularly population stress (Duvick, 2005; Luque et al., 2006; Tollenaar and Lee, 2006).

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These increases in yield potential have been accompanied by large increases in the use of inputs, particularly nitrogen (N) fertilization. A substantial proportion of the massive increase in vield production over the last 60-70 years has been attributed to improve crop management, in particular the amount of N fertilizer use (Duvick, 1992; Sinclair and Muchow, 1995). As modern agriculture must be increasingly concerned with environmental impact of crop management, the potential adverse impact of N fertilization on environment must be minimized without affecting strongly the yield progress that is required. In this context, future genetic gains in yield would be expected to include improvements in N use efficiency (NUE), yield per unit of N available in the soil; resulting from N uptake efficiency (N absorbed per unit of N available; NUPE) and N utilisation efficiency (yield per unit of N absorbed; NUtE) (Moll et al., 1982; Cossani et al., 2012).

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^{*} Corresponding author. Tel.: +34 973 702853; fax: +34 973 702690. *E-mail address:* savin@pvcf.udl.es (R. Savin).

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| Seed company | Hybrid | FAO cycle | Year of release | Characteristics (as described by the seed company) |
|-------------------|--------------|-----------|-----------------|---|
| Caussade semences | Lapopi | 450 | 2003 | Single cross hybrid, dent grain, diseases and fungus attack tolerance, early flowering |
| Caussade semences | Paolis | 650 | 2008 | High yield potential, thick and homogeneous ear, lodging resistant, forage and grain purpose, early flowering. |
| Caussade semences | Franki | 400 | 2005 | Single cross hybrid, semi-dent, semi-precoss, excellent grain yield potential, early vigor, early-lodging tolerance, lodging resistance at harvest, stay-green, rot and fungus resistance, health conditions. |
| Euralis | Eurostar | 400 | 2007 | High stability and productivity, good adaptation to wide range of humid environmental conditions, early maturity. |
| Euralis | Earlystar | 400 | 2006 | High stability and grain potential yield, good quality for forage production, short cycle at physiological maturity. |
| KWS | Kermes | 700 | 2003 | Mainly for grain production, stability and potential yield, vigorous and healthy plant, excellen stay-green, thick and resistant stems, high yield stability, ear rot resistance. |
| Monsanto | DKC6575 | 700 | 2003 | Worm resistance (YieldGard gene), carbon resistance, heat stress tolerance, vigorous and healthy plant, stay-green, thick stem and strong root system, lodging resistance, good adaptability. |
| Limagrain | Beles Sur Bt | 650 | 2006 | Single cross, worn bore resistance (Bt gene), dent grain. |
| Limagrain | Guadiana | 700 | 2006 | Single cross, high yield, high leaf development, grain dent and lodging resistance. |
| Limagrain | Helen Bt | 750 | 2006 | Single cross, high stability and yield potential, flowering semi-precoss, transgenic variety with (Bt gene), worn borer resistance. |
| Pioneer | PR31N28 | 700 | 2006 | Provide with YieldGard gene and Bt gene, recommended for worm attack areas, good adaption in potential yield areas, good stability. |

Selecting for improved NUE would be unlikely in realistic breeding programs unless trustworthy surrogates assessed more easily and quicker than NUE could be identified. Substantial advances have been made in methodologies for phenotyping complex traits in maize breeding (Araus and Cairns, 2014), and many phenotyping tools have been identified (Cairns et al., 2012). Thus, if a trustworthy surrogate could be identified, it might be possible to phenotype for it in order to identify genotypes of putatively improved NUE. Around silking, when yield potential is being determined (Munaro et al., 2011; Paponov et al., 2005; Tollenaar et al., 1992), most plant N is allocated to leaves (Muchow, 1988; Tsai et al., 1991; Van Oosterom et al., 2010). Then, for maximising NUE leaf N at silking must be considered. Several papers have highlighted the critical role of specific leaf N (SLN, the mass of N per unit of leaf area) in maximising crop growth during the critical period of silking, and thereby in maximising yield (DeBruin et al., 2013; Massignam et al., 2011; Muchow and Sinclair, 1994; Sadras et al., 2000). The relationship between yield (or yield-determinant traits) and SLN is largely bi-linear: yield increases linearly with increasing SLN until a critical SLN (SLNc) when yield is maximised and maintained over SLN values higher than SLNc. DeBruin et al. (2013) recently concluded that a SLN of 1.5 gN m^{-2} at silking is sufficient for maximizing yield (in the US Corn Belt). Therefore, it was proposed that it could be possible to phenotype populations to discard genotypes of SLN lower than this SLNc (DeBruin et al., 2013). For this assertion to be widely acceptable the range of variation in SLNc should be very small, at least among modern hybrids. Studies of the range of variation in SLNc are not abundant, as they require a number of genotypes being grown under a wide range of environmental conditions creating a large variation in SLN at silking for each of the genotypes. Thus, with the overall goal of determining the sensibleness of phenotyping for a fixed value of SLN to improve NUE, we aimed specifically to determine the degree of genetic variation, if any, in a range of modern maize hybrids grown under contrasting growing conditions able to generate a wide range of both yield and SLN values for each hybrid.

2. Materials and methods

2.1. Experimental sites

Four field experiments were carried out at two contrasting locations in the province of Lleida (Catalonia; NE Spain) (i) the Plain of Lleida, Menarguens in 2009 (Lat. 41° 43′ 55″ N; Long. 0° 44′ 43″ E) and Algerri in 2010 (Lat. 41° 49′ 3″ N; Long. 0° 38′ 22″ E) representing a relatively warm environment in the Ebro Valley, and (ii) a valley in the Pyrenees, Montferrer in both 2009 and 2010 (Lat. 42° 46′ 20″ N, Long. 2° 35′ 5″ E) representing a relatively cold environment. All experiments were fully irrigated and pests, diseases and weeds were prevented or controlled.

2.2. Treatments and experimental design

All experiments were conducted under field conditions. Treatments included a factorial combination of 11 maize hybrids and two nitrogen levels. The hybrids represent all well adapted commercial hybrids with a range of maturity classes spanning from cycles characterized as FAO400 to FAO750 (Table 1). The two N treatments were an unfertilised control (N₀) and a heavily fertilised condition (N₂₀₀) in which urea was broadcasted at a rate of 200 kgN ha⁻¹ when the plots had the sixth leaf visible.

All experiments were arranged in a split-plot design with three replications, where hybrids were the main plots and N availabilities were the subplots.

In the Plain of Lleida, the main plot consisted of 8 rows 20 m long with a distance between rows of 0.70 m. In the Pyrenees the main plot consisted of 8 rows 15 m long with a distance between rows of 0.75 m. In all experiments we sowed c. 96,000 seeds ha^{-1} and few weeks after seedling emergence we thinned the plots manually to warrant a uniform plant density of 85,000 seedlings ha^{-1} . For this purpose, we inspected every experimental unit and counted the number of plants per meter of row removing plants that were in excess of the desired density.

2.3. Measurements and determinations

Samples (2 m of a central row) were taken both at silking (the R1 stage; Ritchie et al., 1993) and at physiological maturity (when the black layer was formed indicating the end of the grain filling period; Daynard and Duncan, 1969). Sampling was made for each particular experimental unit when that unit reached the specific stage. Plants were cut from ground level weighed immediately in the field. A subsample of three plants per experimental unit was taken randomly from each of the samples and also weighed immediately in the field. Sub-samples were taken to the lab and processed

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