



A note on potential candidate genomic regions with implications for maize stover fodder quality



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ARTICLE INFO

Article history:

Received 18 December 2012

Received in revised form 26 March 2013

Accepted 27 March 2013

Keywords:

Maize stover fodder quality

Genotyping by sequencing

Genomic regions for stover fodder quality

ABSTRACT

A panel of 276 inbred lines from CIMMYT's Drought tolerant maize for Africa program was test crossed to maize line CML312 and the single crosses were evaluated for grain and stover yields, plant height (PH), days to 50% anthesis (DtA₅₀) and silking, stover nitrogen (N), neutral (NDF) and acid detergent fiber (ADF), acid detergent lignin (ADL), *in vitro* organic matter digestibility (IVOMD) and metabolizable energy (ME) content. Most stover fodder quality traits were highly significantly different among the lines except ADF. These differences were substantial among best and worst lines for the traits, with stover N varying threefold and NDF, ADF and IVOMD by more than 10 percentage units. Among the agronomic traits, significant positive associations were observed among grain and stover yield. Grain yield was significantly negatively associated with DtA₅₀ and Anthesis to silking interval (AtS) and positively with PH. Stover yield was significantly negatively associated with DtA₅₀ and positively with PH. Desirable stover quality traits N, IVOMD and ME were significantly negatively associated with grain yield ($R^2 = 0.25\text{--}0.28$) while undesirable quality traits NDF, ADF and ADL were significantly positively associated with grain yield ($R^2 = 0.04\text{--}0.23$). Stover yields were largely unrelated fodder quality traits except for a significant negative association with NDF and ADF ($R^2 = 0.04$ to 0.08). GWAS analysis carried out using GBS (genotyping by sequencing) and a 55K SNPs genotypic dataset revealed several regions of significant association for N, ADF and IVOMD, each explaining from 3 to 9% of phenotypic variance for these fodder quality traits. SYN7725 from the 55K chip on chromosome 4 explained the largest proportion of phenotypic variance (~9%) for ADF and had a robust minor allele frequency (MAF) of 0.35. A specific genomic region on chromosome 3 (132.7–149.2 Mb) was found to be significantly associated with all the three forage quality traits, with the largest effect on IVOMD. This region merits attention for further validation and marker-assisted introgressions. A cellulose-related candidate gene, *Xyloglucan endotransglucosylase/hydrolase (xth1, GRMZM2G119783)* was also identified closer to the peak on chr.10 (~76.9 Mb) for ADF, which has been previously demonstrated to have a significant role in fiber elongation in cotton.

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1. Introduction

Higher stover fodder quantity and quality is emerging as an important trait in maize improvement programs (Berhanu et al., 2012). Genome-wide association study (GWAS) or association

mapping provides a powerful tool for crop improvement and has resulted in identification of several important genomic regions for plant height, flowering time and a range of disease resistance traits in maize (Ducrocq et al., 2008, 2009; McMullen et al., 2009; Kump et al., 2011; Yan et al., 2011). With the discovery of several rapid, cost effective and efficient molecular marker systems in maize, identification of candidate genomic regions with significant effects on fodder quality and their subsequent use in quality improvement program is feasible and practical. The objectives of this investigation were to evaluate a diverse collection of tropical and sub-tropical maize lines for a range of pertinent agronomic and stover fodder quality traits – IVOMD, ADF and N; and to identify tentative candidate genomic regions that are associated with important stover fodder quality parameters for further validation in appropriate populations.

Abbreviations: ADF, acid detergent fiber; ADL, acid detergent lignin; CIMMYT, Centro Internacional de Mejoramiento de Maíz y Trigo; DTMA, drought tolerant maize for Africa; GWAS, Gene Wide Association Study; GBS, genotyping by sequencing; ICRISAT, International Crops Research Institute for the Semi Arid Tropics; ILRI, International Livestock Research Institute; ME, metabolisable energy; N, nitrogen; NIRS, near infrared spectroscopy; NDF, neutral detergent fiber; SAS, statistical analysis systems.

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2. Materials and methods

2.1. Plant material and field trials

A collection of 276 inbred lines from CIMMYT's tropical and sub-tropical programs (DTMA) were test-crossed to CML312 (a widely used sub-tropical tester with a very good general combining ability across germplasm and maturity groups) were evaluated for agronomic and stover fodder quality traits at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) during February–June 2011. These crosses were planted in two row 4 m plots with 2 replications following an α -lattice design. The soil type of the experimental plot was black clay loam with a pH of 8.5. The average daily minimum and maximum temperature during the cropping season was 25 °C and 36 °C, respectively, with an average relative humidity of 32%. Before planting 60 kg nitrogen (N) ha⁻¹ in the form of urea, 60 kg phosphorous ha⁻¹ as single super phosphate, 40 kg potassium ha⁻¹ as muriate of potash and 10 kg zinc as zinc sulfate were applied as a basal dose. Second and third doses of N (each 30 kg N ha⁻¹) were side-dressed when plants were about knee-high and at tasseling, respectively. Pre-emergence application of pendimethalin and atrazine (both at 0.75 kg/ha a.i., tank mixed) were used for weed control.

2.2. Agronomic observations and stover fodder quality traits

Plot-wise five agronomic traits were recorded. Days to 50% anthesis and silking were determined, when 50% of the plants had shed pollen and silk had emerged, respectively. The anthesis silking interval was calculated as the difference between days to 50% silking and 50% anthesis. At physiological maturity, plant height was measured on five representative plants per plot. Grain and stover yields were recorded plot wise and grain weights were adjusted to 12.5% moisture content. Ten representative stover samples from each of the plots harvested were analyzed for stover fodder quality traits [nitrogen (N), neutral (NDF) and acid detergent fiber (ADF), acid detergent lignin (ADL), *in vitro* organic matter digestibility (IVOMD) and metabolizable energy (ME) content] using near infrared spectroscopy (NIRS) (Ramana Reddy et al., 2013).

2.3. Genotyping and association mapping

DNA was extracted from greenhouse grown seedlings at the 3–4 leaves stage. Normalized DNA was used for genotyping with 55K infinium illumina SNP chip and genotyping by sequencing (GBS) platform (Elshire et al., 2011) at Cornell University. SNPs with less than 0.02 Minor Allele Frequency (MAF) and 0.8 call rate (CR) in the 55K genotype dataset were excluded from the analysis. For GBS SNP markers with less than 0.01 MAF and 0.5 CR were eliminated. For the GWAS (genome wide association study) analysis, ~443 K SNPs that remained after filtering for the above-said criterion from both the platforms were combined.

2.4. Statistical analysis

Association test results on three major stover quality traits (N, ADF and IVOMD) were corrected for population structure using general linear model (GLM) algorithm as well as population structure + kinship (Q + K) using Mixed Linear Model (MLM) algorithm (Flint-Garcia et al., 2005; Yu and Buckler, 2006). The GLM and MLM analyses were performed using TASSEL (Bradbury et al., 2007) and SVS (http://www.goldenhelix.com/SNP_Variation/).

The mixed model used for estimating the best linear unbiased estimates (BLUE) for the phenotypes is as: $y = XB + Z\mu + e$ where all fixed effects are modeled in the "XB" term, including the population structure (Q). Random effects are modeled in "Z μ " term including

Table 1

Descriptive statistics for agronomic traits in 276 lines from CIMMYT's tropical and subtropical program for drought tolerant maize for Africa (DTMA).

Trait	Mean	Range	P > F
Grain yield (kg/ha)	1486	150–3356	0.0001
Stover yield (kg/ha)	2816	1453–4757	0.08
Days to 50% Anthesis (d)	58.5	52–65	0.0001
Anthesis to Silking Interval (d)	6.2	0.5–18	0.54
Plant height (cm)	129	94–170	0.96

Table 2

Descriptive statistics for forstover quality traits among 276 lines from CIMMYT's tropical and subtropical program for drought tolerant maize for Africa (DTMA).

Trait	Mean	Range	P > F
Nitrogen (%)	1.1	0.5–1.6	0.0001
Neutral detergent fiber (%)	72.5	62.4–77.9	0.0001
Acid detergent fiber (%)	38.5	31.2–45.3	0.0001
Acid detergent lignin (%) n	4.1	3.1–5.4	0.31
<i>In vitro</i> digestibility (%)	52.6	47.9–60.6	0.0001
Metabolisable energy (MJ/kg)	7.6	7.0–8.9	0.0001

Kinship coefficients (K) and "e" is the vector of residual effects. Analysis of variance and trait relationships were estimated using SAS 9.2 (SAS Institute, 2009). Principal component analysis was performed using TASSEL (Bradbury et al., 2007) and the first 10 principal components (PCs) estimated based on the SNP dataset were used to correct the association tests in the GLM analysis.

3. Results

3.1. Variations in agronomic and stover fodder quality traits

Mean and ranges in grain and stover yields, days to 50% anthesis (DtA₅₀), anthesis to silking (AtS) interval and plant height (PH) in 276 lines from the DTMA association mapping panel are reported in Table 1. Highly significant differences between lines were found for grain yield and DtA₅₀ ($P = 0.08$). Stover yield tended to be different among the lines while differences in AtS and PH were insignificant.

Except for ADL, stover fodder quality traits were highly significantly different among the lines (Table 2). These differences were substantial with stover N varying threefold and NDF, ADF and IVOMD by more than 10 percentage units among the best and the worst lines.

3.2. Relationships between agronomic traits and stover fodder quality traits

Among the agronomic traits, grain and stover yield were highly correlated (Table 3) but the overall relation was weak ($R^2 = 0.08$). Grain yield was significantly negatively associated with DtA₅₀ and AtS and positively with PH. Stover yield was significantly negatively associated with DtA₅₀ and positively with PH.

Desirable stover quality traits N, IVOMD and ME were significantly negatively associated with grain yield ($R^2 = 0.25$ – 0.28) while undesirable stover quality traits NDF, ADF and ADL were significantly positively associated with grain yield ($R^2 = 0.04$ – 0.23). Stover fodder quality traits were largely unrelated to stover yield except for a significant negative association with NDF and ADF ($R^2 = 0.04$ – 0.08).

3.3. Genome wide association study

Based on GLM and MLM P values, significant candidate associations could be identified and their values along with chromosome and physical positions of the top 10 significant associations are reported in Tables 4–6 for three selected stover fodder quality traits N, ADF and IVOMD.

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