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Quantitative trait loci mapping of forage agronomic traits in six mapping populations derived from European elite maize germplasm

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Abstract

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Keywords

DMC, DMY, DPS, forage maize, PHT, QTL analysis

Disciplines

Agronomy and Crop Sciences | Plant Breeding and Genetics | Plant Sciences

Comments

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1 **QTL mapping of forage agronomic traits in six mapping populations derived**
2 **from European elite maize germplasm**

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1 **Abstract**

2 Four agronomic traits were analyzed including dry matter concentration (DMC) and dry
3 matter yield (DMY) for stover, plant height (PHT) and days from planting to silking (DPS). We
4 mapped quantitative trait loci (QTL) in three populations with doubled haploid lines (DHL), one
5 RIL population and two testcross (TC) populations derived from crosses between two of the four
6 populations mentioned above to elite tester lines, based on field phenotyping at multiple locations
7 and years for each. 146 to 168 SSRs were used for genotyping of the four mapping populations.
8 Significant high phenotypic and genotypic correlations were found for all traits at two locations,
9 while DMC was negatively correlated with the other traits. A total of 42, 41, 54, 45 QTL were
10 identified for DMC, DMY, PHT, and DPS, respectively, with 9, 7, 12, and 7 major QTL for each
11 trait. Most detected QTL displayed significant interactions with environment. Major QTL detected
12 in more than two populations will contribute to marker assisted breeding and also to fine mapping
13 candidate genes associated with maize agronomic traits.

14 **Keywords**

15 Forage maize; QTL analysis; DMC; DMY; PHT; DPS

1 **Introduction**

2 In the cooler regions of Europe, maize is primarily grown as a forage crop for feeding of dairy
3 and beef cattle (Lübberstedt et al., 1997a). Major objectives of forage maize breeding are
4 increasing forage yield of the whole above-ground plant materials, enhancing the stover
5 digestibility, and improving the nutritive value for ruminants. Wide genetic variation exists in
6 forage characteristics for maize stover (Leng et al., 2018).

7 Agronomic traits like flowering time and plant height were found to be associated with forage
8 maize stover quality characteristics as polymorphisms in monolignol biosynthetic genes are found
9 to be associated with agronomic traits in European maize (Chen et al., 2010). In addition, anthesis
10 is closely correlated with stalk strength (Peiffer et al., 2013). Transformation of plants from
11 vegetative growth to reproductive growth determines both flowering time, plant height and maize
12 biomass yield. Higher maize plants with larger biomass usually have increased acid detergent fiber
13 (ADF) due to an increased proportion of vegetative parts in the forage as reflected by the positive
14 correlation between ADF and plant height (PHT) (Lübberstedt et al., 1997b). Conversely, early
15 flowering maize with a reduced vegetative growth tends to have a higher ear proportion and, hence,
16 increased *in vitro* digestibility of organic matter (IVDOM), but reduced ADF. Previously, it was
17 believed that the highest grain yield is also suitable for forage use as increased corn yield was
18 associated with increased stover production (Adler et al., 2015), while forage DMY improvement
19 could lead to reduced grain yield (Karlen et al., 2012). However, maize stover accounts for 50%
20 of the total DMY of the whole plant, which is as important as the grain yield (Bertoia et al., 1994).
21 Therefore, improving DMY is the main objective of forage maize breeding for both grain and
22 stover yield.

1 QTL analysis of forage maize agronomic traits including DMY and DMC, which are
2 important forage agronomic traits, has been carried out in various studies (Giraud et al., 2014;
3 Méchin et al., 2001). Most of these studies were conducted using either individual plants or
4 segregating populations derived from biparental crosses by selfing or backcrossing. Using of
5 testcross progenies with multiple testers in QTL mapping studies provides information about the
6 influence of the tester and, hence, is important for both basic research and applications of marker
7 assisted selection (MAS). Three agronomic traits including DMC, DMY, and PHT were analyzed
8 by using testcrossed of European flint lines of maize, and 9 (DMC) to 16 QTL (PHT) were detected
9 by composite interval mapping (Lübberstedt et al., 1997a). QTL for forage maize agronomic traits
10 were characterized in a set of recombinant inbred lines and evaluated in combination with tester
11 lines (Méchin et al., 2001), and close correlations were observed for plant maturity traits like DMC
12 and PHT. PHT and flowering time are closely correlated with DMY and DMC. More QTL for
13 biomass yield and PHT were detected from two nested association mapping DH populations
14 generated from complementary European flint and dent lines (Giraud et al., 2014). Favorable QTL
15 detected in different populations open perspectives for improving forage yield. To identify QTL
16 for flowering time is not only beneficial to analyze the genetic mechanism and molecular control
17 mechanism of flowering traits, but also provide important theoretical basis for the breeding of elite
18 forage maize cultivars.

19 In this study, we characterized QTL for four forage maize agronomic traits in three
20 populations with 250-720 doubled haploid lines (DHL), one RIL population and two TC
21 populations derived from crosses between two of the four populations with tester lines from the
22 opposite heterotic group. The objectives of the project were to: 1) identify and characterize
23 genomic regions for forage maize agronomic traits, 2) evaluate the performance of these

1 populations at per se and testcross level, 3) conduct a comparison across elite maize populations,
2 4) investigate the consistency of these QTL across different populations, and 5) determine the
3 phenotypic and genotypic correlations among important forage maize agronomic characters.

4 **Materials and Methods**

5 **Plant materials**

6 Plants materials used for this study were identical to those employed in a companion study
7 and described in detail by Leng et al. (2018). Briefly, three populations with 250-720 doubled
8 haploid lines (DHLs) and a recombinant inbred lines (RIL) population were used for the
9 investigate the agronomic traits. The choice of parental lines of the GABI, DD (Dent × Dent
10 Doubled Haploid Lines), FF (Flint × Flint-RIL), and FD (Flint × Dent Doubled Haploid Lines)
11 populations were based on their contrasting stover quality (Leng et al., 2018).

12 **SSR assays and linkage maps**

13 SSR genotyping was performed in the laboratory of KWS (Einbeck, Germany). In accordance
14 with their bin location, SSR markers were chosen in the maize genetics database (MaizeGDB,
15 <http://www.maizegdb.org>) throughout the genome. All DNAs were isolated according to Murray
16 & Thompson (1980) with modifications. The linkage maps of all populations were developed
17 using the JoinMap 3.0 program (Van Ooijen & Voorrips, 2001) with LOD threshold of 3.0.

18 **Field experiments**

19 The field experiments with four lines per se and two testcross populations were carried out
20 between 2000 and 2004. Field trials and lines tested were described in a previous report (Leng et
21 al., 2018). In this study, data were analyzed for the following traits: PHT in centimeters, measured

1 from soil level to the lowest tassel branch; DMC of the forage in grams per kilograms, determined
2 from a representative sample of 1.5 kg chopped material per plot; DMY of forage in megagrams
3 per hectare, calculated by multiplying the DMC values with the forage fresh weight per plot; DPS
4 in days, determined by number of days from planting to female flowering at 50% of the plants of
5 a plot had clearly visible silks.

6 **Data analysis**

7 A 10 × 10 lattice designed with two replications were conducted. The lines or testcross
8 progeny of the populations were divided into sub-sets. These each contained 90 families from the
9 population and 10 checks. Analyses of variance were performed on field data according to Cox &
10 Cochran (1957). Lattice adjusted entry means and effective error mean squares were used to
11 compute the combined analyses of variance across environments for each experiment (Cox &
12 Cochran, 1957). Heritability coefficients were estimated with their 95% confidence intervals
13 (Knapp & Bridges, 1987) on an entry mean basis as the ratio between the estimated genetic σ^2_g
14 and phenotypic variance σ^2_p . In addition, heritability estimates on a plot basis were computed
15 (Wricke & Weber, 1986). Coefficients of genetic correlation and their standard errors (SE) were
16 calculated from the analysis of variance and covariance according to Mode & Robinson (1959).
17 All statistical computations were performed with the PLABSTAT software (Utz, 1993).
18 Phenotypic and genotypic correlation coefficients for quality-determining characteristics were
19 calculated according to Presterl et al. (2007).

20 **Linkage mapping**

21 Linkage mapping and genetic map distances was carried out by using the Kosambi mapping
22 function implemented in the JoinMap 3.0 program (Kosambi, 1943). Associations between

1 phenotypes and genotypes were performed using "composite interval mapping" (CIM)
2 implemented in PLABQTL (Utz & Melchinger, 1996). PLABQTL follows the regression
3 approach as proposed by Haley & Knott (1992) and extended by using cofactors. Cofactors were
4 identified as previously described (Presterl et al., 2007). A LOD threshold (\log_{10} of the likelihood
5 odds ratio) of 3.0 was chosen for declaring a putative QTL significance. The QTL position was
6 estimated where the LOD score reached its maximum in the region concerned.

7 For each region, a 1-LOD support interval was constructed as described by Lander & Botstein
8 (1989). QTL shared by different traits were considered to be co-segregating when their 1-LOD
9 support intervals overlapped (Presterl et al., 2007). The effect of QTL \times environment interactions
10 was calculated according to Presterl et al. (2007). The additive effects of QTL were estimated as
11 half the difference between the phenotypic values of the respective homozygotes. The maize bin
12 was given for each QTL as the position of the left flanking marker, according to MaizeGDB
13 (<http://www.maizegdb.org>).

14 **Results**

15 **Agronomic Trait analysis**

16 **GABI Population**

17 The GABI population was planted in Grucking in 2000 and 2001. The plant harvests were
18 carried out in two years, with about the same DMC (24.07% and 23.76%, respectively). In 2001,
19 DMY was with 4.9 t/ha lower than in 2000 (6.2 t/ha). PHT was significantly higher (201.8 cm) in
20 2001, compared to 2000 (164.1 cm), the same was true for DPS 93.7 d and 98.0 d for 2000 and
21 2001, respectively. The GABI population had the longest DPS (98.4 d) among the four populations
22 used in this study (Table 1). Significant genotypic variance component estimates (σ^2_g) were found

1 for all four traits. Genotype by location interaction variance component estimates (σ_{ge}^2) were also
2 significant ($P = 0.01$) for all traits, but were not as pronounced as respective σ_g^2 values between
3 the two locations, except for DMC (Table 1). Heritabilities were higher than 83% for all traits
4 except 59.4% for DMC (Table 1). Close significant ($P = 0.01$) phenotypic (r_p) and genotypic (r_g)
5 correlations were found among all investigated traits (Table S1).

6 **DD Population**

7 The parental line AS30 was characterized with significantly higher agronomic traits than
8 AS29, however, there is no distinguished DMY difference, 5.2 t/ha for both AS29 and AS30.
9 Significant σ_g^2 estimates were found for all four traits, while significant σ_{ge}^2 estimates were only
10 found for DMC and DPS (Table 1), which were of less importance than σ_g^2 . Heritabilities ranged
11 from 71.8% (DMY) to 93.7% (PHT) (Table 1). r_p and r_g were significant ($P = 0.01$) for all trait
12 pairs, and highest r_p and r_g values were detected between PHT and DMY, 0.69 and 0.79,
13 respectively (Table S3).

14 The DD \times F TC population matured earlier at both locations compared to the DD per se lines,
15 resulting in the lowest DPS (70.6 d) and highest DMC (37.4%), also due to a very hot and dry
16 summer in 2003 (Table 1). The DMY of DD \times F TC population was significantly higher (8.0 t/ha)
17 than that of the DD population (6.2 t/ha). σ_g^2 estimates were significant for all investigated traits
18 ($P = 0.01$), σ_{ge}^2 estimates exceeded those for σ_g^2 with lower heritabilities, ranged from 4.2% to
19 45.6% (Table 1). Significant negative correlations were found between DMC and DMY (Table
20 S4). r_p and r_g for DMC and DMY between per se and TC performance were significant ($P = 0.05$)
21 (Table S5).

1 **FF Population**

2 The DMC of parent line AS07 was 26.3%, significant lower than AS17 (31.76%), the DMC
3 of the FF population progenies were ranged from 21.0% to 42.7% (Table 1). Highly significant σ_g^2
4 were found for all investigated agronomic traits, the σ_{ge}^2 were also always significant (Table 1),
5 but had a minor effect compared to the σ_g^2 . The heritabilities ranged from 76.2% (DMC) to 89.34%
6 (PHT). The r_p and r_g of correlation between traits were significantly different (Table S6).

7 Testcrossed AS17 had slightly lower tested agronomic traits than testcrossed AS07,
8 completely different to per se results. The FF \times D TC progenies showed a highly significant
9 difference among all tested traits. The σ_{ge}^2 was also always significant, but considerably less
10 important than the corresponding σ_g^2 (Table 1). Heritabilities were moderate, from 55.7% (DMC)
11 to 86.0% (PHT). r_p were significant ($P = 0.05$) for all trait combinations except PHT and DMC
12 (Table S7). Highly significant correlations were found for all traits when comparing per se and
13 testcross performance in the FF population (Table S8).

14 **FD Population**

15 The FD population was significantly affected by leaf diseases, especially *Puccinia sorghi* in
16 Grucking, but it had no effect (data not shown) on DMC variation. There is almost no difference
17 for the DMC and PHT between the parental lines, 28.6% and 27.1%, and 147.6 cm and 147.3 cm
18 for AS06 and AS08. AS06 anthesis was a few days later than AS08, 80.6 d and 76.4 d respectively.
19 AS06 showed a significantly higher DMY (5.7 t/ha) than AS08 (4.6 t/ha). The remaining FD
20 progeny ranged from 0.3 t/ha to 8.4 t/ha for DMY and 70.7 d to 88.4 d for DPS (Table 1). Highly
21 significant σ_g^2 and σ_{ge}^2 were found for all traits ($P = 0.01$) (Table 1). The genotype environment
22 interaction variance (σ_{ge}^2) and the errors (σ^2) were mostly of less importance compared to
23 genotypic variance (σ_g^2), which was also indicated by the high heritability for agronomic traits,

1 ranged from 76.6% (DMC) to 89.8% (DPS) (Table 1). r_p and r_g were significant ($P = 0.01$) for all
2 trait combinations, and negative (low) correlations were found between DMC and other agronomic
3 traits (Table S2).

4 **QTL Analyses**

5 **DMC**

6 Totally, 4 to 13 QTL were identified for DMC from the six populations distributed on 10
7 chromosomes explaining 25.7% to 64.2% of the phenotypic (r_p^2) and 36.2% to 100% of the
8 genotypic variation (r_g^2) (Table 2). QTL identified from GABI, DD, and FD populations showed
9 significant interactions with environment ($P = 0.05$). The largest number of 13 QTL for DMC were
10 identified in the GABI population, explaining 65.3% of r_p^2 and 56.4% of r_g^2 respectively. Three
11 major QTL on chromosomes 4 (bin 4.04-4.06), 5 (bin 5.07), and 6 (bin 6.05) explaining 13.0%,
12 11.3%, and 10.5% of r_p^2 were identified (Table S9). Two major QTL on chromosome 6 (bin 6.00-
13 6.01) and chromosome 8 (bin 8.03) were detected in the DD population, explaining 11.9% and
14 18.9% of r_p^2 (Table S9). One major QTL on chromosome 6 (bin 6.02-6.03) were identified from
15 the DD \times F TC population explained 16.3% of r_p^2 (Table S9). Six QTL for DMC were detected in
16 the FF population, explained 35.5% r_p^2 and 36.2% r_g^2 , one major QTL on chromosome 2 (bin 2.08)
17 explained 13.7% of r_p^2 (Table S9). Four QTL were identified in the FF \times D TC population
18 explained 25.7% of r_p^2 and 40.3% of r_g^2 (Table 2). Six QTL were identified for DMC in the FD
19 population, explained 44.4% of r_p^2 and 47.5% of r_g^2 (Table 2), two QTL on chromosome 7 (bin
20 7.05-7.06) and chromosome 10 (bin 10.04-10.06) explained $> 10\%$ of r_p^2 (Table S9).

1 **DMY**

2 5 to 12 QTL were identified for DMY distributed from the six populations on all 10
3 chromosomes, which explained 25.3% to 85.4% of r^2_p and 25.3% to 77.6% of r^2_g (Table 2). QTL
4 identified from GABI, DD, and DD \times F TC populations showed significant interactions with
5 environment ($P = 0.01$). Three major QTL on chromosomes 2 (bin 2.06-2.08), 4 (bin 4.03-4.04),
6 and 8 (bin 8.05-8.06) were identified in the GABI population explaining 11.7%, 18.3%, and 23.2%
7 of r^2_p (Table S9). Six QTL were detected in the DD population, explaining 50.7% of r^2_p and 49.4%
8 of r^2_g . Two major QTL on chromosomes 5 (bin 5.04-5.05) and 9 (bin 9.03) identified in the DD
9 population explained 13.1% and 11.7% of r^2_g , respectively. One major QTL on chromosome 1
10 (bin 1.08) in the DD \times F TC population explained 10.2% of r^2_p (Table S9). Five QTL for DMY
11 were detected in the FF population, explained between 5.5% (bin 10.03-10.04) to 7.5% (bin 5.02-
12 5.03) of r^2_p (Table S9). One major QTL on chromosome 4 (bin 4.07-4.08) were identified for DMY
13 in the FD population, explaining 10.6% of r^2_p (Table S9).

14 **PHT**

15 6 to 17 putative QTL were identified for PHT from the five populations distributed on all 10
16 chromosomes, explaining 40.8% to 100% of r^2_p and 47.0% to 77.4% of r^2_g , significant QTL \times
17 environment interactions were detected for all these QTL ($P = 0.01$) (Table 2). Seven major QTL
18 on chromosomes 2 (bin 2.08), 3 (bin 3.05-3.06), 6 (bin 6.03-6.05), 7 (bin 7.02), and 8 (bin 8.05)
19 with $r^2_p > 10\%$ were identified in the GABI population (Table S9). Nine QTL were detected in the
20 DD population explaining 67.1% of r^2_p and 57.4% of r^2_g , with two major QTL on chromosomes 3
21 (bin 3.05) and 10 (bin 10.07) explaining 18.3% and 11.4% of r^2_p (Table 2). Eight QTL were
22 detected for PHT in the FF population, and three major QTL on chromosomes 1 (bin 1.06), 3 (bin
23 3.04), and 5 (bin 5.05-5.06) explained 13.1%, 11.6%, and 13.3% of r^2_p (Table S9). Six QTL were

1 identified in the FF × D TC population, one major QTL on chromosome 1 (bin 1.06) explaining
2 17.3% of r^2_p (Table S9). Twelve QTL were identified for PHT in the FD population, explaining
3 100% of r^2_p and 63.3% of r^2_g (Table 2), three major QTL on chromosomes 3 (bin 3.06), 4 (bin
4 4.07-4.08), and 9 (bin 9.04) explained 13.2%, 21.4%, and 10.3% of r^2_p (Table S9).

5 **DPS**

6 4 to 16 putative QTL were identified for DPS from the five populations distributed on 10
7 chromosomes, explaining 25.7% to 91.8% of r^2_p and 37.8% to 60.3% of r^2_g , significant QTL ×
8 environment interactions were detected for all these QTL ($P = 0.05$) (Table 2). The highest number
9 of 16 QTL detected in the GABI population explained 91.8% of r^2_p and 54.6% of r^2_g (Table 2),
10 four major QTL were detected on chromosomes 2 (bin 2.06-2.08), 3 (bin 3.04), 6 (bin 6.06-6.07),
11 and 8 (8.05), explained > 10% of r^2_p (Table S9). Seven QTL on were identified in the FF population,
12 explaining 62.1% of r^2_p and 49.1% of r^2_g (Table 2), one major QTL on chromosome 5 (bin 5.03-
13 5.04) explaining 21.1% of r^2_p (Table S9). Four QTL were detected in the FF × D TC population
14 (Table 2), one major QTL on chromosome 3 (bin 3.04) explained 10.1% of r^2_p (Table S9). Eleven
15 QTL were identified for DPS in the FD population, explaining 77.9% of r^2_p and 60.3% of r^2_g (Table
16 2), three major QTL were detected on chromosomes 1 (bin 1.06), 2 (bin 2.08-2.09), and 8 (bin
17 8.05), explained > 10% of r^2_p (Table S9).

18 **Consistency of QTL between line per se and TC evaluation**

19 The correlation between the line per se and testcross performance was significant for DMC
20 and DMY (Table 3), it was expected to find common QTL across the DD and DD × F TC
21 population. Two consistent QTL were found for DMC (bins 7.03 and 7.05-7.06) from the line per
22 se and TC population (Table 3). Two consistent QTL were found for DMY (bins 3.04 and 5.07)

1 from the line per se and TC population (Table 3). The correlations between the corresponding traits
2 were always significant in the FF × D TC population (Table S8). Therefore, it is not surprising to
3 detect consistent QTL corresponding to these agronomic traits across the line per se and TC. One
4 common QTL for DMC (bin 2.04), two for DMY (bins 8.03, 10.04), three for PHT (bins 1.06,
5 1.07, 2.06), and three for DPS (bins 2.04, 3.04, 3.05-06) were identified in the lines per se and TC
6 of FF population (Table 4). Especially the two hot spots bin 2.04 (for DMC, PHT and DPS) and
7 bin 3.04-3.05 (for DMC, DMY, PHT, and DPS).

8 **Correlations among forage agronomic traits and stover quality traits**

9 We analyzed the correlations between forage maize agronomic/forage yield and stover quality
10 traits, which was conducted by our previous research (Leng et al., 2018). Negative r_p existed
11 between DMC, DMY, and NDF (neutral detergent fiber), DNDF (digestibility of NDF) in all four
12 populations (Table S1-S4, S6-S7). In addition, loose negative genotypic correlations were found
13 between DMY, DMC and IVDOM, NDF. PHT and DPS were significantly ($P = 0.01$) positive
14 phenotypically and genetically correlated with stover quality traits like IVDOM and WSC (water
15 soluble carbohydrates). DPS was negatively correlated with cell wall digestibility traits like NDF
16 and DNDF. In this study, it seems there is negative correlation between plant height and cell wall
17 digestibility (IVDOM, NDF, and DNDF), which indicates that taller plants possess poorer cell
18 wall digestibility than shorter plants. However, no correlation was found among nutrient quality
19 traits, agronomic traits and yield traits. Negative r_p and r_g were found between NDF and all the
20 four agronomic traits in the six populations (Table S1-S4, S6-S7), and also DNDF.

1 **Consistency of QTL for both agronomic and quality traits**

2 In this study, a total of 42, 41, 54, 45 QTL were identified for DMC, DMY, PHT, and DPS,
3 respectively (Table S9). Previously, 33, 23, 32, 38 QTL were identified for IVDOM, NDF, WSC,
4 and DNDF by using the same six populations (Leng et al., 2018). Here, we summarized QTL
5 shared between traits across populations for both agronomic and quality traits, and 5 (NDF and
6 DPS) to 17 (PHT and DMC, DNDF and DMC) common QTL were identified totally (Table S10).
7 The largest number of 9 to 17 common QTL were found between DMC and other traits, supported
8 by significant correlations (Table S1-S4, S6-S7). Major QTL for agronomic and stover quality
9 traits co-localized in the same chromosome regions, such as bins 2.08, 3.05, and 8.05. QTL for
10 WSC, DMC, DMY, PHT, and DPS shared the same chromosome region in bin 2.08. A major QTL
11 in bin 3.05 was associated with NDF, DNDF, and PHT. In bin 8.05, major QTL were identified
12 for IVDOM, WSC, PHT, and DPS. In addition, there were also few consistent minor QTL such as
13 in bins 1.06, 7.02, and 10.03-10.04, where both forage maize agronomic and quality traits
14 colocalized.

15 **Discussion**

16 **Consistency of QTL across populations**

17 One QTL for DMC located in bin 7.05-7.06 was detected in five populations except the FF
18 × D population, and bins 5.05 and 10.04-10.06 were detected in three populations, explaining more
19 than 10% of phenotypic variation. A QTL in bin 5.05 was also identified in the RIL population by
20 Mechin et al. (2001). One common QTL for DMY in bin 3.05-3.06 was found in three populations
21 (Table S9). A major QTL in bin 1.06 was commonly identified for PHT explaining more than 10%
22 phenotypic variation, was also reported by Lübberstedt et al. (1997a) and Schön et al. (1994)

1 although each with a minor effect. One major QTL in bin 5.03-5.04 was associated with DPS twice
2 (Table S9). According to the report of QTL for flowering time traits was observed in bins 1.05,
3 7.02, and 9.02-9.03, and a QTL for days to silking was also observed in bin 7.02 (Hu et al., 2008;
4 Zhang et al., 2004). Major QTL in bin 8.05 were detected for DPS by Frascaroli et al. (2009), and
5 other bins 1.07, 2.02, 7.02, and 8.03 were found in our study. Hot spot regions for flowering time
6 in chromosomal regions like 1.05-06, 3.04-06, 8.05, 10.04 and 10.05-06 were identified through
7 meta-analysis (Xu et al., 2012). These common QTL indicate that there exist dominant genes
8 controlling agronomic traits, which involved in controlling both inflorescence and vegetative
9 development in maize (McSteen et al., 2007).

10 **QTL hot spots associated with agronomic and forage quality traits**

11 There are some common major QTL which were identified for different agronomic traits
12 (Table S9), in agreement with higher correlations among these traits. It was not surprising to see
13 that chromosome hot spots in bins 1.06, 2.08, 3.04-3.06, 7.02, and 8.05 contained QTL for PHT
14 and DPS, as flowering time determines PHT (Irish & Nelson, 1991). Two important regions of the
15 genome were bins 3.05-3.06 and 8.05, which contained QTL for DMV, PHT and DPS. Bin regions
16 1.06, 2.08, 3.04-06 and 8.05 were identified by different linkage mapping populations (Frascaroli
17 et al., 2009; Lübberstedt et al., 1997a). QTL for NDF and DNDF also share the same chromosome
18 region in bin 3.05 (Leng et al., 2018), containing QTL for PHT and DPS. QTL hotspots in bins
19 7.02 and 8.05 were exclusively found to be associated with flowering traits and DMC (Frascaroli
20 et al., 2009; Hu et al., 2008; Méchin et al., 2001; Zhang et al., 2004). In addition, bin 8.05 was an
21 important region, where three major QTL for IVDOM, WSC, and DNDF clustered (Leng et al.,
22 2018), consistent with QTL identified by Roussel et al. (2002). A number of consistent QTL in
23 bins 4.08, 9.04, and 10.03-10.04 were identified for maize flowering by meta-QTL analysis

1 (Chardon et al., 2004; Xu et al., 2012). A major QTL for DMY was also estimated in bin 10.03-
2 10.04 from the TC population (Méchin et al., 2001). Another hotspot was in bin 5.05-5.06, with
3 three major QTL for DMC, DMY, and DPS clustering in this region, while this region was
4 identified for PHT by Frascaroli et al. (2009) for and DMC by Méchin et al. (2001). DMY was
5 usually higher for late maturing plants, while those earliest maturing had the highest NDFD.
6 Generally, reduced lignin content resulted in higher stover digestibility, reduced grain yield, and
7 delayed maturity (Pedersen et al., 2005). Cell wall lignification is not always negatively correlated
8 with DMY and other agronomic traits, while no pleiotropic polymorphisms affecting both DNDF
9 and PHT or DMY were detected (Chen et al., 2010). Thus, different gene/s may affect both
10 agronomic and cell wall digestibility traits. Common QTL detected in this study might be caused
11 by pleiotropy or closely linked QTL located in the same chromosomal region. These QTL hotspots
12 show that agronomic and feeding values traits need to be addressed simultaneously.

13 **Co-segregation of QTL with known genes**

14 Most QTL identified in this study were co-localized with known genes associated with
15 specific agronomic traits. A *dwarfplant10* gene co-localized in bin 2.08, the *D10* mutant is a dwarf
16 with fair tassel and shortened internodes (Neuffer & England, 1995), in accordance with QTL for
17 PHT and DPS in this region. Tassel development is tightly correlated PHT and DPS, and two well
18 characterized genes associated with tassel development were found in bin 3.04. *Tasselseed4* (*ts4*)
19 determines the sex and cell fate of meristems forming tassel (Mendes-Moreira et al., 2015) and
20 *tassels replace upper ears1* (*tru1*) associated with shortened tassel length (Sheridan, 1988). A
21 *ga20ox3* gene encoding gibberellin 20-oxidase3 is located in bin 3.06, which is another hot spot
22 for DMY, PHT and DPS. Ga20ox family genes regulate GA levels, and are associated with
23 internode elongation and stem node number, respectively (Rieu et al., 2008). *Vgt1* (*Vegetative to*

1 *generative transition1*) in bin 8.05 is a cis-acting regulatory element for the *rap2* flowering time
2 gene, which confers advanced timing of transition of the apical meristem from vegetative to
3 generative state, reducing node number (Salvi et al., 2007). In addition, other well characterized
4 genes associated with forage agronomic and stover quality traits, were co-localized with QTL
5 detected in this study. Flowering time is a complex quantitative trait, controlled by a small number
6 of major effect genes, but also a large number of minor effect genes. Consistent QTL together with
7 the new QTL identified in this study may help to elucidate the genetic basis of maize agronomic
8 traits and also to broaden the utilization of MAS in maize breeding programs.

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12 **Conflict of Interest**

13 The authors declare that they have no conflict of interest.

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Table 1. Mean values, least significant differences (GD 5%), minimum and maximum values across two years, and estimates of variance components, heritabilities (h^2), and 95% confidence intervals of heritabilities (CI) for quality traits.

Populations [#]	Traits	Mean	GD 5%	Min.	Max.	Source of variation			h^2	CI
						σ^2_g	σ^2_{ge}	σ^2		
GABI	IVDOM	71.5	4.74	54.1	80.9	7.26**	4.31**	1.52	71.4	66.8-75.4
	NDF	55.8	5.69	43.5	76.2	10.94**	6.32**	2.09	72.3	67.8-76.1
	WSC	19.2	5.56	0.6	30.8	12.41**	5.48**	2.55	75.6	71.6-79.0
DD	IVDOM	75.8	3.79	70.4	81.2	1.72**	1.92**	1.78	48.2	33.6-59.7
	NDF	53.8	4.73	46.5	60.3	2.48**	4.07**	1.70	46.2	31.0-58.1
	WSC	23.0	5.33	15.9	31.4	3.83**	5.33**	2.00	51.1	37.3-61.9
	DNDF	57.4	3.47	52.0	64.9	3.30**	2.94**	0.15	68.1	59.15-75.1
DD × F TC	IVDOM	64.9	2.84	60.4	69.5	2.04**	0.65**	1.43	66.1	56.6-73.6
	NDF	69.5	2.94	65.0	74.1	0.54**	1.68**	1.68	62.0	51.3-70.4
	WSC	8.6	2.50	4.8	12.1	0.67**	0.67**	0.95	45.2	29.8-57.3

	DNDF	55.1	2.91	50.3	59.0	1.99**	0.97**	1.21	64.6	54.6-72.4
FF	IVDOM	72.5	3.94	64.9	78.9	4.58**	1.79**	2.21	69.6	61.4-76.1
	NDF	58.0	5.43	48.6	67.7	9.57**	3.58**	4.02	71.6	63.9-77.6
	WSC	14.6	5.42	5.8	23.2	8.76**	3.19**	4.40	69.8	61.6-76.2
	DNDF	57.4	4.00	45.2	65.2	4.88**	2.21**	1.93	70.3	62.2-76.6
FF × D TC	IVDOM	69.6	2.43	64.8	73.4	1.67**	0.44**	1.08	68.6	60.2-75.3
	NDF	63.3	3.64	58.1	68.1	2.15**	1.72**	1.70	55.7	43.7-65.2
	WSC	14.9	4.03	10.3	20.7	1.78**	2.11**	2.09	45.9	31.3-57.4
	DNDF	56.6	3.41	52.4	60.1	0.61**	1.90**	1.09	28.8	9.6-44.0
FD	IVDOM	74.1	3.96	67.3	81.2	3.57**	2.77**	1.29	63.8	54.7-71.0
	NDF	56.4	4.91	48.6	64.9	6.90**	4.39**	1.84	68.9	61.2-75.1
	WSC	20.7	5.50	11.7	30.0	8.12**	5.52**	2.29	67.5	59.4-74.0
	DNDF	56.4	4.74	48.5	66.4	4.30**	4.15**	1.64	59.7	49.7-67.8

GABI: The German Plant Genome Research Program population; DD: Dent × Dent Double Haploid Lines; DD × F TC: (Dent × Dent) × Flint Test cross; FF: Flint × Flint-RIL; FF × D TC: (Flint × Flint) × Dent Test Cross; FD: Flint × Dent Double Haploid Lines.

*, ** significant at $P = 0.05, 0.01$ (F-Test).

Table 2. Number of QTL, variance components, percentages of phenotypic (r^2_p) and genotypic variation (r^2_g), explained by all QTL for forage quality traits IVDOM, NDF, WSC, and DNDF in six populations.

Traits	Populations	Number of QTL	F	QTL \times E	r^2_p	r^2_g
IVDOM	GABI	16	7.21**	0.63**	77.3	74.6
	DD	4	1.72**	0.16**	31.7	54.3
	DD \times F TC	1	2.04**	0.08**	5.0	4.9
	FF	3	4.58**	-0.02	22.6	33.8
	FF \times D TC	2	1.67**	0.05*	11.4	21.9
	FD	7	3.54**	0.45**	46.7	48.9
NDF	GABI	8	10.97**	1.34**	35.3	55.3
	DD	3	2.48**	0.08	36.3	57.2
	DD \times F TC	1	1.82**	0.11**	5.7	5.6
	FF	3	9.57**	0.21*	17.7	20.4
	FF \times D TC	3	2.15**	0.09*	14.9	18.1

	FD	5	6.88**	1.19**	46.1	45.5
WSC	GABI	15	12.38**	1.33**	86	69.0
	DD	2	3.84**	0.05	12	26.7
	DD × F TC	3	0.67**	0.01	19.8	43.4
	FF	3	8.67**	0.06	20.4	28.0
	FF × D TC	3	1.78**	0.02	13	29.4
	FD	6	8.13**	1.27**	62.3	45.6
DNDF	DD	4	3.30**	0.04	28.9	36.2
	DD × F TC	1	1.99**	0.02	7.7	10.8
	FF	6	4.88**	0.16*	49.9	49.1
	FF × D TC	7	0.61**	0.17**	49.9	97.6
	FD	7	4.36**	0.11	47.5	53.6

*, ** significant at $P = 0.05, 0.01$ (F-Test).

Table 3. Overview over consistent QTL positions in the DD and the DD × F TC populations.

Traits	bin	DD				DD × F TC			
		Pos.#	LOD	R ² p‡	Effect	Pos.#	LOD	R ² p‡	Effect
IVDOM	9.02-03	50	9.93	14.3	+	34	3.21	5.0	+
NDF	9.02-03	54	4.67	17.0	-	34	3.65	5.7	-
DNDF	3.04	2	2.13	3.2	+	12	4.09	7.7	+
	9.02-03	48	3.68	7.6	+	10	2.20	2.9	+

Position on the chromosome in cM in distance from the first marker.

‡ Proportion of phenotypic variance that is explained by the QTL.

Table 4. Overview of consistent QTL positions in the FF and FF × D TC populations.

Traits	bin	FF				FF × D TC			
		Pos.#	LOD	R ² _p [§]	Effect	Pos.#	LOD	R ² _p [§]	Effect
IVDOM	3.05	68	6.12	7.5	-	68	2.89	5.9	-
WSC	10.04	16	4.29	6.8	-	18	4.91	6.1	-
DNDF	3.05	66	10.25	17.4	-	70	2.99	4.4	-
	5.03-04	94	6.72	9.6	-	86	3.67	6.2	-
	6.02	64	3.47	3.3	-	66	4.90	9.2	-
	6.05	108	5.43	7.2	-	104	2.06	3.5	-
	10.06	66	4.42	5.9	+	64	5.53	7.4	+

Position on the in cM in distance from the first marker.

§ Proportion of phenotypic variance that is explained by the QTL.

Table 5. Results of QTL analyses for DNDF and overview of QTL found in more than one population.

Populations	QTL	Max. LOD	R^2_p †	R^2_g ‡	bin region ³										
					1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	
DD	2	8.3	8.3	35.0	05					04-05			05*		06
FF	5	10.3	17.4	48.6	09*	03-04	05			04	05				06
FD	7	7.9	12.8	52.7	09	04-05	05-06			06	05				06*

† Proportion of phenotypic variance explained by a QTL.

‡ Proportion of phenotypic variance explained by all QTL.

3 Bin region of nearest SSR markers, based on MaizeGDB.

* Peak, LOD < 3.5

Table S1 Coefficient of phenotypic (above the diagonal) and genotypic correlation (below the diagonal) for agronomic and stover quality related traits of the GABI population

Traits	DMC	DMY	IVDOM	NDF	WSC	DNDF	PHT	DPS
DMC		0.14**	0.00	-0.01	0.09*	-0.03	0.10**	0.09*
DMY	0.13++		0.46**	-0.49**	0.60**	0.21**	0.68**	0.50**
IVDOM	-0.05	0.54++		-0.90**	0.86**	0.89**	0.14**	0.45**
NDF	-0.02	-0.56++	-1.00++		-0.92**	-0.63**	-0.15**	-0.48**
WSC	0.07+	0.69++	0.93++	-0.92++		0.58**	0.33**	0.47**
DNDF	-0.13+	0.34++	0.97++	-1.00++	0.83++		-0.05	0.29**
PHT	0.18++	0.75++	0.16++	-0.16++	0.38++	-0.08+		0.31**
DPS	0.05	0.54++	0.53++	-0.53++	0.51++	0.47++	0.34++	

Table S2 Coefficient of phenotypic (above the diagonal) and genotypic correlation (below the diagonal) for agronomic and stover quality related traits of the FD population

Traits	DMC	DMY	IVDOM	NDF	WSC	DNDF	PHT	DPS
DMC		-0.27**	-0.06	0.10	-0.10	-0.21**	-0.22**	-0.17**
DMY	-0.32++		0.09	-0.21**	0.38**	-0.01	0.52**	0.24**
IVDOM	-0.05	0.05		-0.76**	0.70**	0.74**	-0.13*	0.28**
NDF	0.13+	-0.17++	-0.74++		-0.90**	-0.23**	-0.14*	-0.28**
WSC	-0.07	0.35++	0.72++	-0.93++		0.20**	0.27**	0.37**
DNDF	-0.27++	-0.01	0.72++	-0.18++	0.20++		-0.20**	0.15**
PHT	-0.25++	0.56++	-0.19++	-0.14+	0.31++	-0.27++		0.34**
DPS	-0.20++	0.26++	0.31++	-0.29++	0.42++	0.20++	0.40++	

Table S3 Coefficient of phenotypic (above the diagonal) and genotypic correlation (below the diagonal) for agronomic and stover quality related traits of the DD population

Traits	DMC	DMY	IVDOM	NDF	WSC	DNDF	PHT	DPS
DMC		0.19**	0.07	-0.03	-0.23**	-0.37**	0.14*	0.50**
DMY	0.21++		-0.04	-0.04	0.28**	-0.21**	0.69**	0.42**
IVDOM	0.04	-0.23+		-0.73**	0.47**	0.70**	-0.36**	0.08
NDF	0.00	0.15+	-0.55++		-0.75**	-0.22**	0.26**	-0.04
WSC	-0.40++	0.20+	0.29++	-0.74++		0.16**	0.12	0.04
DNDF	-0.47++	-0.35++	0.63++	0.07	0.09		-0.37**	-0.22**
PHT	0.14++	0.79++	-0.54++	0.42++	0.12+	-0.46++		0.41**
DPS	0.57++	0.50++	0.07	0.03	-0.03	-0.29++	0.47++	

Table S4 Coefficient of phenotypic (above the diagonal) and genotypic correlation (below the diagonal) for agronomic and stover quality related traits of the DD × F TC population

Traits	DMC	DMY	IVDOM	NDF	WSC	DNDF
DMC		-0.28**	-0.11	0.25**	-0.34**	0.02
DMY	-1.00++		0.28**	-0.33**	0.35**	0.23**
IVDOM	0.14	0.62++		-0.88**	0.67**	0.91**
NDF	0.46++	-0.48++	-0.93++		-0.86**	-0.66**
WSC	-0.46++	0.70++	0.67++	-0.95++		0.39**
DNDF	0.58++	0.71++	0.97++	-0.84++	0.44++	

Table S5 Coefficient of phenotypic (r_p) and genotypic correlation (r_g) between the intrinsic power of 250 lines of DD population and the performance of the 250 test crosses the DD \times F TC population for agronomic traits

Trait	r_p	r_g
DMC \times DMC	0.15*	0.46++
DMY \times DMY	0.36**	0.46++

Table S6 Coefficient of phenotypic (above the diagonal) and genotypic correlation (below the diagonal) for agronomic and stover quality related traits of the FF population

Traits	DMC	DMY	IVDOM	NDF	WSC	DNDF	PHT	DPS
DMC		-0.19**	-0.28**	0.32**	-0.32**	-0.08	-0.16*	-0.36**
DMY	-0.26++		0.01	-0.20**	0.33**	-0.22**	0.55**	0.32**
IVDOM	-0.39++	-0.06		-0.80**	0.69**	0.56**	-0.21**	0.11
NDF	0.45++	-0.18++	-0.81++		-0.93**	-0.03	0.04	-0.28**
WSC	-0.46++	0.36++	0.69++	-0.94++		-0.23**	0.23**	0.37**
DNDF	-0.14+	-0.30++	0.58++	-0.05	-0.29++		-0.35**	-0.28**
PHT	-0.17++	0.60++	-0.23++	0.04	0.30++	-0.44++		0.27**
DPS	-0.42++	0.39++	0.16++	-0.35++	0.49++	-0.32++	0.31++	

Table S7 Coefficient of phenotypic (above the diagonal) and genotypic correlation (below the diagonal) for agronomic and stover quality related traits of the FF × D TC population

Traits	DMC	DMY	IVDOM	NDF	WSC	DNDF	PHT	DPS
DMC		-0.15*	-0.17**	0.20**	-0.07	-0.13*	0.02	-0.26**
DMY	-0.33++		0.28**	-0.45**	0.57**	-0.01	0.64**	0.59**
IVDOM	-0.40++	0.27++		-0.84**	0.71**	0.76**	-0.03	0.06
NDF	0.83++	-0.56++	-1.00++		-0.92**	-0.32**	-0.17**	-0.19**
WSC	-0.75++	0.78++	0.93++	-0.91++		0.15*	0.36**	0.26**
DNDF	0.14	-0.14+	1.00++	-1.00++	0.93++		-0.27**	-0.10
PHT	0.06	0.74++	-0.03	-0.28++	0.61++	-0.59++		
DPS	-0.58++	0.80++	0.16+	-0.24++	0.37++	0.09	0.72++	

Table S8 Coefficient of phenotypic (r_p) and genotypic correlation (r_g) between the intrinsic performance of the lines of the FF-pop and performance of test crosses of FF \times D TC for agronomic traits

Trait combination	r_p	r_g
DMC \times DMC	0.41**	0.58++
DMY \times DMY	0.53**	0.63++
PHT \times PHT	0.74**	0.81++
DPS \times DPS	0.62**	0.78++

Table S9 Statistical parameters that are associated with the QTL of six populations for agronomic traits

Chr.	Position#	Support Interval	Left Marker	bin	Right Marker	bin	LOD	R ² _p [§]	Effect [‡]	Effect (2000)	Effect (2001)
DMC											
GABI										Bernburg	Grucking
2	86	82-92	phi00092	2.05	bnlg1138	2.06	5.26	2.9	-0.279	-0.165	-0.398
2	138	126-144	bnlg1233	2.08	bnlg1520	2.09	3.99	2.4	0.283	0.411	0.160
3	160	156-168	bnlg1257	3.09	bnlg1754	3.09	6.96	4.5	0.344	0.240	0.444
4	24	16-30	phi00096	4.04	bnlg2291	4.06	10.76	13.0	0.656	0.435	0.880
4	66	54-78	bnlg1189	4.07	dupssr28	4.08	3.74	2.3	-0.278	-0.176	-0.378
5	4	0-14	bnlg1879	5.03	bnlg1046	5.03	3.65	2.2	0.280	0.147	0.409
5	36	32-44	bnlg0150	5.04	bnlg2323	5.04	3.06	1.1	-0.205	-0.263	-0.148
5	92	72-114	phi00085	5.07	bnlg1885	5.07	4.15	11.3	0.762	0.482	1.038
6	0	0-10	bnlg1043	6.00	bnlg2243	6.01	5.12	2.8	-0.265	-0.196	-0.331
6	70	66-76	umc01413	6.05	phi00025	6.05	12.57	10.5	-0.551	-0.401	-0.639
7	46	40-52	bnlg1808	7.02	bnlg1305	7.03	5.95	3.8	0.308	0.207	0.408
8	36	32-44	bnlg1067	8.03	bnlg1834	8.03	3.81	2.5	-0.249	-0.542	0.039
10	52	48-60	bnlg1655	10.04	phi00035	10.06	10.38	6.0	-0.397	-0.315	-0.476
DD										Bernburg	Grucking
1	8	2-12	umc01071	1.01	umc01948	1.01	4.49	7.7	0.691	0.639	0.743
1	72	68-88	bnlg2086	1.05	bnlg1884	1.05	3.14	14.9	-1.018	-0.824	-1.213
5	6	0-10	bnlg1006	5.00	MA003663	5.00	4.51	5.7	0.573	0.505	0.641
6	4	0-10	phi00126	6.00	bnlg0249	6.01	6.58	11.9	-0.862	-0.741	-0.983
7	76	64-84	bnlg2203	7.02	bnlg1305	7.03	3.71	5.4	-0.581	-0.566	-0.596
7	186	180-188	phi00082	7.05	phi00116	7.06	4.25	5.3	-0.561	-0.435	-0.688
8	34	32-42	bnlg1067	8.03	umc01807	8.03	10.56	18.9	-1.111	-1.290	-0.933
DD × F TC										Bernburg	Grucking
3	32	18-44	bnlg1456	3.05	umc01539	3.05	5.51	6.8	-0.494	-0.486	-0.502
5	86	74-94	bnlg1208	5.04	umc02111	5.05	3.50	3.2	0.284	0.203	0.365

6	24	18-30	umc01006	6.02	umc01572	6.03	11.15	16.3	-0.700	-0.397	-1.003
6	172	164-172	dupssr15	6.06	phi00089	6.08	3.14	4.0	-0.331	-0.388	-0.274
7	86	80-98	bnlg1070	7.03	umc01324	7.03	6.25	6.2	-0.414	-0.355	-0.473
7	188	184-188	phi00082	7.05	phi00116	7.06	4.65	5.6	-0.370	-0.488	-0.251
FF										Bernburg	Grucking
1	144	140-146	bnlg1057	1.06	umc01035	1.06	3.71	6.5	0.785	0.877	0.692
1	164	160-170	bnlg1556	1.06	bnlg1025	1.07	4.04	2.9	-0.522	-0.665	-0.378
2	46	34-50	umc01448	2.04	bnlg1018	2.04	7.09	6.9	0.695	0.671	0.718
2	134	128-138	bnlg1233	2.08	bnlg1940	2.08	10.70	13.7	1.012	0.842	1.182
5	168	164-170	umc01822	5.05	umc01941	5.06	5.68	2.1	0.350*	0.364	0.336
7	164	150-170	bnlg2259	7.04	phi00082	7.05	3.35	3.4	0.554	0.673	0.434
FF × D TC										Bernburg	Grucking
1	32	20-44	bnlg1429	1.02	bnlg0176	1.03	3.75	6.1	0.263	0.356	0.169
1	248	244-254	bnlg1055	1.11	umc01325	1.11	6.36	7.9	0.248	0.286	0.211
2	42	32-50	bnlg1017	2.02	umc01448	2.04	5.22	7.6	0.246	0.257	0.234
10	62	50-70	umc01407	10.04	bnlg2190	10.06	3.02	4.1	-0.179	-0.183	-0.176
FD										Bernburg	Grucking
1	104	400-114	MA003701	1.05	bnlg1057	1.06	3.31	4.7	-0.499	-0.456	-0.523
2	48	32-62	bnlg1017	2.02	bnlg1537	2.03	5.63	6.1	0.693	0.291	1.084
5	110	100-112	bnlg0278	5.06	bnlg0609	5.06	4.00	6.4	0.654	0.480	0.770
7	124	108-128	phi00082	7.05	phi00116	7.06	8.72	10.8	0.793	0.906	0.702
9	42	38-48	phi00065	9.03	MA003325	9.03	4.05	5.5	-0.561	-0.795	-0.367
10	56	50-62	bnlg1074	10.04	phi00035	10.06	8.47	10.9	-0.846	-1.020	-0.682
DMY											
GABI										2000	2001
1	190	174-200	bnlg1643	1.08	phi00011	1.09	5.64	3.6	-19.855	-21.092	-18.618
2	94	90-108	bnlg1138	2.06	bnlg1329	2.08	19.63	11.7	35.500	41.333	29.667
3	80	74-88	bnlg0420	3.05	bnlg1449	3.06	8.35	4.6	-21.810	-28.022	-15.597

4	18	14-24	bnlg1126	4.03	phi00096	4.04	29.68	18.3	48.841	51.524	46.158
4	100	86-112	bnlg0292	4.08	umc01101	4.09	4.19	2.5	17.259	25.434	9.084
5	46	42-60	mmc00081	5.05	umc01502	5.05	3.07	1.8	-13.385	-18.554	-8.217
6	4	0-10	bnlg2243	6.01	umc01006	6.02	7.27	4.9	22.084	26.385	17.783
6	88	76-102	nc000013	6.05	dupssr15	6.06	4.99	3.2	-20.365	-21.722	-19.007
7	24	18-34	bnlg1292	7.01	phi00112	7.01	11.33	6.5	-27.396	-32.509	-22.282
8	4	0-16	bnlg1194	8.01	bnlg2235	8.02	4.92	3.3	-19.643	-21.807	-17.480
8	56	52-58	bnlg0666	8.05	bnlg1812	8.06	14.21	23.2	-54.413	-53.107	-55.718
9	34	20-50	bnlg1583	9.01	dupssr06	9.02	3.74	1.8	-13.955	-14.596	-13.314
DD										Bernburg	Grucking
3	8	6-14	bnlg1904	3.04	bnlg1601	3.04	3.16	5.7	0.027	0.022	0.033
5	86	80-94	bnlg1208	5.04	umc02111	5.05	6.93	13.1	-0.043	-0.033	-0.053
5	142	136-150	phi00085	5.07	MA003713	5.07	4.96	6.9	-0.030	-0.009	-0.051
6	26	18-34	umc01006	6.02	umc01572	6.03	6.14	8.6	0.033	0.029	0.039
8	76	68-82	bnlg0240	8.06	bnlg1065	8.07	4.33	4.7	-0.024	-0.021	-0.028
9	46	40-52	phi00061	9.03	MA003415	9.03	8.41	11.7	-0.040	-0.026	-0.054
DD × F TC										Bernburg	Grucking
1	102	94-112	umc01972	1.06	bnlg1057	1.06	6.93	8.4	0.159	0.107	0.211
1	162	156-170	umc01446	1.08	bnlg1643	1.08	6.59	10.2	-0.173	-0.132	-0.213
3	0	0-6	bnlg1647	3.04	bnlg1904	3.04	3.11	4.5	0.101	0.076	0.126
4	76	66-84	mmc00471	4.04	umc01329	4.06	4.80	2.8	0.081	0.009	0.152
5	82	74-90	bnlg1046	5.03	bnlg1208	5.04	7.23	8.4	-0.160	-0.117	-0.204
5	136	130-140	bnlg0278	5.06	phi00085	5.07	4.68	6.9	-0.135	-0.080	-0.190
6	16	8-20	bnlg0249	6.01	MA003444	6.01	4.50	7.9	0.138	0.082	0.195
6	92	86-96	umc01413	6.05	umc01314	6.05	7.36	9.3	0.156	0.113	0.199
FF × D TC										Bernburg	Grucking
1	44	34-50	bnlg0176	1.03	bnlg1484	1.03	3.07	2.0	-0.116*	-0.075	-0.157
3	50	44-56	phi00029	3.04	dupssr05	3.04	5.28	4.5	0.200	0.204	0.197

3	88	80-100	bnlg1456	3.05	bnlg1063	3.06	5.93	4.3	0.201	0.196	0.205
8	40	30-48	bnlg1834	8.03	phi00081	8.03	4.18	7.4	0.263	0.265	0.262
10	18	12-22	umc01246	10.04	bnlg1526	10.04	6.10	7.1	-0.224	-0.187	-0.261
FF										Bernburg	Grucking
1	178	170-188	umc01147	1.07	bnlg1331	1.10	4.81	5.8	0.295	0.301	0.278
5	62	54-72	bnlg1879	5.02	bnlg1700	5.03	3.33	7.5	0.322	0.247	0.402
8	40	30-48	bnlg1834	8.03	phi00081	8.03	5.11	7.1	0.352	0.316	0.401
9	76	72-84	umc01492	9.04	umc01657	9.05	4.71	5.8	-0.271	-0.196	-0.338
10	16	12-22	bnlg1655	10.03	umc01246	10.04	4.38	5.5	-0.269	-0.252	-0.294
FD										Bernburg	Grucking
1	114	106-124	MA003701	1.05	bnlg1057	1.06	6.25	5.4	31.166	28.059	31.511
3	104	90-120	MA003699	3.06	umc01674	3.06	5.07	4.5	-30.977	-30.996	-30.643
4	48	40-68	bnlg1189	4.07	dupssr28	4.08	9.74	10.6	-46.320	-42.107	-50.935
9	8	0-18	bnlg1583	9.01	dupssr06	9.02	3.10	1.4	-	-12.099	-26.229
9	100	92-104	dupssr29	9.08	bnlg0619	9.08	3.36	5.1	17.679	29.553	20.465
PH											
GABI										2000	2001
1	126	122-130	bnlg2086	1.05	bnlg1884	1.05	4.23	1.4	1.293	0.996	1.473
2	56	48-66	bnlg2277	2.02	bnlg1537	2.03	5.85	3.9	2.635	2.606	2.714
2	96	92-102	bnlg1329	2.08	dupssr24	2.08	16.43	11.3	4.470	4.108	4.917
3	60	52-64	bnlg1904	3.04	umc01012	3.04	3.52	2.1	-2.257	-1.548	-3.090
3	84	80-88	bnlg0420	3.05	bnlg1449	3.06	32.01	15.9	-6.933	-6.829	-7.047
4	22	18-28	bnlg1126	4.03	phi00096	4.04	25.80	23.4	7.467	6.652	8.321
4	54	48-64	bnlg1189	4.07	dupssr28	4.08	4.09	2.3	2.433	1.956	2.852
4	84	80-88	phi00093	4.08	bnlg0292	4.08	18.10	10.6	4.764	4.837	4.665
5	26	20-32	bnlg1700	5.03	bnlg0150	5.04	3.02	0.8	-1.474*	-0.865	-1.810
5	42	38-50	bnlg2323	5.04	mmc00081	5.05	6.66	4.8	-3.749	-3.931	-3.695
5	150	116-150	phi00085	5.07	bnlg1885	5.07	3.28	1.7	-1.490	-1.389	-1.572

6	24	12-42	umc01572	6.03	umc01413	6.05	4.18	10.3	4.476	4.077	4.775
6	92	80-102	nc000013	6.05	dupssr15	6.05	18.31	12.8	-5.400	-5.469	-5.518
7	36	30-38	bnlg1200	7.02	bnlg1792	7.02	7.26	11.9	-4.022	-4.082	-3.923
8	56	50-58	bnlg0666	8.05	bnlg1812	8.05	3.84	10.1	-3.734	-1.721	-5.687
8	132	128-140	dupssr14	8.09	umc01069	8.09	10.76	9.2	-3.548	-3.086	-4.189
10	30	22-40	umc01152	10.01	bnlg1079	10.03	9.85	5.2	-2.822	-2.268	-3.326
DD										Bernburg	Grucking
2	104	96-110	bnlg1831	2.06	bnlg1138	2.06	8.00	7.9	-5.178	-4.582	-5.775
3	22	18-32	bnlg1456	3.05	umc01539	3.05	14.37	18.3	6.106	7.111	5.101
3	116	98-140	bnlg0197	3.09	bnlg1257	3.09	3.30	6.8	-3.958	-4.364	-3.551
5	10	4-14	bnlg1006	5.00	MA003663	5.00	4.62	3.3	2.317	2.435	2.198
6	30	20-42	umc01006	6.02	umc1572	6.03	4.10	6.3	3.339	3.848	2.829
9	26	8-34	dupssr06	9.02	bnlg0244	9.02	3.04	1.5	-2.145n	-2.565	-1.725
9	48	44-52	phi00061	9.03	MA003415	9.03	6.48	7.9	-6.355	-5.977	-6.734
9	68	64-76	umc01357	9.05	bnlg1191	9.06	4.54	5.2	-4.041	-3.450	-4.630
10	92	86-92	bnlg1450	10.07	MA003685	10.07	5.90	11.4	-4.520	-4.376	-4.664
FF										Bernburg	Grucking
1	132	128-136	umc01972	1.06	bnlg1057	1.06	11.25	13.1	6.402	5.133	7.672
1	166	162-170	bnlg1556	1.06	bnlg1025	1.07	8.15	9.0	5.041	4.762	5.320
2	72	64-78	bnlg1138	2.06	umc01946	2.07	5.19	6.4	-3.991	-2.948	-5.035
3	58	50-68	phi00029	3.04	dupssr05	3.04	5.62	11.6	5.406	5.094	5.719
4	110	92-124	dupssr34	4.07	dupssr28	4.08	3.36	3.1	3.275	2.751	3.798
5	168	160-170	umc01822	5.05	umc01941	5.06	12.02	13.3	-5.397	-5.228	-5.565
6	64	54-70	umc01133	6.01	umc01796	6.02	3.80	5.8	3.649	3.447	3.852
8	90	88-102	bnlg1607	8.06	bnlg1065	8.06	2.82	2.6	2.519	1.946	3.093
FF × D-TC										Bernburg	Grucking
1	132	126-138	umc01972	1.06	bnlg1057	1.06	6.92	17.3	5.361	3.981	6.742
1	172	166-176	bnlg1025	1.07	umc01147	1.07	3.74	3.9	2.184	2.512	1.857

2	68	64-74	bnlg1831	2.05	bnlg1138	2.06	5.45	5.1	2.391	2.265	2.518
3	48	42-56	phi00029	3.04	dupssr05	3.04	3.01	5.4	2.869	2.551	3.188
3	76	64-84	bnlg1456	3.05	bnlg1063	3.06	5.16	2.8	2.810	2.347	3.273
7	58	48-66	bnlg2203	7.02	bnlg1022	7.02	4.02	6.3	2.957	1.946	3.967
FD										Bernburg	Grucking
1	32	24-36	bnlg1014	1.01	MA003666	1.01	6.29	8.8	3.987	4.252	3.918
1	116	112-118	MA003701	1.05	bnlg1057	1.06	5.87	9.2	6.002	5.768	6.460
2	72	62-84	MA003398	2.03	bnlg1175	2.04	5.58	8.4	4.401	4.104	4.897
3	68	66-76	phi00029	3.04	MA003693	3.04	3.16	7.1	-3.954	-3.282	-4.759
3	116	108-122	umc01674	3.06	MA003430	3.06	3.82	13.2	-5.594	-4.848	-6.518
4	6	2-8	comtghs1	4.05	bnlg1265	4.05	3.28	5.0	-3.203	-3.685	-2.931
4	46	42-52	bnlg1189	4.07	dupssr28	4.08	15.97	21.4	-7.905	-6.918	-9.095
7	20	8-24	bnlg1292	7.01	bnlg1200	7.01	3.27	3.7	2.769	3.325	2.049
7	60	58-62	umc01134	7.03	umc01251	7.04	3.76	4.5	2.981	3.221	2.670
9	54	48-66	phi00032	9.04	umc01733	9.04	9.89	10.3	4.352	3.914	4.639
9	120	106-128	bnlg0128	9.07	bnlg1129	9.08	4.04	5.6	3.485	3.371	3.373
10	108	98-114	MA003416	10.07	MA003685	10.07	4.55	6.2	3.328	3.936	2.473
DPS											
GABI										Bernburg	Grucking
1	0	0-36	phi00056	1.01	bnlg0176	1.03	4.06	3.1	-0.356	-0.391	-0.313
1	102	96-106	phi00001	1.03	umc01849	1.04	7.46	3.6	-0.515	-0.629	-0.408
1	126	122-128	bnlg2086	1.05	bnlg1884	1.05	3.22	1.3	0.303	0.536	0.074
2	44	40-52	bnlg2277	2.02	bnlg1537	2.03	6.52	3.4	-0.420	-0.428	-0.415
2	100	92-108	bnlg1329	2.06	dupssr24	2.08	17.78	13.2	0.910	1.051	0.764
3	62	56-68	bnlg1904	3.04	umc01012	3.04	4.59	11.9	-0.756	-0.840	-0.678
4	76	66-82	dupssr28	4.08	phi00093	4.08	5.55	2.6	-0.350	-0.181	-0.510
5	70	68-74	bnlg0278	5.06	bnlg0609	5.06	5.40	4.6	-0.439	-0.741	-0.139
6	132	106-138	dupssr15	6.06	bnlg1740	6.07	18.03	10.0	-0.681	-0.630	-0.732

7	38	34-44	bnlg1792	7.02	bnlg1808	7.02	3.71	5.3	-0.609	-0.716	-0.506
7	70	68-72	umc01134	7.03	bnlg2271	7.04	3.16	1.4	0.269	0.195	0.344
8	54	52-56	phi00081	8.04	bnlg0666	8.05	30.49	19.9	-1.035	-0.895	-1.166
9	22	10-34	bnlg1583	9.01	dupssr06	9.02	5.21	2.1	-0.314	-0.266	-0.362
9	144	130-144	bnlg0128	9.07	bnlg1129	9.08	6.08	3.5	0.394	0.450	0.339
10	16	0-40	phi00118	10.00	umc01152	10.01	3.18	1.7	0.338	0.322	0.348
10	52	48-62	bnlg1655	10.03	phi00035	10.06	4.78	4.2	0.514	0.590	0.446
DD										Bernburg	Grucking
2	64	52-66	umc01024	2.04	umc01448	2.04	4.44	3.5	0.426	0.228	0.596
2	130	126-134	bnlg1329	2.08	umc01108	2.08	3.98	0.6	-0.163n	-0.140	-0.155
3	20	12-38	phi00029	3.05	bnlg1456	3.05	3.51	2.5	0.336	0.254	0.435
6	106	90-132	umc01314	6.05	MA003671	6.06	3.75	3.5	0.503	0.439	0.603
8	34	32-40	bnlg1067	8.03	umc01807	8.03	3.33	6.9	-0.583	-0.591	-0.554
9	66	56-68	umc01107	9.04	umc01357	9.05	4.96	6.5	-0.560	-0.174	-0.931
10	88	82-82	bnlg1450	10.07	MA003685	10.07	3.98	2.2	-0.331*	-0.089	-0.556
FF										Bernburg	Grucking
1	192	180-206	umc01147	1.07	bnlg1331	1.10	3.85	7.2	0.839	0.883	0.795
2	46	42-60	umc01448	2.04	bnlg1018	2.04	3.95	7.8	-0.764	-0.779	-0.750
2	130	120-142	bnlg1233	2.08	bnlg1940	2.08	4.39	7.3	-0.793	-0.899	-0.688
3	46	42-56	umc01012	3.04	phi00029	3.04	3.70	5.9	0.722	0.651	0.794
3	74	64-82	bnlg1456	3.05	bnlg1063	3.06	5.68	5.2	0.750	0.576	0.923
5	96	90-100	bnlg1700	5.03	bnlg0653	5.04	15.61	21.1	1.534	1.496	1.571
6	74	66-82	umc01979	6.04	umc02006	6.04	5.26	7.6	0.744	0.573	0.915
FF × D-TC										Bernburg	Grucking
2	34	28-42	bnlg1017	2.02	umc01448	2.04	5.98	6.9	0.364	0.356	0.371
3	48	42-54	phi00029	3.04	dupssr05	3.04	5.65	10.1	0.344	0.385	0.303
3	84	76-92	bnlg1456	3.05	bnlg1063	3.06	8.25	8.2	0.364	0.111	0.618
5	0	0-8	umc01308	5.00	bnlg1006	5.00	3.56	3.2	0.168	0.101	0.237

FD											Bernburg	Grucking
1	116	110-124	MA003701	1.05	bnlg1057	1.06	13.43	10.6	0.881	0.988	0.842	
2	134	128-142	dupssr24	2.08	bnlg1520	2.09	9.74	11.7	-0.957	-0.868	-1.083	
4	14	8-22	MA003326	4.05	umc01329	4.06	7.87	8.6	-0.833	-0.726	-0.991	
4	82	68-100	dupssr28	4.08	umc01101	4.09	6.54	8.8	-0.950	-0.849	-1.003	
5	72	68-78	MA003682	5.03	MA003667	5.03	7.78	5.5	0.848	0.672	0.940	
5	96	82-108	umc01502	5.05	bnlg0278	5.06	3.00	4.9	-0.817	-0.690	-0.914	
6	2	0-10	phi00075	6.00	MA003323	6.00	3.47	4.5	-0.620	-0.560	-0.650	
6	52	30-56	coaomt1d1	6.01	umc01014	6.04	4.37	1.3	-0.499n	-0.329	-0.718	
6	68	64-92	umc01413	6.05	nc000013	6.05	3.26	4.0	-0.883	-1.052	-0.754	
8	40	30-46	c4hxxxs1	8.03	bnlg0666	8.05	7.52	10.7	0.873	0.569	1.181	
9	36	28-44	bnlg1401	9.02	MA003480	9.03	5.67	7.3	0.751	0.510	0.942	

Table S10 QTL shared between traits for both agronomic and quality traits

Traits	DMC	DMY	IVDOM	NDF	WSC	DNDF	PHT	DPS
DMC								
DMY	13							
IVDOM	11	9						
NDF	9	7	10					
WSC	13	8	8	10				
DNDF	17	11	15	8	8			
PHT	17	13	10	7	11	11		
DPS	14	16	9	5	7	13	13	