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# **Quantitative trait loci (QTL) mapping in multi-line crosses of European maize**

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<sup>1</sup>Steinhoff J, Liu W, Maurer HP, Würschum T, Longin FH, Ranc N, Reif JC (2011) Multiple-Line Cross QTL-Mapping in European Elite Maize. *Crop Sci* 51:2505-2516

<sup>2</sup>Steinhoff J, Liu W, Maurer HP, Würschum T, Longin FH, Ranc N, Reif JC (2012a) Exploitation of Elite Maize (*Zea mays* L.) Germplasm Across Maturity Zones. *Crop Sci* 52:1534-1542

<sup>3</sup>Steinhoff J, Liu W, Reif JC, Della Porta G, Ranc N, Würschum T (2012b) Detection of QTL for Flowering Time in Multiple Families of Elite Maize. *Theor Appl Genet* 125:1539-1551



## General Introduction

Maize (*Zea mays* L.) was domesticated in Central America and its adaptation to different climatic conditions was facilitated by tremendous natural variation (Camus-Kulandaivelu et al. 2006). Maize is worldwide a major staple crop for human nutrition and animal feed: 20 % of the calories produced worldwide are provided by maize (FAOSTAT 2012), which is the highest supply followed by wheat and rice. Agronomic important traits in maize breeding are grain yield, grain moisture, adaptation to climatic conditions and flowering time (Veldboom and Lee 1996; Mechin et al. 2001). Selection gain for these traits can be increased by profound knowledge of their genetic architecture. Abundance of molecular markers allows investigating the genomic regions underlying quantitative traits so called Quantitative Trait Loci (QTL) (Geldermann 1975) in detail.

### *Multiple-line cross QTL studies*

The genetic architecture of complex traits in maize has been studied using classical QTL mapping approaches (Melchinger et al. 1998; Utz et al. 2000). These are based on single segregating biparental populations and were accepted as a promising approach for crop improvement in maize (Stuber et al. 1999; Tuberosa et al. 2003). The use of single biparental populations in QTL studies is constricted due to a non-compliance of the respective germplasm (Crepieux et al. 2004). This implies a deficient applicability of single biparental populations in routine plant breeding programs.

The use of biparental populations for QTL detection shows limitations in statistical power, resolution of estimated QTL positions and a decreased transferability of QTL between populations (Mihaljevic et al. 2004). In single populations, the sample size is mostly too small and therefore QTL are not detectable due to different genetic subsets per population (Holland 2007).

These problems can be overcome by using designs based on several segregating populations (Rebai and Goffinet 1993; Muranty 1996). In these populations, the number of tested progeny is sufficiently high to overcome the problem of limited sample size. The additional advantage of multiple-line cross (MC) QTL mapping approaches is that the underlying population structure reflects the data routinely produced in applied plant breeding programs. Such routinely generated data of breeding programs can therefore be used to study the genetic architecture of complex traits.

First studies based on MC-designs have been published in maize, investigating the genetic basis of grain yield (Blanc et al. 2006), dry matter content (Blanc et al. 2006), flowering time (Blanc et al. 2006; Coles et al. 2010), and the genetics of heterosis of these traits (Lari pe et al. 2012). All the above-mentioned studies were either based on genetic resources or crosses among lines of public breeding programs. To our knowledge, no study has been published based on elite germplasm of commercial maize breeding programs yet.

Following the proposal of Reba  and Goffinet (2000), Blanc et al. (2006) suggested two biometrical models to analyze multiple-line cross QTL mapping experiments. The disconnected model assumes QTL substitution effects being specific for every single segregating population and therefore fits QTL effects as nested effects within populations. The genetic assumption underlying the connected model is that allele substitution effects are specific for every parental line. Until now, in a very limited number of studies the power to map QTL with both approaches has been empirically compared

#### *Reliability of the genetic consensus map*

The reliability of MC-QTL mapping depends on the quality of the underlying consensus map (Beavis and Grant 1991). Several experimental studies reported high colinearity between different genetic maps across different maize populations (Blanc et al. 2006; Coles et al. 2010). These

findings are in contrast to the results based on sequencing reported by Fu and Dooner (2002) who observed that genes present in the maize line B73 in several instances had no allelic counterpart in line McC. Therefore, colinearity among genetic maps has to be investigated to assess the reliability of results from multiple-line cross QTL mapping studies.

#### *Variation in allelic substitution effect*

One disadvantage of biparental QTL mapping experiments is the difficulty to transfer QTL to other populations, even when the populations have one parent in common (Mihaljevic et al. 2004). Until now, little is known about the proportion of variation caused by a QTL that is unique for a certain cross and how much of the variation is transferable across crosses. MC-QTL mapping based on diallel crosses among parents allow the analysis of this question in more detail.

#### *Epistasis*

Epistasis refers to interactions between two or more loci in the genome (Carlborg and Haley 2004) and is a popular explanation for the background dependency of QTL (Jannink and Jansen 2001). Comparing the lack of fit of the disconnected versus the connected model was suggested as a one-dimensional scan for QTL x genetic background epistasis (Jannink and Jansen 2001). Applying this test for QTL with significant main effects, Blanc et al. (2006) observed the presence of significant QTL × background epistasis for grain yield, grain moisture, and silking date in maize. For flowering time, epistatic interactions have been detected in the self-pollinating plants *Arabidopsis* and rice (El-Lithy et al. 2006; Uwatoko et al. 2008), whereas in the outbreeding species maize epistasis for flowering time appears to be less prominent (Buckler et al. 2009; Coles et al. 2010).

A constraint for the one-dimensional scan for epistasis is the fact that positive and negative epistatic effects can compensate each other (Mihaljevic et al. 2004). As a consequence one-dimensional scans for epistasis can fail to detect significant effects. Two-dimensional scans for epistasis allow exploring the interactions between single markers. Due to non-significant QTL  $\times$  background epistatic interactions of flowering time reported in literature (Coles et al. 2010), the application of two-dimensional scans for epistasis was conducted in this study.

### *Objectives*

In this thesis multiple-line cross QTL mapping was applied based on six commercial maize breeding populations based on a diallel mating design. In particular, the objectives were to

- (i) assess the reliability of the maize genetic consensus map by comparing it to its six single population linkage maps,
- (ii) exploit the benefits of a combined analysis by applying two MC-QTL mapping models and to compare the results to single-population analyses, and
- (iii) investigate the genetic architecture for grain yield, grain moisture, adaptation and flowering time in elite maize.



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## **Publication 1:**

### **Multiple-Line Cross Quantitative Trait Locus Mapping in European Elite Maize**

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**Abstract**

Multiple-line cross QTL mapping is proposed as a promising tool to detect QTL with high power and substantial accuracy. The main aim of this study was to assess the benefits of combined QTL analysis by applying two biometrical models compared to single-population analyses. For the combined QTL analysis we used a biometrical model which assumes allele substitution effects specific for every biparental population (disconnected model). Moreover, we applied a biometrical model which assumes allele substitution effects specific for every parent (connected model). Six testcross populations of maize derived from a diallel cross of four parents were tested in 10 environments for grain yield and grain moisture. The 788 genotypes were genotyped with 857 SNP markers. Our findings clearly underline the potential to improve the power to detect QTL and the resolution to localize the QTL in the genome switching from single population QTL mapping towards joint QTL analysis across populations. The disconnected model outperformed the connected model with regard to the power to detect QTL. Consequently, our results suggest that the disconnected model is the model of choice for multiple-line cross QTL mapping in elite maize germplasm.

## **Publication 2:**

### **Exploitation of elite maize (*Zea mays* L.) germplasm across maturity zones**

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**Abstract**

Transfer of elite lines across maturity zones is of crucial interest because it facilitates the exploitation of indirect selection gain. The main goal of this study was to investigate strategies to guide the transfer of elite lines from Southern Europe to the U.S. Corn Belt. Testcrosses of progenies of six biparental populations derived from a diallel cross of four Southern European elite lines were evaluated together with adapted commercial checks in 10 Southern European and six U.S. Corn Belt environments in 2007 for grain yield and grain moisture when mated to adapted testers. Moreover, the 788 genotypes were genotyped with 857 single nucleotide polymorphism (SNP) markers and multiple-line cross QTL mapping was performed. Some testcross progenies in the U.S. Corn Belt reached grain yield performance comparable to the best check, which suggests that direct use of Southern European lines is promising. The success of using grain yield or grain moisture data determined in Southern Europe to pre-select Southern European lines for use in the U.S. Corn Belt is limited. Moreover, we observed a complex genetic architecture of adaptation with absence of major QTL and strong QTL by background interactions. We found evidence that epistasis influences adaptation, additionally hampering the success of marker guided transfer of germplasm from Southern Europe to the U.S. Corn Belt.

## **Publication 3:**

### **Detection of QTL for flowering time in multiple families of elite maize**

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**Abstract**

Flowering time is a fundamental quantitative trait in maize that has played a key role in the postdomestication process and the adaptation to a wide range of climatic conditions. Flowering time has been broadly studied and recent QTL mapping results based on diverse ancestors suggest that the genetic architecture underlying this trait is mainly based on numerous minor QTL. Here, we used a population of 684 progenies from five connected families to investigate the genetic architecture of flowering time in elite maize. We used a joint analysis and identified 9 main effect QTL explaining approximately 50% of the genotypic variation of the trait. The QTL effects were small compared to the observed phenotypic variation and showed strong differences between families. We detected no epistasis with the genetic background but four digenic epistatic interactions in a full 2-dimensional genome scan. Our results suggest that flowering time in elite maize is mainly controlled by main effect QTL with rather small effects but that epistasis may also contribute to the genetic architecture of the trait.

## General Discussion

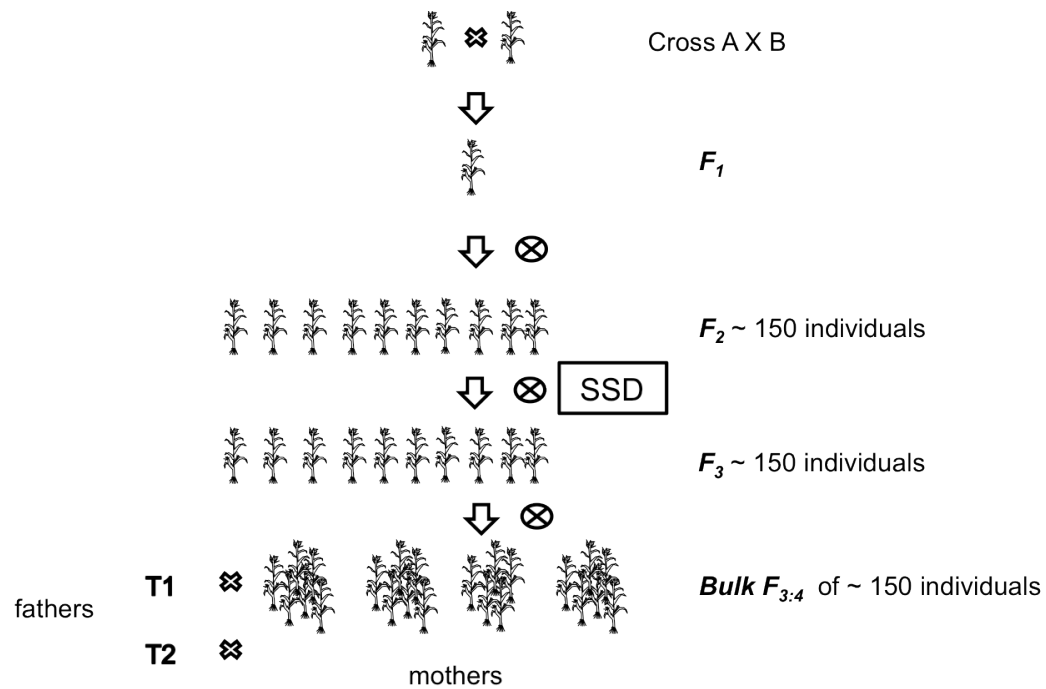
Multiple-line crosses have been proposed as a promising method for QTL detection to unravel the genetic architecture of quantitative traits in maize (Blanc et al. 2006; Coles et al. 2010). In commercial plant breeding programs, breeders generate many segregating biparental populations of elite material which are phenotyped and mostly genotyped with molecular markers. Especially in crosses of elite x elite lines, population sizes of more than 100 individuals are reached (Longin, pers. comm.). The present work was conducted within a project funded by the German Federal Ministry of Education and Research (BMBF) with the goal to use data routinely generated in breeding programs for multiple-line cross QTL mapping studies.

### *Experimental design of the study*

In the present work, six  $F_3$  populations, with a total of 788 individuals (for flowering time five  $F_3$  populations, with a total of 684 individuals) were obtained from a diallel cross between four dent inbred lines (A, B, C, and D) (Figure 1). Lines C and D were related by pedigree. This relationship also became apparent in the molecular analyses of the parental lines (Steinhoff et al. 2011). The underlying genetic pattern is typical for elite lines of the first GCA tests. The phenotyping intensity was high because it was based on field evaluation in up to ten locations. The number of locations is double as high as commonly applied in maize breeding programs at this stage of the first GCA tests.

Progenies of the six crosses were unselected with regard to their testcross-performance for the target traits. This is relevant for the MC-QTL mapping study, because even a moderate selection can reduce the QTL detection power and result in biased estimates of the QTL effects (Melchinger et al. 2012). For biparental populations, biometrical approaches have been developed to overcome the problem of selection of

unbiased estimates of QTL effects (Melchinger et al. 2012). In contrast, for MC-QTL mapping there is still a need to find a suitable way to handle this problem biometrically.

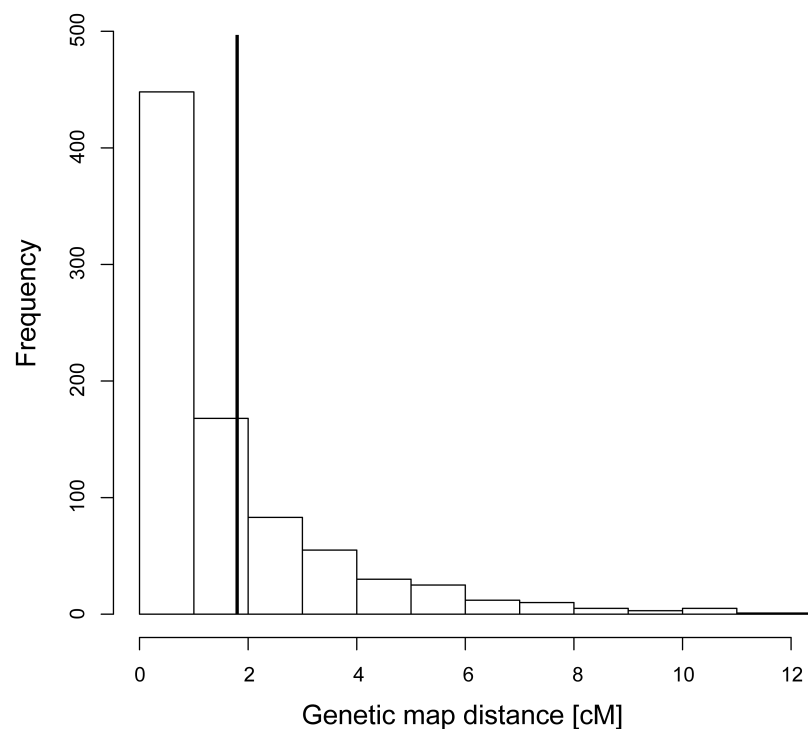


**Figure 1** Mating design of the populations under study.

The 788 individuals have been fingerprinted with a total of 857 SNP markers. In a first step, genetic linkage maps of the single populations were generated (Steinhoff et al. 2011). Afterwards, an integrated consensus map was established based on the data of the single populations. For testing the reliability of results of MC-QTL mapping studies, the colinearity between genetic linkage maps of the single biparental founder populations and the integrated consensus map was checked. In accordance with previous studies in maize reporting a high colinearity between genetic maps of single populations and the respective

consensus maps (Blanc et al. 2006; Coles et al. 2010), we detected a high colinearity between single population genetic maps and the consensus map (Steinhoff et al. 2011). This clearly indicates that QTL mapping across single populations is not hampered by a large variation of recombination frequencies across populations (Steinhoff et al. 2011).

The marker density is a crucial factor when deciding which QTL mapping strategy should be chosen (for review, see Würschum 2012). The consensus map comprised 857 polymorphic markers and had a total length of 1580 cM. The average interval length between markers was 1.84 cM (Figure 2).



**Figure 2** Histogram of the distribution of genetic map distances between adjacent markers of the consensus map and the mean distance, displayed by the vertical line.

As the four parents are related by pedigree, the application of association mapping approaches would be of interest. Dense genetic linkage maps would alternatively enable mapping strategies estimating identical by descent relationships among the parental lines (e.g. Van Eeuwijk et al. 2010; Meuwissen et al. 2001) with the potential to increase QTL detection power (Jansen et al. 2003; Jannink et al. 2009). For our data set, the observed marker density was at the lower limit and, consequently, association mapping and identical by descent approaches have not been applied in this thesis.

For linkage mapping approaches, the required marker density is substantially lower compared to that of association mapping. Results of theoretical studies suggested that the power of QTL detection for linkage mapping does not considerably increase if the distance between adjacent markers decreases below 10 cM (Davarsi 1993; Piepho 2000). For the six populations used in the underlying study, more than 90 % of the genetic map distances between adjacent polymorphic markers were smaller than 10 cM. This fact suggests that marker density is no major limiting factor for QTL detection applying linkage mapping approaches. Nevertheless, for some of the six populations we also observed few large gaps of up to 30 cM (Steinhoff et al. 2011). These, however, may rather point to identity by descent than to a too low number of markers. Consequently, owing to the marker density underlying this study, we applied linkage mapping approaches, in which we assumed that the parents are unrelated.

#### *Choice of a biometrical approach for MC-QTL*

Several biometrical models have been suggested for MC-QTL mapping. They can be grouped into fixed and random allele effect models (for review see Jannink and Wu 2003). Random allele effect models are very powerful for a large number of segregating families, because the number of QTL parameter is independent of the number of families (Wu and Jannink 2004). In contrast, power of QTL detection is higher for fixed

compared to random allele effect models if the number of segregating families is low (Xu 1998). Therefore, two alternative fixed allele effect models described in detail by Blanc et al. (2006) were used in our studies.

For the disconnected model, QTL allele substitution effects are assumed to be specific for every single segregating population (Blanc et al. 2006). This model is equivalent to the full model introduced by Jannink and Jansen (2001). In the connected model, allele substitution effects are assumed to be specific for every parental line (Blanc et al. 2006). For the diallel mating design, this assumption leads to a higher number of degrees of freedom for QTL detection based on the connected model in comparison to the disconnected model.

Blanc et al. (2006) compared the disconnected and the connected model empirically. They found that the connected model led to a substantial increased QTL detection power owing to a reduced number of estimated allele substitution effects. In contrast, we observed uniformly across traits that the disconnected model outperformed the connected model in terms of number of QTL and confidence intervals (Steinhoff et al. 2011; 2012a). This superiority of the disconnected versus the connected model can be explained by high background dependencies of QTL effects (Steinhoff et al. 2011).

The use of a diallel mating design facilitates a one-dimensional scan for epistasis. In this test, described in detail by Blanc et al. (2006), a model with QTL as defined in the disconnected analysis and cofactors as defined in the connected analysis, and a model with QTL and cofactors as defined in the connected analysis are compared to each other. A first version of this test was described in a theoretical study by Jannink and Jansen (2001). The one-dimensional scan does not detect epistatic effects if negative and positive effects cancel each other out (Mihaljevic et al. 2004). Therefore, the disconnected model was extended and a full two-dimensional test for epistasis was applied.

*Genetic architecture of grain yield*

For grain yield, seven QTL explaining a total of 43.6 % of the genotypic variance were detected using the disconnected model (Steinhoff et al. 2011). None of these QTL was a major QTL explaining more than 10 % of the genotypic variation of the trait. This finding is in accordance with results of Huang et al. (2010), who reported only small effect QTL contributing to grain yield. Applying cross-validation revealed that only 10% of the variance can be reliably explained for grain yield based on the QTL detected in the MC-QTL mapping approach (Liu et al. 2012). Using a genomic selection approach as applied in a companion study shows that the inheritance of grain yield is closer to the infinity model (Zhao et al. 2011). Therefore, grain yield cannot appropriately be tackled with conventional QTL mapping approaches.

One- and two-dimensional tests for epistasis did not reveal any significant interaction. The results show, however, that peaks are very close to the significance threshold and in some of these cases, the peaks occurred in the same regions where main QTL had been detected. In addition, the modified diallel analysis based on estimated QTL effects within populations revealed a strong dependency on the genetic background (Steinhoff et al. 2011). Consequently, epistasis as one explanation of this background dependency cannot be ruled out for grain yield.

*Genetic architecture of grain moisture*

For grain moisture, nine QTL explaining a total of 63.2 % of the genotypic variance were found by applying the MC-QTL approach (Steinhoff et al. 2011). The result is comparable to that of grain yield, showing no major QTL for this trait in the adapted environments (Steinhoff et al. 2012a). After a cross-validation step, the explained genotypic variance of the trait dropped down to 15 % (Liu et al. 2012). In accordance with grain yield, one- and two-dimensional scans suggested that epistasis plays only a

minor role. The small QTL x background interaction, however, can be interpreted as an indicator for presence of epistasis.

#### *Genetic architecture of adaptation*

The immediate use of non-adapted inbred lines without selection, serving as parents in hybrid combinations with adapted lines, is a promising strategy to exploit the genetic diversity of elite breeding pools (Hallauer and Miranda 1988). Although phenotypic correlations revealed a low association between the European and US-Cornbelt maturity zone, some testcrosses reached the yield level of the best check (Steinhoff et al. 2012a). Due to the low correlations between genotypic values determined in the European and US-Cornbelt maturity zone, we investigated whether adaptation is influenced by major QTL (Steinhoff et al. 2012a). Adaptation was also not influenced by major QTL and, thus, marker-assisted transfer of germplasm across maturity zones is not feasible.

#### *Genetic architecture of flowering time*

A previous study in maize showed that flowering time is a complex trait with no major QTL being expected (Buckler et al. 2009). In the underlying study, nine QTL were identified using the disconnected model, explaining 48.4% of the genotypic variation of the trait in total (Steinhoff et al. 2012b). In accordance to Buckler et al. (2009), it has been shown that flowering time is inherited rather by several QTL with minor effects than by a few major QTL.

Interestingly, our QTL study indicate a significant impact of digenic epistasis on female flowering time (Steinhoff et al. 2012b), which is divergent to Buckler et al. (2009) who reported no or little impact of epistasis on the trait. This discrepancy can be explained by the difference in the genetic material in the studies. As Buckler et al. (2009) reported their



results on the basis of a diverse panel of maize, there is evidence that in elite maize, epistatic interactions may have been conserved.

### *Conclusions and outlook*

The results of this thesis showed that grain yield, grain moisture, adaptation to different climatic zones and flowering time have a complex genetic architecture with an absence of major QTL. As a consequence, the application of marker assisted selection is not promising and more appropriated strategies such as genomic selection should be applied. The joint analyses across populations result in higher QTL detection power and resolution compared to single population analyses. Consequently, the tested QTL mapping approaches are well suited to identify diagnostic markers for more simply inherited traits such as southern corn leaf blight (Negeri et al. 2011). Nevertheless, conducting joint analyses, the reliability of the results should be validated by a cross validation process.

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## Summary

Multiple-line crosses (MC) have been proposed as promising mapping resource for quantitative trait loci (QTL) detection for agronomic important traits. In contrast to mapping populations derived from a single biparental population, MC can increase the statistical power of QTL detection, the accuracy of QTL location and of QTL effect estimates. Additionally, MC-QTL mapping has the advantage of using data routinely collected in plant breeding programs.

The objectives of this study were to (i) assess the reliability of the maize genetic consensus map by comparing it to its six single population linkage maps, (ii) exploit the benefits of a combined analysis by applying two MC-QTL mapping models and to compare the results to single-population analyses, and (iii) investigate the genetic architecture of grain yield, grain moisture, adaptation, and flowering time in elite maize.

The experiment comprised six populations with 109 to 150 individuals, resulting from crosses of elite maize breeding material. The germplasm was provided by Syngenta Seeds, Bad Salzflen, Germany. The 788 genotypes were genotyped with 857 SNP markers. After constructing genetic linkage maps of the six single populations, the genotypic information of the single populations was integrated in a consensus map and its reliability was tested for QTL studies. The average distance between adjacent markers was 1.84 cM suggesting that the marker density is not a limiting factor for QTL analyses. Moreover, we observed medium to high heritabilities for all traits. Consequently, the quality of both genotypic and phenotypic data should allow QTL detection with substantial power.

We applied two different MC-QTL mapping models on the data assuming fixed allele effects. The disconnected model estimates QTL effects nested within populations, whereas the connected model takes into account the relationship between the populations. Both models outperformed the single population analyses with regard to QTL detection

rate, variance explained by the detected QTL, and the size of the confidence intervals. In all analyses, the disconnected model outperformed the connected model in terms of number of QTL and size of confidence intervals. This superiority seems to be caused by the high background dependencies of QTL effects in connected crosses, which was revealed by a modified diallel analysis of the QTL effects.

We investigated the genetic architecture of grain yield, grain moisture, adaptation to maturity zones, and flowering time. Our findings suggest that all traits exhibit a complex genetic architecture with an absence of large QTL effects. Some of the studied traits appear to be influenced by epistasis, interactions between loci. In particular, for flowering time, the two-dimensional scan for epistatic interactions suggested the presence of digenic epistasis.

The absence of QTL with large effects suggests that marker-assisted selection is not an appropriate tool to breed for adapted maize hybrids with improved grain yield. Consequently, more suitable approaches for complex traits such as genomic selection should be applied. The joint analyses across populations resulted in higher QTL detection power and resolution compared to single population analyses. Thus, for traits with a less complex genetic architecture, MC-QTL mapping is a powerful tool for the identification of robust diagnostic markers.

## Zusammenfassung

Mehrlinien-Kreuzungen (MK) wurden in der Literatur als vielversprechende Ausgangspopulation zur Kartierung von *quantitative trait loci* (QTL) für agronomisch wichtige Merkmale vorgeschlagen. Im Unterschied zu Kartierungspopulationen, die auf einzelne biparentale Populationen zurückgehen, lässt sich durch die Verwendung von MK die statistische Güte der QTL-Detektion erhöhen, sowie die Lage der QTL und deren Effektgröße präziser bestimmen. Zusätzlich ist es möglich, die in Pflanzenzüchtungsprogrammen routinemäßig gesammelten Daten zu verwenden.

Die Ziele der vorliegenden Arbeit waren (i) die Verlässlichkeit der integrierten genetischen Karte im Vergleich zu den sechs genetischen Kopplungskarten der Einzelpopulationen einzuschätzen, (ii) die Vorteile der kombinierten QTL-Analyse durch die Anwendung von zwei MK-QTL Kartierungs-Modellen, auch im Vergleich der Ergebnisse mit der Einzelpopulationsanalyse, zu analysieren und (iii) die genetische Architektur der Merkmale Kornertrag, Kornfeuchte, klimatische Anpassung und Blühzeitpunkt zu untersuchen.

Der Versuch bestand aus sechs Populationen mit jeweiligen Größen zwischen 109 und 150 Individuen. Das genetische Material entstammt einem Mais-Elitepool, den die Firma Syngenta in Bad Salzuflen bereitstellte. Die 788 Genotypen wurden mit 857 SNP Markern genotypisiert und anhand dieser Ergebnisse wurde für jede Population eine genetische Karte berechnet. Auf den genetischen Informationen der Einzelpopulationen basierend wurde eine genetische Konsensuskarte erstellt und deren Güte für die Verwendung in der QTL Studie getestet. Die durchschnittliche Entfernung zwischen benachbarten Markern betrug 1.84 cM. Diese Markerdichte ist ausreichend und stellt keinen limitierenden Faktor für die QTL-Analyse dar. Die berechneten Heritabilitäten wurden für alle Merkmale als mittel bis hoch geschätzt. Demzufolge sollte die Qualität der genotypischen sowie der



phänotypischen Daten eine QTL-Analyse von ausreichender statistischer Güte erlauben.

Es wurden zwei verschiedene Kartierungs-Modelle mit fixen Alleleffekten verwendet. Während im nicht-verbundenen Modell QTL-Effekte hierarchisch für jede spaltende Population angepasst werden, werden im verbundenen Modell die Beziehungen zwischen den Populationen berücksichtigt. In Bezug auf die QTL Detektionsrate, die durch den QTL erklärte Varianz und die Größe der Vertrauensintervalle zeigten beide Modelle bessere Ergebnisse im Vergleich zu den Analysen der Einzelpopulationen. Im direkten Vergleich zwischen beiden Modellen erzielte das nicht-verbundene Modell im Bezug auf die QTL Detektionsrate und die Größe der Vertrauensintervalle die besten Ergebnisse. Die bessere Leistung des nicht-verbundenen Modells kann durch die hohe Abhängigkeit der QTL vom genetischen Hintergrund erklärt werden. Dies wurde in einer veränderten Diallel-Analyse der QTL-Effekte offensichtlich.

In der vorliegenden Studie wurde die genetische Architektur der Merkmale Kornertrag, Kornfeuchte, Anpassung an Reifezonen und Blühzeitpunkt analysiert. Unsere Ergebnisse zeigen, dass alle der untersuchten Merkmale eine sehr komplexe genetische Struktur aufweisen. Bei keinem der Merkmale konnte ein großer QTL-Effekt detektiert werden. Einige Merkmale scheinen von Epistasie, der Interaktion zwischen Loci, beeinflusst zu sein. Insbesondere für den Blühzeitpunkt deuten die Ergebnisse des zwei-dimensionalen Epistasie-Tests auf signifikante digenische Interaktionen hin.

Das Fehlen von QTL mit großen Effekten weist darauf hin, dass die marker-gestützte Selektion für die Züchtung von angepassten Maishybriden mit verbessertem Kornertrag kein geeigneter Ansatz ist. Für komplexe Merkmale sollten folglich passendere Ansätze wie die genomische Selektion benutzt werden. Im Vergleich zur Analyse der Einzelpopulationen erzielte die verbundene Analyse über Populationen hinweg eine höhere Güte, QTL aufzufinden und eine präzisere

Lagebestimmung der QTL. Demnach ist die MK-QTL Kartierung ein leistungsfähiges Werkzeug für die Entwicklung robuster diagnostischer Marker bei Merkmalen mit einer einfachen genetischen Architektur.

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## **Erklärung**

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Stuttgart, im Oktober 2012

Jana Steinhoff