DASHE DENTSEN FORTUNE

GENOME-WIDE ASSOCIATION STUDIES FOR MAIZE YIELD AT THREE CONTRASTING SITES

Dissertation submitted to the Genetics and Breeding Graduate Program of the Universidade Federal de Viçosa in partial fulfillment of the requirements for the degree of *Magister Scientiae*.

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Adviser

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Viçosa, 2023.

ABSTRACT

Dashe, Dentsen Fortune, Universidade Federal de Viçosa, 2023. **Genome-wide Association studies for maize yield at three contrasting sites**. Adviser: Luiz Alexandre Peternelli. Co-adviser: Andréa Carla Bastos Andrade.

In the present study, genome-wide association study (GWAS) was used to identify marker association in three different environments. The study analyzed the 2018 maize dataset from the genome-2-field (G2F) initiative for yield trait marker association using three bi-parental populations and a total of 936 hybrid individuals. The GWAS analysis was performed by implementing two models: generalized linear model (GLM) (population structure (Q) accounted for), and mixed linear model (MLM) (population structure (Q) and kinship (K) accounted for), in order to minimize spurious associations and control for types I and II error rates. A total of 791 significantly associated SNPs were detected for the yield trait ($p>0.0001$) but overlaps in SNPs were identified from the different models in each site and thereafter, a total of 39 unique loci overlapped from the 791 loci from both models in all three sites were noted, out of which 25 loci were located on chromosome 1, 1 on chromosome 3, 6 on chromosome 7 and 7 on chromosome 8. The presence of these unique loci across the two models and three diverse environments suggests their robustness and potential relevance and warrants further investigation into the specific genetic factors and molecular mechanisms underlying their association with maize yield across varying growing conditions. Therefore further validation study and fine mapping of these loci will provide valuable information for understanding the genetic and environmental components of grain yield in maize.

Keywords: GWAS. *Zea mays*. Principal components. MLM. GLM.

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LIST OF ACRONYMS AND ABBREVIATIONS

Genome-wide association studies (GWAS)
genome-2-field initiative (g2f)
generalized linear model (GLM)
mixed linear model (MLM)
Single nucleotide polymorphism (SNP)
Principal Component Analysis (PC)
Population structure (Q)
Kinship (K)
Memory-efficient, Visualization-enhanced, and Parallel-accelerated tool in R (rMVP)

SUMMARY

1. INTRODUCTION

Plant breeding is one of man's most prolonged continuous activities with a progressive contribution (Lee, Joohyun, et al., 2015). The general concept involves human activities in selecting plants with more productive and desirable characteristics (Lee, Joohyun, et al., 2015). Modern breeding has improved with the advent of genetic markers. Breeding tools such as Marker-assisted Selection (MAS), Genomic selection (GS), Genome-wide association studies (GWAS), and quantitative trait loci (QTL) have played a significant role in enabling the great leap and results experienced from breeding programs (Lamichhane and Sapana, 2022; Lee, Joohyun, et al., 2015).

GWAS and GS are potent tools that exploit DNA sequence polymorphisms to improve breeding by predicting breeding values using markers distributed across the whole genome (Xiao et al., 2017). These tools take advantage of the advances in sequencing and genotyping technologies. They exploit the relationship between the genotypic and phenotypic data/information available on a particular population and trait of interest (Uffelmann et al., 2021). GWAS analysis tests hundreds of thousands of genetic variants across several genomes to find those variants statistically associated with a specific trait or disease. Generally, GWAS aims to identify associations of genotypes with phenotypes by assessing differences in the allele frequency of genetic variants between individuals with similar ancestry but are different phenotypically (Uffelmann et al., 2021).

GWAS and other molecular breeding methodologies owe their success to the advances in molecular markers and sequencing technologies (Zargar et al., 2015). GWAS was first developed and applied in human studies and has significantly contributed to understanding thousands of genetic variants that have significant associations with diseases (Bush and Jason, 2012). GWAS relies on linkage disequilibrium (LD) between markers under testing and functional polymorphisms of causative genes (Korte and Ashley, 2013). The idea behind GWAS is that genetic variants physically close to each other on a chromosome are more likely to be inherited together (Tibbs et al., 2021; Gupta et al., 2019; Bush and Jason, 2012). Thus, single nucleotide polymorphisms (SNPs) near the causative locus can be in high LD with the functional polymorphisms, and therein, an association can be assumed with the phenotype of interest. GWAS methodologies, therefore, detect the associations and mark up the regions where these significant SNPs have been detected, and the gene implicated can be observed (Tibbs et al., 2021; Gupta et al., 2019; Bush and Jason, 2012).

GWAS study uses statistical methods to establish an association between markers and observed phenotypes. Statistical tests such as ANOVA can be used in a naïve approach on each SNP individually to detect association (Marees et al., 2018). A significant challenge of using such a simple naïve approach and any naïve method for GWAS is the possibility of generating a high rate of false positives as the number of markers increases (Bush and Jason, 2012). To overcome this, a standard method used is by limiting the proportion of all positive results that are expected to be false positives (limiting the false discovery rate FDR) or by using Bonferroni correction (Gao et al., 2010; Gupta et al., 2019; Bush and Jason, 2012). Another major contributor to false positives in GWAS is the relatedness among individuals where SNPs that are more common in a given subpopulation would be observed to show spurious association with the phenotype of interest, mainly if that phenotype is observed at a higher frequency within that subpopulation (Thomson, Russell and Rebekah McWhirter, 2017; Korte and Ashley, 2013).

Several methods have been developed to overcome these challenges for improving computational speed and memory efficiency, including statistical power (Eu-Ahsunthornwattana et al., 2014). Some examples of these methods are mixed linear model (MLM), generalized linear model (GLM), compressed mixed linear model (CMLM) (Zhang et al., 2010), enriched compressed mixed linear model (ECMLM) (Li et al., 2014), efficient mixed-model association (EMMA) (Kang et al., 2008), efficient mixed-model association expedited (EMMAX) (Kang et al. 2010), factored spectrally transformed linear mixed models (FaST-LMM) (Lippert et al., 2011), and genome-wide efficient mixed model analysis (GEMMA) (Zhou and Matthew, 2012).

The Mixed linear model (MLM) is one of the models that handle spurious associations arising from population structure. The unified mixed-model approach developed by Yu Jianming et al. (2006) accounted for multiple levels of relatedness simultaneously using the information provided by the random genetic markers. The mixed linear model displays control for types I and II error rates and is flexible in handling family-based samples and/or samples with familial relationships within a structured population. MLM uses a relative kinship matrix derived from marker data to account for co-ancestry effects, which overcomes the problems of incomplete pedigree data or bias arising from breeding studies. To account for the multiple relatednesses within a population, the population structure (Q) and relative kinship (K) are both fit into the model (Wang et al., 2014).

The generalized linear model (GLM) usually uses the principal components analysis to model ancestry differences explicitly (Schein et al., 2003). This model also efficiently minimizes spurious associations from population stratification (Pritchard et al., 2000). The correction implemented in this model is specific to a candidate marker's variation in frequency across ancestry populations on a genome-wide scale, increasing the detection of genuine associations (Pritchard et al., 2000). GLMs are commonly used in GWAS to test the association between genetic variants and complex traits (Tibbs et al., 2021). GLMs are a generalization of the linear regression model, allowing for non-normal error distributions and non-constant variance (Guisan et al. 2002). GLMs can analyze continuous and binary traits (Zhang and Lei, 2023).

Maize is one of the most important cereal crops worldwide (Tagne et al., 2008). Understanding its yield's genetic basis can help breeders develop new varieties with improved potential, which can increase food production and help address food insecurity. GWAS has been widely applied in maize breeding due to the genetic variability, distinct population, and availability of marker information from maize studies (Shikha et al., 2021). Several yield-related traits have been studied in maize because the genetic basis of such traits has been identified. Zhang et al. (2020) used a combination of linkage mapping and GWAS to provide an understanding of some of the genetic basis of yield-related traits in maize across multiple environments. The study identified several QTLs and SNPs that control yield-related traits in maize. Related GWAS studies for plant height (Zhang et al., 2019), kernel row numbers (An et al., 2020), yield, plant height, and silking (Malvar et al., 2018), among others, have equally enhanced the understanding of the genetic basis of maize yield which paved the way for improvement in maize variety improvement and breeding.

Improvement in crop varieties is always aided by results from continuous studies arising from improved breeding techniques and methodologies. The major challenge is identifying and organizing those underlying genetic mechanisms of crop traits for improvement. GWAS is an appropriate tool for unraveling the genetic bases of complex agronomic traits. The GWAS tool would identify potential locations associated with the yield trait under study. To understand how different environments affect the performance of the maize variety, a study of the association between the trait under study and molecular markers in a multi-environment trial is essential. Therefore, a genome-wide association study on maize yield from the genome-to-field initiative multi-site data can provide valuable insights into the genetic basis of maize yield. Therefore, this study aims to explore the effect of different environments on maize yield using Genome-Wide Association studies (GWAS) tool by identifying markers associated with maize yield in multi-site trials.

2. MATERIAL AND METHODS

2.1 Maize dataset description

The dataset contains results from phenotypic evaluations of multi-location field trials and genotypic evaluation using practical haplotype graphs of multiple maize populations. Field-level weather and soil data for the multiple locations where field testing was conducted were also included. Collaborators collected data in the Genomes to Fields (G2F) initiative (https://www.genomes2fields.org/home/). The dataset used for this analysis is from the 2018 planting season, which utilized genetic materials with a relatively narrow maturity window across all locations. This reduced the impact on flowering time, giving more uniform data and simplifying plot management for collaborators. Traits evaluated in the 2018 dataset included stand count, stalk lodging, root lodging, days to anthesis, days to silking, plot weight, plant height, ear height, ear height, grain yield, and grain moisture.

The plant material and phenotypic datasets were described in more detail in previous publications (AlKhalifah et al., 2018; McFarland et al., 2020; Lima et al., 2023) and on the project website (https://www.genomes2fields.org/home/).

2.1.1. Phenotypic data

The phenotypic dataset is the product of an extensive collection of trials from different collaborator institutions. Thirty fields located on the North American continent were used for the 2018 planting season. The experimental design for the hybrid trials was a randomized complete block design with two replications per environment. PHW65 was used as the reference design population, which includes double haploids derived from PHW65-PHN11, PHW65-Mo44, and PHW65-MoG families. For phenotypic pre-processing, environments with critical missing information were eliminated, and the dataset was further filtered to include only the three families (Mo44, PHN11, and MoG) with a common parent, PHW65. Of the 19,608 individuals recorded in the planting season, after filtering, 12,591 individuals were retained, with the Mo44 family having 3,876 individuals, PHN11 having 5996 individuals, and MoG having 2,719 individuals. From this population, three locations selected based on extreme weather correlations were analyzed separately for association analysis of each hybrid in each environment for grain yield.

2.1.2. Genotypic data

The 2018-2019 dataset contains filtered genomic data, which was processed following a GBS procedure reported by Gage et al. (2017). Filtered genotype-by-sequencing (GBS) data of inbred lines used in Genomes to Fields hybrid experiments were downloaded from CyVerse (https://datacommons.cyverse.org/browse/iplant/home/shared/commons_repo/curated/GenomesToFields_G2F_Data_2018). The dataset consisted of 312 individuals genotyped at 1.3 million SNPs. According to the supplementary material of the G2F genomic data, the G2F genomic materials were genotyped using the Practical Haplotype Graph.

The GBS procedure implemented by the G2F project was previously reported and published by (Gage et al., 2017). Briefly, samples that had >2% mismatch to their corresponding GBS calls were removed, but the only exceptions were the parental lines: Mo44, MoG, PHW65, PHT69, and LH195, which were included regardless of how well their PHG SNP calls matched GBS SNPs. SNPs were filtered by removing monomorphic markers ('--maf 0.000001' in vcftools) and markers missing calls in all samples ('--max-missing 0.000001' in vcftools), resulting in a final dataset of 312 individuals genotyped at 1.3 million SNPs. This final dataset was downloaded from the Cyverse site and used for this analysis.

2.2. Statistical analysis

2.2.1. About the locations

The choice of locations to include for this study was possible after evaluating the available weather data by performing the multivariate exploratory technique of principal components (PC). Three sites were selected based on a more significant divergence among weather variables (soil temperature, temperature, dew point, solar radiation, photoperiod, soil moisture, and rainfall).

2.2.2. Models used for GWAS analysis

To determine the potential association between SNPs and phenotypic variants, we carried out statistical analysis for the yield trait with each SNP across the maize genome for each site. For the association test, the generalized linear model (GLM) accounting for population structure (Q) and the mixed linear model (MLM) accounting for population structure (Q) and kinship matrix (k) were implemented. Therefore, GLM and MLM were implemented for each site analyzed.

A kinship matrix was included in the analysis to account for familial relatedness. For all models used, we included the first three principal components (PC) derived from the PC analysis of the SNP data. The PC values were treated as fixed covariates in these models and were used to adjust for population structure. From the results for each model in each site, we generated Manhattan plots (MP) of the observed versus the expected p-values at each SNP.

Generalized Linear Model (GLM)

The basic model equation for a GLM in GWAS is

$$g(E(y)) = X\beta + Z\gamma + e$$

Where $g(.)$ is a link function, which relates the expected value of the trait $(E(y))$ to the linear predictor $X\beta + Z\gamma$. X is a design matrix associated with the fixed effects, including genetic variants of interest and covariates. β is a vector of coefficients associated with the predictor variables in the design matrix. These coefficients represent the effect of each predictor on the response variable. Z is a design matrix for random effects, accounting for the population structure based on relatedness among individuals (or kinship matrix). γ is a vector of coefficients associated with the predictor variable in Z. e is a vector of residual errors. The choice of the link function depends on the nature of the trait being analyzed. In the case of yield evaluated here, the link function was an identity link function.

Mixed Linear Model (MLM)

The mixed model equation incorporating both the population structure and kinship matrix method is expressed as

$$y = X\beta + S\alpha + Qv + Z\mu + e$$

Where y is a vector of phenotypic observations; β represents the fixed effects other than the SNP under testing and the population structure; β is a vector of fixed effects other than SNP or population group effects; α is a vector of SNP effects; v is a vector of population fixed effects; μ is a vector of polygenic background effects; e is a vector of residual effects; Q is a matrix relating y to v; and X, S, and Z are incidence matrices of 1s and 0s relating y to β, α and μ respectively.

2.2.3. Computational resources

All the analyses were carried out within the R environment (Team, R. 2022), using the packages: 'stats' (Team, R. 2022), 'factoextra' (Kassambara and Mundt, 2020), and 'rMVP' (Yin, Lilin, et al., 2021).

3. RESULTS

3.1. Phenotypic data analysis

The means of each of the seven weather variables (soil temperature, temperature, dew point, solar radiation, photoperiod, soil moisture, and rainfall) were analyzed to evaluate the variations among the different sites selected for the study. These variables were analyzed using principal coordinate analysis (PCoA). The first two PCs were selected from the analysis, explaining 76.4% of the variance. The first PC (Dim1) is strongly negatively associated with soil temperature, temperature, dew point, and solar radiation. In contrast, the second PC (Dim2) strongly correlates positively with photoperiod and rainfall (Table 1).

Table 1. PC results for weather variables.

Weather variable	Dim1	Dim2
Soil temperature	**-0.5046374**	-0.2330772
Temperature	**-0.4598559**	0.3400268
Dew point	**-0.4472682**	0.3407735
Solar radiation	**-0.3796722**	-0.3556440
Photoperiod	-0.3032594	**0.4437022**
Soil moisture	0.1022570	0.3278176
Rainfall	0.2953830	**0.5320822**

The sites NYH2 and IAH3 show specific properties concerning the evaluated variables (Tables 2 and 3), especially for variables with strong associations in each PC. In the evaluated agricultural season, these sites had a lower average temperature, low dew point, and soil temperature. IAH3 differs from NYH2 due to its lower incidence of solar radiation, higher rainfall, and, consequently, higher soil moisture. In this same season, GAH2 presented higher average temperature, dew point, soil temperature, and solar radiation, with low rainfall and higher soil moisture. Although this site presents different climatic characteristics from the other selected sites, it presents similarities with most other sites evaluated in the PC. The photoperiod was shorter in all sites (IAH3, NYH2, and GAH2) compared to all evaluated sites in the entire dataset.

The yield trait from the three sites showed abundant phenotypic variations and an approximate normal distribution (Figure 2), indicating that the trait is a quantitative trait controlled by multiple genes (Zeng et al., 2022). Shapiro-Wilk test of normality was conducted to determine if the yield was normally distributed. From the output, GAH2 (p=0.1245), IAH3 (p=0.08115), and NYH3 (p=0.2919), the data are not significantly different from a normal distribution, and therefore we can assume the normality in the yield data from the three sites.

Table 2. Means environmental variables for the selected sites.

Site	GAH2	IAH3	NYH2
STATE	Georgia	Wisconsin	New York
TEMP (°C)	25.34	20.44	15.4
DP (°C)	19.83	15.49	9.36
SR (W/m^2)	254.16	14.71	170.29
RAIN (mm)	0.05	186.29	0.04
ST (°C)	28.08	4.51	16.92
SM (%VWC)	51.44	66.66	13.49
PHOTO (hr)	13.83	13.95	12.89

temperature (TEMP), dew point (DP), solar radiation (SR), rainfall (RAIN), soil temperature (ST), soil moisture (SM), and photoperiod (PHOTO)

Table 3. PC results for all sites.

SITE	PC1	PC2	SITE	PC1	PC2
IAH3	**4.616285**	**5.23102**	ARH1	-0.35002	0.190131
NYH2	**3.116513**	**-2.67125**	WIH1	-0.35662	-1.12757
NYH3	2.26837	-1.54318	OHH1	-0.55165	0.30768
MNH1	2.070811	-1.06291	NEH2	-0.87889	0.764219
NYH1	1.3138	-0.98529	DEH1	-0.97241	0.624546
ONH2	1.254893	-1.66052	ILH1	-1.3568	0.645998
IAH2	0.988758	0.091855	ARH2	-1.47757	0.213282
WIH2	0.564543	-1.26739	INH1	-1.69311	0.940958
IAH4	0.550662	-0.19256	MOH1	-1.8962	0.345094
TXH1	0.107006	-0.31573	GAH1	-1.99937	0.033189
TXH2	-0.18498	1.187585	NCH1	-2.31364	-0.01771
IAH1	-0.32332	-0.23491	**GAH2**	**-2.49707**	**0.503458**

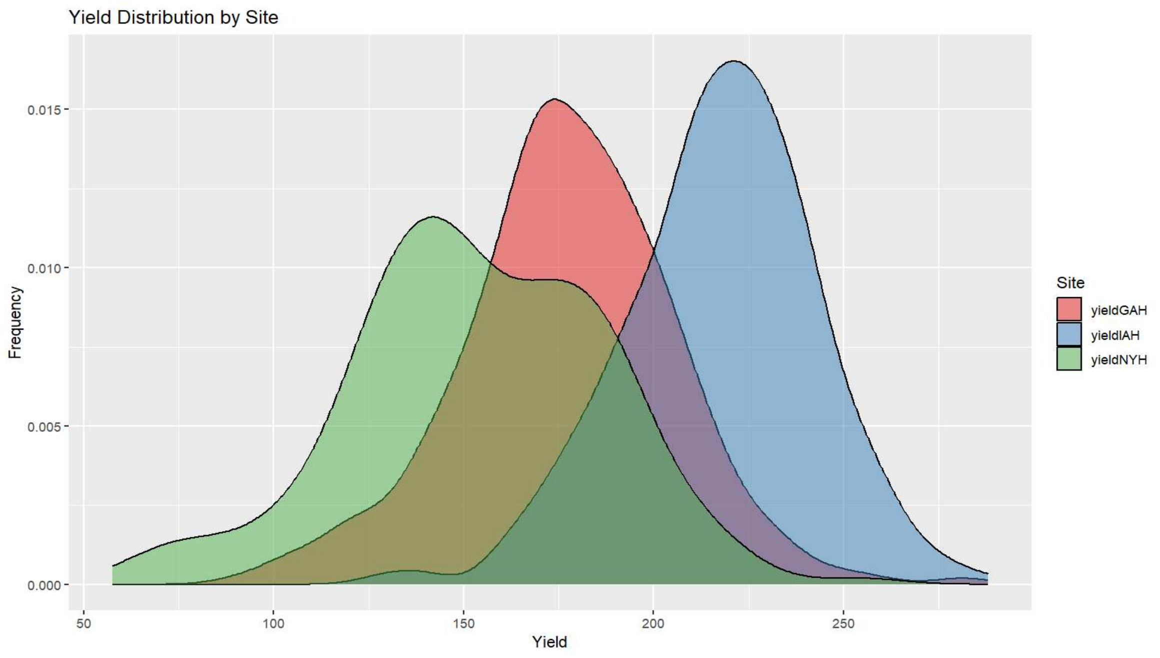

Figure 1. Phenotypic variation and distribution of yield trait for sites GAH2, IAH3, and NYH2.

3.2. Population structure assessment

The population structure of the 312 maize samples was estimated by PC analysis using the 1,353,525 SNPs. Distinct subpopulations matching the three families (MO44 x PHW65, PHN11 x PHW65, and PHW65 x MOG) were noted with the SNP density plotted on a 1MB window size (Figure 3).

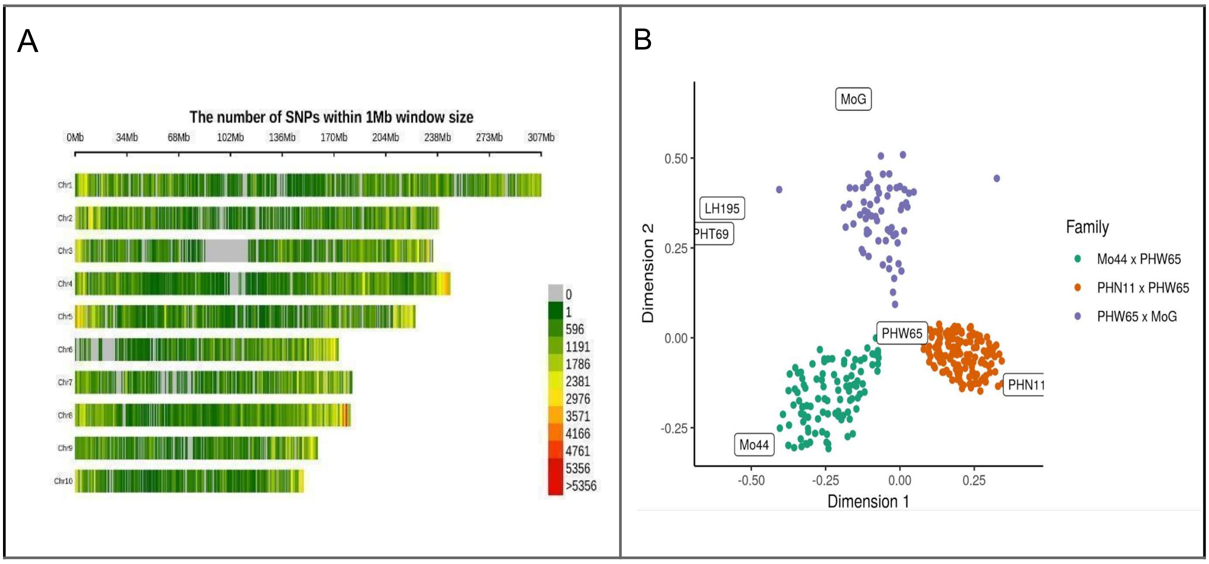

Figure 2. PC analysis of SNP data. A. Marker density. B. Population structure in two dimensions of the three sub-populations.

3.3. Genome-wide marker-trait associations

The association results (p-values of the marker-trait association in a Manhattan plot) are shown in Figures 3, 4, and 5 for the sites GAH2, IAH3, and NYH2, respectively. In total, 1,353,525 SNPs were used to perform GWAS for the yield trait from the three sites.

It was too strict to discover the significant sites when setting the threshold P-value for associated SNPs as 1/n (n being the number of SNP makers) or 0.05/n. Therefore, a threshold P-value of 1.00e04 was used for the three sites. Regarding the results, with the p-value threshold of 1.00e-04, we observed 39 significantly associated SNPs for the yield trait using the MLM method across all three sites (GAH2, IAH3, and NYH2) and 791 significantly associated SNPs for the GLM method for all three sites (GAH2, IAH3, and NYH2) (Figure 3, 4, 5 and Table S1). For all three site observations, based on the two models (MLM and GLM) in each site, there were overlaps of significant SNPs, where the SNPs identified were the same. The MLM model identified fewer SNPs than the GLM model. Of the 39 SNPs identified in the MLM model, 25 unique loci were found on chromosome 1, 1 unique loci on chromosome 3, 6 unique loci on chromosome 7, and 7 unique loci on chromosome 8. For the GLM model, 791 unique loci were identified to be associated with the yield trait from all three sites, where 265 unique loci were identified on chromosome 1, 486 unique loci on chromosome 2, 3 unique loci on chromosome 3, 6 unique loci on chromosome 4, 1 unique loci each on chromosome 5, 6, 7, 9 and 10, and 26 unique loci on chromosome 8.

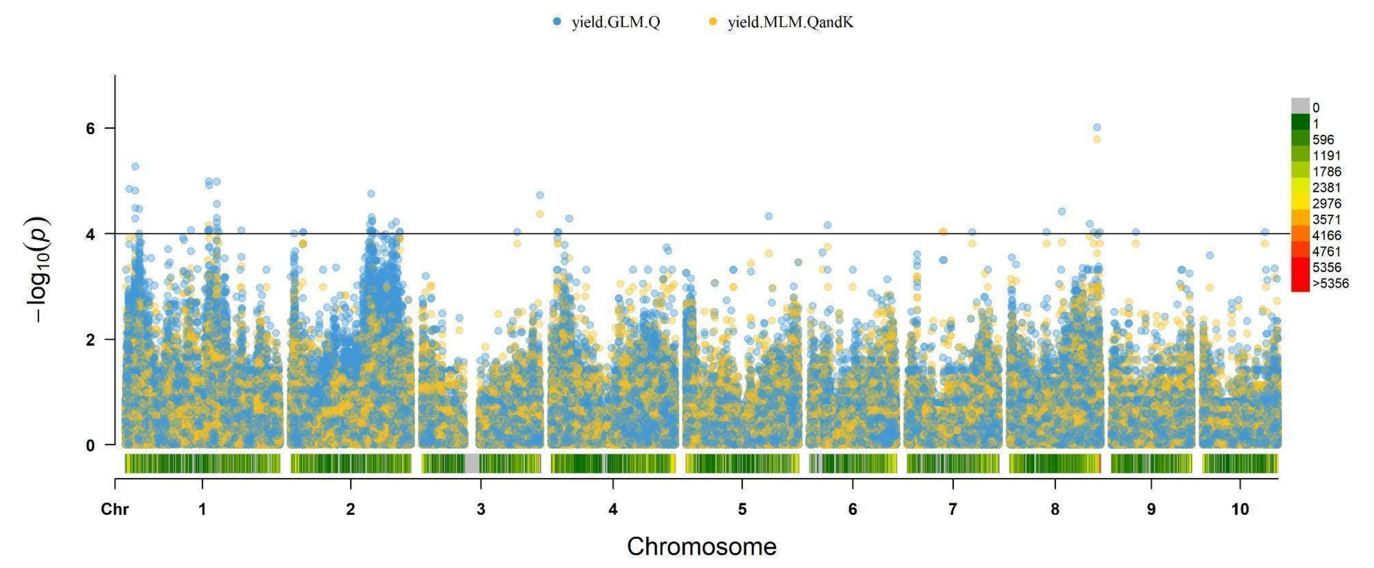

Figure 3. GWAS results for GAH2 site. Manhattan plot for the significant marker-trait association for the individually evaluated models. The black line represents the genome-wide significance threshold 1e-04 for all evaluated models.

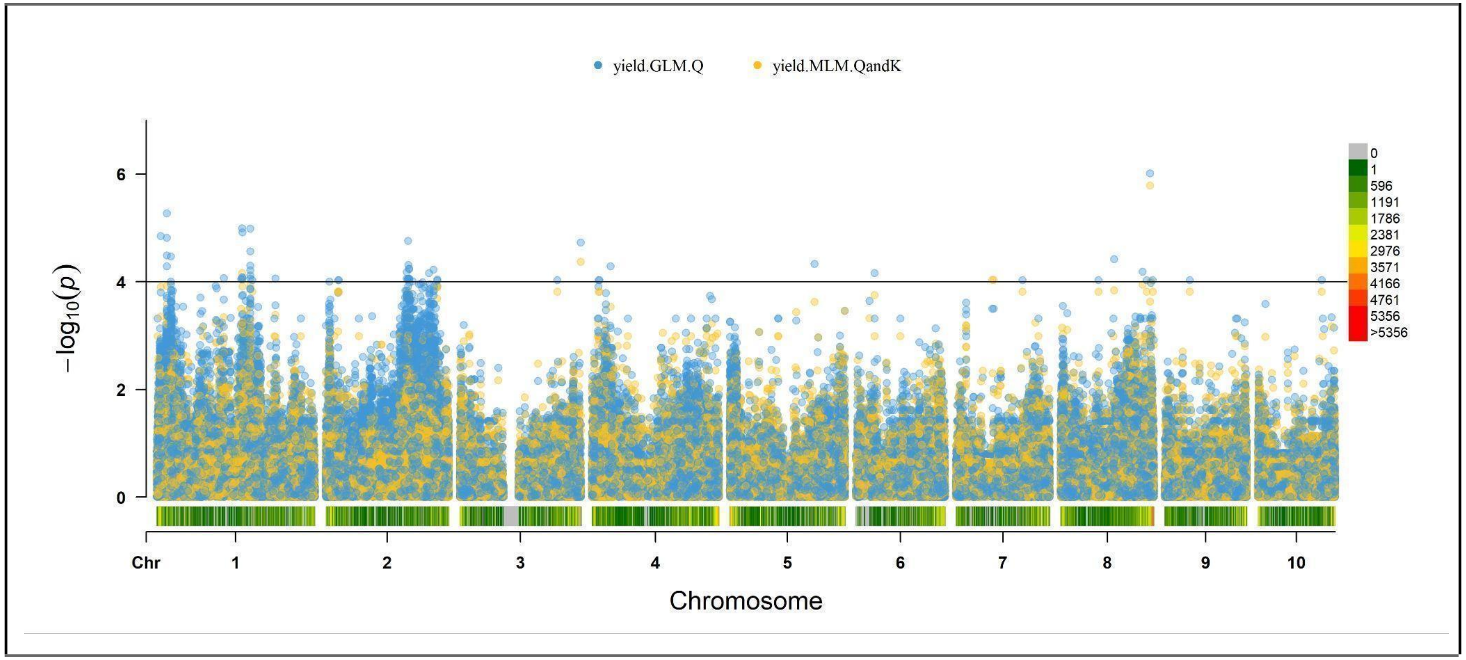

Figure 4. GWAS results for IAH3 site. Manhattan plot for the significant marker-trait association for the individually evaluated models. The black line represents the genome-wide significance threshold 1e-04 for all evaluated models.

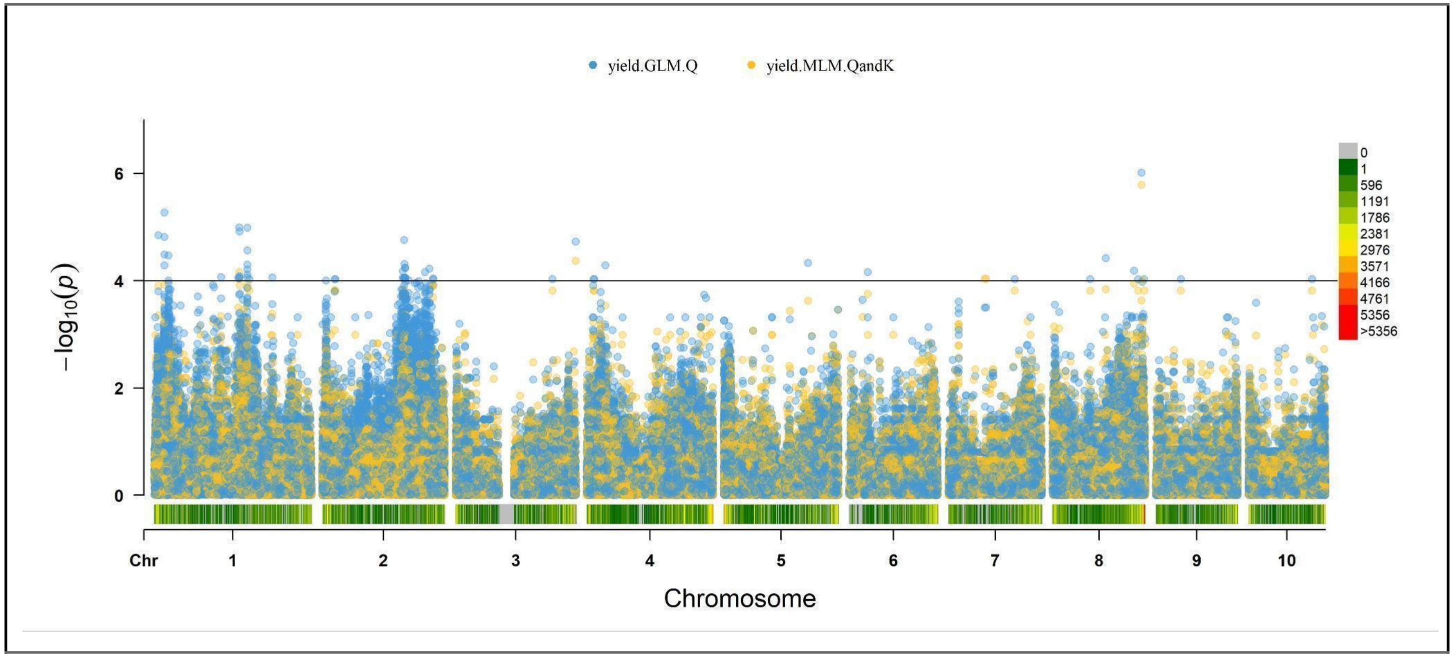

Figure 5.GWAS results for NYH2 site. Manhattan plot for the significant marker-trait association for the individually evaluated models. The black line represents the genome-wide significance threshold 1e-04 for all evaluated models.

4. DISCUSSION

The exploration of maize yield in three contrasting environments unveils a nuanced understanding of the genetic underpinnings of this vital agricultural trait. The distinct environmental conditions at each site—Wisconsin, characterized by moderate summers; Georgia, marked by hot summers and mild winters; and New York, undergoing diverse agricultural challenges due to climate change—provide a rich tapestry for investigating the adaptability of maize varieties. The three sites under study have unique environmental conditions that affect agricultural activities. For instance, Wisconsin is well known for its maize production (Moran and Edward et al., 2002). The region is characterized by seasonal changes and moderate summers with cooler temperatures (Moran and Edward et al., 2002). Maize production in Site IAH3, Wisconsin, is conditioned based on farmers' adaptation to shorter growing seasons and cooler temperatures. Where site GAH2 is located, Georgia experiences hot summers and mild winters. The state has abundant rainfall and fertile soils, contributing significantly to agricultural productivity (Carter 1974). The state of New York, where the site NYH2 is located, experiences diverse agricultural practices that contribute significantly to the state's economy (New York, 2015). Due to the effects of climate change, the state experiences short, extreme precipitation events with mild drought, introducing pressure on agriculture due to increased disease, heat, and reduced productivity.

The phenotypic analysis, notably the Principal Component Analysis (PCA), sheds light on specific properties of sites GAH2, IAH3, and NYH2. Variables with strong associations in each of the Principal Components (PCs) revealed the uniqueness of these sites concerning the evaluated yield trait. This distinction in phenotypic characterization provided data for a more informed exploration of the genetic factors influencing maize yield. From the results of the phenotypic analysis, it was observed that both IAH3 and NYH2 show specific properties concerning the evaluated variables in Table 3, especially for variables with strong associations in each of the PCs.

GWAS is a powerful tool for identifying the genetic basis of complex traits such as yield. By analyzing large sets of genetic markers across the genome, GWAS can identify genomic regions associated with yield, even if the effect of individual variants is small. Multi-environment trials are essential for evaluating the performance of maize varieties under different environmental conditions.

GWAS models have been designed with different assumptions and conditions and perform differently with each data under study. In our study, GLM and MLM models were adopted to estimate the effect of each SNP marker for the yield trait. The MLM models included the kinship (k) and population structure (Q) as covariates. In contrast, only the population structure (Q) was included as a covariate for the GLM model. From the resulting number of identified significantly associated SNPs, we observe that the GLM model identified more single loci significantly associated with the trait than the MLM model (Table S1).

Our study showed an overlapping representation pattern in the Manhattan plot of the observations for the GLM model in all three sites and the representation pattern from the MLM model within all three sites. The study identified 25, 1, 6, and 7 significant SNPs located on chromosomes 1, 3, 7, and 8, respectively, from the MLM model and 265, 486, 3, 6, 1, 1, 1, 26, 1 and 1 significant SNPs in chromosomes 1, 2, 3, 4, 5, 6, 7, 8, 9, 10 respectively from the GLM model. These findings align with several other studies available in literature. For example, in a GWAS study by Zeng et al. (2022) for grain yield-related traits using 291 maize inbred lines as materials and six yield-related traits of maize, the study used the MLM with PCA model and identified 59 significantly associated SNPs at $p<0.0001$ based on 38,683 high-quality SNP markers. SNPs were detected on chromosomes 1, 2, 3, 7, 8, 9, and 10 for the grain yield per plant (GYP) trait, while for the grain weight (GW) trait, SNPs were located on all chromosomes. Also, for the grain length (GL) trait, SNPs were detected on chromosomes 2, 7, and 10.

Similarly, a study by Zhang, Chaoshu, et al. (2017) analyzed the genetic architecture of maize ear and grain morphological traits using a compressed mixed linear model (CMLM) in GAPIT. Using a less stringent threshold of $-\log_{10}(P) > 4$, the authors detected 64 highly significant SNPs (from 40,757 SNPs which were generated from 240 accession maize panels and used for their study) associated with the trait under study in three environments. These SNPs were identified on chromosomes 1, 2, 3, 4, 5, 6, 8, 9, and 10

Despite the initial expectation of identifying differences in the identified markers across the different environments, the study revealed that 791 SNPs were detected using the GLM model in all three locations, and 39 SNPs were detected using the MLM model in all three locations. This unexpected result suggests that the same set of SNPs may be consistently associated with maize yield across diverse environments, indicating their robustness and potential relevance for marker-assisted selection in maize breeding programs. The consistent presence of these SNPs across different environments highlights their importance and warrants further investigation into the specific genetic factors and molecular mechanisms underlying their association with maize yield across varying growing conditions. Therefore, further studies, including validation experiments and fine-mapping of identified loci, are crucial to validate the observed associations and refine the understanding of the genetic basis of maize yield. Although limited, the findings from this study will contribute to future studies and contribute to understanding complex traits in maize.

5. CONCLUSION

This Genome-Wide Association Study (GWAS) of maize yield in three contrasting environments provided valuable insights into the genetic basis of this complex trait. The three sites under study, each with unique environmental conditions, presented diverse challenges and opportunities for maize production. The phenotypic analysis highlighted specific properties of sites GAH2, IAH3, and NYH2, emphasizing the importance of considering environment-specific factors in GWAS.

The adoption of both the Generalized Linear Model (GLM) and Mixed Linear Model (MLM) allowed us to estimate the effects of Single Nucleotide Polymorphism (SNP) markers on the yield trait. Notably, incorporating kinship and population structure as covariates, the MLM model outperformed the GLM model in identifying significantly associated SNPs. This observation aligns with recognizing that different GWAS models may perform differently under varying conditions.

The Manhattan plot representation exhibited overlapping patterns between the MLM and GLM models across all three sites, revealing significant SNPs on chromosomes 1, 3, 7, and 8. These findings resonate with existing literature, validating our results against previous GWAS studies in maize. The identified loci contribute to the growing knowledge of the genetic architecture of maize yield.

Comparison with studies such as Zeng et al. (2022) and Zhang et al. (2017) further strengthens our findings. The overlap in chromosomal locations of significant SNPs underscores the reliability of our results and supports the consistency of specific genomic regions influencing maize yield across different studies.

While our study has provided valuable insights, it is essential to acknowledge its limitations. The identified loci offer suggestive evidence, but further validation through experimental studies and fine mapping is imperative. This step will enhance the robustness of our observations and refine our understanding of the genetic determinants of maize yield.

Despite the preliminary nature of our findings, this study contributes valuable information to the field of maize genetics. The identified loci and their associations with yield serve as a foundation for future investigations. As we progress, continued research, including validation experiments and collaborative efforts, will be crucial for unraveling the intricate genetic mechanisms governing maize yield in diverse environmental conditions.

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APPENDIX - Supplementary material

Table S1. GWAS result for site GAH2, IAH3 and NYH2: Significant markers post-GWAS.

SNP	CHR	POS	GLM	MLM	SNP	CHR	POS	GLM	MLM
S1_7694009	1	7694009	1.42E-05		S1_130030123	1	1.3E+08	8.58E-05	
S1_7694010	1	7694010	1.42E-05		S1_130030182	1	1.3E+08	8.58E-05	
S1_7694023	1	7694023	1.42E-05		S1_130030245	1	1.3E+08	8.58E-05	
S1_19930113	1	19930113	1.53E-05		S1_130030306	1	1.3E+08	8.58E-05	
S1_19930330	1	19930330	3.24E-05		S1_130030365	1	1.3E+08	8.58E-05	
S1_19930743	1	19930743	3.24E-05		S1_130030395	1	1.3E+08	8.58E-05	
S1_19931290	1	19931290	3.24E-05		S1_130030522	1	1.3E+08	8.58E-05	
S1_19939791	1	19939791	3.24E-05		S1_130030584	1	1.3E+08	8.58E-05	
S1_19940738	1	19940738	3.24E-05		S1_130030603	1	1.3E+08	8.58E-05	
S1_19941809	1	19941809	5.38E-06		S1_130030688	1	1.3E+08	8.58E-05	
S1_19943712	1	19943712	5.15E-05		S1_130030729	1	1.3E+08	8.58E-05	
S1_27839685	1	27839685	3.42E-05		S1_130030762	1	1.3E+08	8.58E-05	

S1_130029430	1	1.3E+08	8.58E-05	S1_130030782	1	1.3E+08	8.58E-05
S1_130029448	1	1.3E+08	8.58E-05	S1_130030938	1	1.3E+08	8.58E-05
S1_130029478	1	1.3E+08	8.58E-05	S1_130030946	1	1.3E+08	8.58E-05
S1_130029490	1	1.3E+08	8.58E-05	S1_130030977	1	1.3E+08	8.58E-05
S1_130029491	1	1.3E+08	8.58E-05	S1_130031128	1	1.3E+08	8.58E-05
S1_130029547	1	1.3E+08	8.58E-05	S1_130031129	1	1.3E+08	8.58E-05
S1_130029604	1	1.3E+08	8.58E-05	S1_130031179	1	1.3E+08	8.58E-05
S1_130029704	1	1.3E+08	8.58E-05	S1_130031190	1	1.3E+08	8.58E-05
S1_130029745	1	1.3E+08	8.58E-05	S1_130031237	1	1.3E+08	8.58E-05
S1_130029858	1	1.3E+08	8.58E-05	S1_130031367	1	1.3E+08	8.58E-05
S1_130029983	1	1.3E+08	8.58E-05	S1_130031436	1	1.3E+08	8.58E-05
S1_130029995	1	1.3E+08	8.58E-05	S1_130031487	1	1.3E+08	8.58E-05
S1_130030040	1	1.3E+08	8.58E-05	S1_130031563	1	1.3E+08	8.58E-05
S1_130030054	1	1.3E+08	8.58E-05	S1_130031653	1	1.3E+08	8.58E-05
S1_130031693	1	1.3E+08	8.58E-05	S1_130033340	1	1.3E+08	8.58E-05
S1_130031696	1	1.3E+08	8.58E-05	S1_130033378	1	1.3E+08	8.58E-05
S1_130031957	1	1.3E+08	8.58E-05	S1_130033406	1	1.3E+08	8.58E-05
S1_130031993	1	1.3E+08	8.58E-05	S1_130033475	1	1.3E+08	8.58E-05

S1_130032027	1	1.3E+08	8.58E-05
S1_130032053	1	1.3E+08	8.58E-05
S1_130032079	1	1.3E+08	8.58E-05
S1_130032162	1	1.3E+08	8.58E-05
S1_130032188	1	1.3E+08	8.58E-05
S1_130032209	1	1.3E+08	8.58E-05
S1_130032289	1	1.3E+08	8.58E-05
S1_130032475	1	1.3E+08	8.58E-05
S1_130032498	1	1.3E+08	8.58E-05
S1_130032499	1	1.3E+08	8.58E-05
S1_130032534	1	1.3E+08	8.58E-05
S1_130032580	1	1.3E+08	8.58E-05
S1_130032612	1	1.3E+08	8.58E-05
S1_130032661	1	1.3E+08	8.58E-05
S1_130032683	1	1.3E+08	8.58E-05
S1_130032811	1	1.3E+08	8.58E-05
S1_130032839	1	1.3E+08	8.58E-05
S1_130032855	1	1.3E+08	8.58E-05
S1_130033489	1	1.3E+08	8.58E-05
S1_130033499	1	1.3E+08	8.58E-05
S1_130033502	1	1.3E+08	8.58E-05
S1_130033658	1	1.3E+08	8.58E-05
S1_130033771	1	1.3E+08	8.58E-05
S1_130034009	1	1.3E+08	8.58E-05
S1_130034092	1	1.3E+08	8.58E-05
S1_130034104	1	1.3E+08	8.58E-05
S1_130034149	1	1.3E+08	8.58E-05
S1_130034150	1	1.3E+08	8.58E-05
S1_130034222	1	1.3E+08	8.58E-05
S1_130034225	1	1.3E+08	8.58E-05
S1_130034235	1	1.3E+08	8.58E-05
S1_130034253	1	1.3E+08	8.58E-05
S1_130034337	1	1.3E+08	8.58E-05
S1_130034387	1	1.3E+08	8.58E-05
S1_130034396	1	1.3E+08	8.58E-05
S1_130034400	1	1.3E+08	8.58E-05

S1_130032872	1	1.3E+08	8.58E-05	S1_130034483	1	1.3E+08	8.58E-05
S1_130032962	1	1.3E+08	8.58E-05	S1_130034523	1	1.3E+08	8.58E-05
S1_130032988	1	1.3E+08	8.58E-05	S1_130034539	1	1.3E+08	8.58E-05
S1_130033110	1	1.3E+08	8.58E-05	S1_130034578	1	1.3E+08	8.58E-05
S1_130033212	1	1.3E+08	8.58E-05	S1_130034658	1	1.3E+08	8.58E-05
S1_130033323	1	1.3E+08	8.58E-05	S1_130034696	1	1.3E+08	8.58E-05
S1_130034702	1	1.3E+08	8.58E-05	S1_130036404	1	1.3E+08	8.58E-05
S1_130034793	1	1.3E+08	8.58E-05	S1_130036444	1	1.3E+08	8.58E-05
S1_130034835	1	1.3E+08	8.58E-05	S1_130036476	1	1.3E+08	8.58E-05
S1_130034910	1	1.3E+08	8.58E-05	S1_130036533	1	1.3E+08	8.58E-05
S1_130034949	1	1.3E+08	8.58E-05	S1_130036708	1	1.3E+08	8.58E-05
S1_130034958	1	1.3E+08	8.58E-05	S1_130037055	1	1.3E+08	8.58E-05
S1_130035003	1	1.3E+08	8.58E-05	S1_130037173	1	1.3E+08	8.58E-05
S1_130035064	1	1.3E+08	8.58E-05	S1_130037276	1	1.3E+08	8.58E-05
S1_130035220	1	1.3E+08	8.58E-05	S1_130037348	1	1.3E+08	8.58E-05
S1_130035235	1	1.3E+08	8.58E-05	S1_130037384	1	1.3E+08	8.58E-05
S1_130035264	1	1.3E+08	8.58E-05	S1_130037424	1	1.3E+08	8.58E-05
S1_130035294	1	1.3E+08	8.58E-05	S1_130037427	1	1.3E+08	8.58E-05

S1_130035360	1	1.3E+08	8.58E-05	S1_130037453	1	1.3E+08	8.58E-05
S1_130035375	1	1.3E+08	8.58E-05	S1_130037496	1	1.3E+08	8.58E-05
S1_130035394	1	1.3E+08	8.58E-05	S1_130037514	1	1.3E+08	8.58E-05
S1_130035433	1	1.3E+08	8.58E-05	S1_130037601	1	1.3E+08	8.58E-05
S1_130035505	1	1.3E+08	8.58E-05	S1_130037708	1	1.3E+08	8.58E-05
S1_130035534	1	1.3E+08	8.58E-05	S1_130037803	1	1.3E+08	8.58E-05
S1_130035641	1	1.3E+08	8.58E-05	S1_130037844	1	1.3E+08	8.58E-05
S1_130035693	1	1.3E+08	8.58E-05	S1_130037960	1	1.3E+08	8.58E-05
S1_130035709	1	1.3E+08	8.58E-05	S1_130038037	1	1.3E+08	8.58E-05
S1_130035826	1	1.3E+08	8.58E-05	S1_130038142	1	1.3E+08	8.58E-05
S1_130035882	1	1.3E+08	8.58E-05	S1_130038317	1	1.3E+08	8.58E-05
S1_130035982	1	1.3E+08	8.58E-05	S1_130038764	1	1.3E+08	8.58E-05
S1_130036029	1	1.3E+08	8.58E-05	S1_130038772	1	1.3E+08	8.58E-05
S1_130036153	1	1.3E+08	8.58E-05	S1_130038784	1	1.3E+08	8.58E-05
S1_130036221	1	1.3E+08	8.58E-05	S1_130038816	1	1.3E+08	8.58E-05
S1_130036326	1	1.3E+08	8.58E-05	S1_130038843	1	1.3E+08	8.58E-05
S1_130038925	1	1.3E+08	8.58E-05	S1_166142267	1	1.66E+08	8.20E-05
S1_130038945	1	1.3E+08	8.58E-05	S1_166142273	1	1.66E+08	8.20E-05

S1_130038953	1	1.3E+08	8.58E-05		S1_166142882	1	1.66E+08	9.08E-05	
S1_130038970	1	1.3E+08	8.58E-05		S1_166143056	1	1.66E+08	1.02E-05	6.88E-05
S1_130039095	1	1.3E+08	8.58E-05		S1_166143239	1	1.66E+08	1.02E-05	6.88E-05
S1_130039151	1	1.3E+08	8.58E-05		S1_166143313	1	1.66E+08	8.20E-05	
S1_130039190	1	1.3E+08	8.58E-05		S1_166143315	1	1.66E+08	8.20E-05	
S1_130039195	1	1.3E+08	8.58E-05		S1_166143316	1	1.66E+08	8.20E-05	
S1_130039324	1	1.3E+08	8.58E-05		S1_166143317	1	1.66E+08	8.20E-05	
S1_130039345	1	1.3E+08	8.58E-05		S1_166143319	1	1.66E+08	8.20E-05	
S1_130039409	1	1.3E+08	8.58E-05		S1_166143321	1	1.66E+08	8.20E-05	
S1_130039511	1	1.3E+08	8.58E-05		S1_166143454	1	1.66E+08	1.02E-05	6.88E-05
S1_130039589	1	1.3E+08	8.58E-05		S1_166143489	1	1.66E+08	1.02E-05	6.88E-05
S1_130039619	1	1.3E+08	8.58E-05		S1_166143798	1	1.66E+08	1.02E-05	6.88E-05
S1_130039704	1	1.3E+08	8.58E-05		S1_166144914	1	1.66E+08	1.02E-05	6.88E-05
S1_130039733	1	1.3E+08	8.58E-05		S1_166144950	1	1.66E+08	1.02E-05	6.88E-05
S1_130039818	1	1.3E+08	8.58E-05		S1_166145254	1	1.66E+08	1.02E-05	6.88E-05
S1_130039907	1	1.3E+08	8.58E-05		S1_166145427	1	1.66E+08	9.08E-05	
S1_164202781	1	1.64E+08	9.02E-05		S1_166146484	1	1.66E+08	1.02E-05	6.88E-05
S1_166141969	1	1.66E+08	1.02E-05	6.88E-05	S1_166146570	1	1.66E+08	9.08E-05	
S1_166141979	1	1.66E+08	1.02E-05	6.88E-05	S1_166146632	1	1.66E+08	1.02E-05	6.88E-05

S1_166142016	1	1.66E+08	1.02E-05	6.88E-05	S1_166146973	1	1.66E+08	1.02E-05	6.88E-05
S1_166142100	1	1.66E+08	1.02E-05	6.88E-05	S1_166147113	1	1.66E+08	1.02E-05	6.88E-05
S1_166142101	1	1.66E+08	1.02E-05	6.88E-05	S1_166147117	1	1.66E+08	1.02E-05	6.88E-05
S1_166142102	1	1.66E+08	1.02E-05	6.88E-05	S1_166147185	1	1.66E+08	1.02E-05	6.88E-05
S1_166142105	1	1.66E+08	1.02E-05	6.88E-05	S1_166147199	1	1.66E+08	1.02E-05	6.88E-05
S1_166142107	1	1.66E+08	1.02E-05	6.88E-05	S1_166147253	1	1.66E+08	1.02E-05	6.88E-05
S1_166142108	1	1.66E+08	1.02E-05	6.88E-05	S1_166147270	1	1.66E+08	8.20E-05	
S1_166147535	1	1.66E+08	8.20E-05		S1_181979538	1	1.82E+08	8.67E-05	
S1_166147545	1	1.66E+08	8.20E-05		S1_181979754	1	1.82E+08	2.73E-05	
S1_166147587	1	1.66E+08	8.20E-05		S1_181979793	1	1.82E+08	2.73E-05	
S1_166147596	1	1.66E+08	8.20E-05		S1_181979848	1	1.82E+08	8.67E-05	
S1_166147600	1	1.66E+08	8.20E-05		S1_181979894	1	1.82E+08	2.73E-05	
S1_166147716	1	1.66E+08	8.20E-05		S1_181979926	1	1.82E+08	8.67E-05	
S1_166147920	1	1.66E+08	8.20E-05		S1_181979927	1	1.82E+08	8.67E-05	
S1_166147957	1	1.66E+08	8.20E-05		S1_181980304	1	1.82E+08	7.69E-05	
S1_166148048	1	1.66E+08	8.20E-05		S1_181980506	1	1.82E+08	7.69E-05	
S1_166148052	1	1.66E+08	8.20E-05		S1_181980740	1	1.82E+08	6.15E-05	
S1_166624720	1	1.67E+08	8.59E-05		S1_181981154	1	1.82E+08	7.69E-05	
S1_166624747	1	1.67E+08	8.59E-05		S1_181981777	1	1.82E+08	7.69E-05	
S1_166624793	1	1.67E+08	8.59E-05		S1_181983149	1	1.82E+08	7.69E-05	

S1_166625011	1	1.67E+08	8.59E-05	S1_185851418	1	1.86E+08	9.40E-05
S1_166626144	1	1.67E+08	8.59E-05	S1_185851441	1	1.86E+08	9.40E-05
S1_166627003	1	1.67E+08	8.59E-05	S1_185851478	1	1.86E+08	9.40E-05
S1_166758910	1	1.67E+08	1.22E-05	S1_230668606	1	2.31E+08	8.71E-05
S1_181978368	1	1.82E+08	8.67E-05	S2_7733348	2	7733348	9.97E-05
S1_181978427	1	1.82E+08	8.67E-05	S2_7733357	2	7733357	9.97E-05
S1_181978470	1	1.82E+08	5.04E-05	S2_7733795	2	7733795	9.97E-05
S1_181978764	1	1.82E+08	8.67E-05	S2_24693010	2	24693010	9.40E-05
S1_181978819	1	1.82E+08	1.03E-05	S2_26144925	2	26144925	9.40E-05
S1_181978823	1	1.82E+08	1.03E-05	S2_26145084	2	26145084	9.40E-05
S1_181978873	1	1.82E+08	2.73E-05	S2_26145267	2	26145267	9.40E-05
S1_181978879	1	1.82E+08	1.03E-05	S2_157947394	2	1.58E+08	8.83E-05
S1_181979132	1	1.82E+08	8.67E-05	S2_157947699	2	1.58E+08	8.83E-05
S1_181979156	1	1.82E+08	2.73E-05	S2_157947707	2	1.58E+08	8.83E-05
S1_181979239	1	1.82E+08	8.67E-05	S2_157947893	2	1.58E+08	8.83E-05
S2_157947940	2	1.58E+08	8.83E-05	S2_157950068	2	1.58E+08	8.83E-05
S2_157947962	2	1.58E+08	8.83E-05	S2_157950078	2	1.58E+08	8.83E-05
S2_157948092	2	1.58E+08	8.83E-05	S2_157950121	2	1.58E+08	8.83E-05

S2_157948125	2	1.58E+08	8.83E-05
S2_157948153	2	1.58E+08	8.83E-05
S2_157948295	2	1.58E+08	8.83E-05
S2_157948491	2	1.58E+08	8.83E-05
S2_157948654	2	1.58E+08	8.83E-05
S2_157948683	2	1.58E+08	8.83E-05
S2_157948768	2	1.58E+08	8.83E-05
S2_157948772	2	1.58E+08	8.83E-05
S2_157948896	2	1.58E+08	8.83E-05
S2_157948956	2	1.58E+08	8.83E-05
S2_157948970	2	1.58E+08	8.83E-05
S2_157949017	2	1.58E+08	8.83E-05
S2_157949099	2	1.58E+08	8.83E-05
S2_157949115	2	1.58E+08	8.83E-05
S2_157949122	2	1.58E+08	8.83E-05
S2_157949197	2	1.58E+08	8.83E-05
S2_157949485	2	1.58E+08	8.83E-05
S2_157949629	2	1.58E+08	8.83E-05
S2_157950183	2	1.58E+08	8.83E-05
S2_157950348	2	1.58E+08	8.83E-05
S2_157950548	2	1.58E+08	6.67E-05
S2_157950770	2	1.58E+08	8.83E-05
S2_158026772	2	1.58E+08	8.83E-05
S2_158026790	2	1.58E+08	8.83E-05
S2_158026863	2	1.58E+08	8.83E-05
S2_158026914	2	1.58E+08	8.83E-05
S2_158026945	2	1.58E+08	8.83E-05
S2_158027081	2	1.58E+08	8.83E-05
S2_158027168	2	1.58E+08	8.83E-05
S2_158027171	2	1.58E+08	8.83E-05
S2_158027335	2	1.58E+08	8.83E-05
S2_158027337	2	1.58E+08	8.83E-05
S2_158027618	2	1.58E+08	8.83E-05
S2_158027712	2	1.58E+08	8.83E-05
S2_158027715	2	1.58E+08	8.83E-05
S2_158027722	2	1.58E+08	8.83E-05

S2_157949635	2	1.58E+08	8.83E-05	S2_158027757	2	1.58E+08	8.83E-05
S2_157949642	2	1.58E+08	8.83E-05	S2_158027758	2	1.58E+08	8.83E-05
S2_157949644	2	1.58E+08	8.83E-05	S2_158027776	2	1.58E+08	8.83E-05
S2_157949650	2	1.58E+08	8.83E-05	S2_158027785	2	1.58E+08	8.83E-05
S2_157949675	2	1.58E+08	8.83E-05	S2_158027881	2	1.58E+08	8.83E-05
S2_157949759	2	1.58E+08	8.83E-05	S2_158027899	2	1.58E+08	8.83E-05
S2_157950050	2	1.58E+08	8.83E-05	S2_158027912	2	1.58E+08	8.83E-05
S2_158027926	2	1.58E+08	8.83E-05	S2_160530430	2	1.61E+08	8.83E-05
S2_158027939	2	1.58E+08	8.83E-05	S2_160530456	2	1.61E+08	8.83E-05
S2_158028099	2	1.58E+08	8.83E-05	S2_160530457	2	1.61E+08	8.83E-05
S2_158028121	2	1.58E+08	8.83E-05	S2_160530500	2	1.61E+08	8.83E-05
S2_158028203	2	1.58E+08	8.83E-05	S2_160530510	2	1.61E+08	8.83E-05
S2_158028282	2	1.58E+08	8.83E-05	S2_160530827	2	1.61E+08	8.83E-05
S2_158028356	2	1.58E+08	8.83E-05	S2_160530900	2	1.61E+08	8.83E-05
S2_158028397	2	1.58E+08	8.83E-05	S2_160530942	2	1.61E+08	8.83E-05
S2_158028444	2	1.58E+08	8.83E-05	S2_160530943	2	1.61E+08	8.83E-05
S2_158028490	2	1.58E+08	8.83E-05	S2_160530998	2	1.61E+08	8.83E-05
S2_158028615	2	1.58E+08	8.83E-05	S2_160531016	2	1.61E+08	8.83E-05

S2_158028765	2	1.58E+08	8.83E-05	S2_160531088	2	1.61E+08	8.83E-05
S2_158028788	2	1.58E+08	8.83E-05	S2_160531286	2	1.61E+08	8.83E-05
S2_158028815	2	1.58E+08	8.83E-05	S2_160531605	2	1.61E+08	8.83E-05
S2_158028897	2	1.58E+08	8.83E-05	S2_160531607	2	1.61E+08	8.83E-05
S2_158028968	2	1.58E+08	8.83E-05	S2_160531696	2	1.61E+08	8.83E-05
S2_158028984	2	1.58E+08	8.83E-05	S2_160531711	2	1.61E+08	8.83E-05
S2_158029006	2	1.58E+08	8.83E-05	S2_160531952	2	1.61E+08	8.83E-05
S2_158029020	2	1.58E+08	8.83E-05	S2_160532154	2	1.61E+08	8.83E-05
S2_159762406	2	1.6E+08	9.07E-05	S2_160532210	2	1.61E+08	8.83E-05
S2_159762574	2	1.6E+08	9.07E-05	S2_160532332	2	1.61E+08	8.83E-05
S2_159762587	2	1.6E+08	9.07E-05	S2_160532374	2	1.61E+08	8.83E-05
S2_160529248	2	1.61E+08	8.83E-05	S2_160532420	2	1.61E+08	8.83E-05
S2_160530163	2	1.61E+08	8.83E-05	S2_160532460	2	1.61E+08	8.83E-05
S2_160530168	2	1.61E+08	8.83E-05	S2_160532465	2	1.61E+08	8.83E-05
S2_160530280	2	1.61E+08	8.83E-05	S2_160532468	2	1.61E+08	8.83E-05
S2_160530353	2	1.61E+08	8.83E-05	S2_160532475	2	1.61E+08	8.83E-05
S2_160530356	2	1.61E+08	8.83E-05	S2_160532680	2	1.61E+08	8.83E-05
S2_160532808	2	1.61E+08	8.83E-05	S2_160539919	2	1.61E+08	8.83E-05

S2_160532904	2	1.61E+08	1.74E-05
S2_160534561	2	1.61E+08	8.83E-05
S2_160534656	2	1.61E+08	8.83E-05
S2_160534768	2	1.61E+08	8.83E-05
S2_160534862	2	1.61E+08	8.83E-05
S2_160534883	2	1.61E+08	8.83E-05
S2_160534914	2	1.61E+08	8.83E-05
S2_160535010	2	1.61E+08	8.83E-05
S2_160535215	2	1.61E+08	8.83E-05
S2_160535399	2	1.61E+08	8.83E-05
S2_160535684	2	1.61E+08	8.83E-05
S2_160535863	2	1.61E+08	8.83E-05
S2_160536170	2	1.61E+08	8.83E-05
S2_160536171	2	1.61E+08	8.83E-05
S2_160536694	2	1.61E+08	8.83E-05
S2_160536797	2	1.61E+08	8.83E-05
S2_160537416	2	1.61E+08	8.83E-05
S2_160537541	2	1.61E+08	8.83E-05
S2_160540404	2	1.61E+08	8.83E-05
S2_160540483	2	1.61E+08	8.83E-05
S2_160540486	2	1.61E+08	8.83E-05
S2_160540832	2	1.61E+08	8.83E-05
S2_160540917	2	1.61E+08	8.83E-05
S2_160542040	2	1.61E+08	8.83E-05
S2_160542274	2	1.61E+08	8.83E-05
S2_160542879	2	1.61E+08	8.83E-05
S2_160542901	2	1.61E+08	8.83E-05
S2_160542911	2	1.61E+08	8.83E-05
S2_160542924	2	1.61E+08	8.83E-05
S2_160542927	2	1.61E+08	8.83E-05
S2_160543066	2	1.61E+08	8.83E-05
S2_160543067	2	1.61E+08	8.83E-05
S2_160543096	2	1.61E+08	8.83E-05
S2_160543142	2	1.61E+08	8.83E-05
S2_160543159	2	1.61E+08	8.83E-05
S2_160543211	2	1.61E+08	8.83E-05

S2_160537660	2	1.61E+08	8.83E-05
S2_160537913	2	1.61E+08	8.83E-05
S2_160537934	2	1.61E+08	8.83E-05
S2_160538075	2	1.61E+08	8.83E-05
S2_160538126	2	1.61E+08	8.83E-05
S2_160538485	2	1.61E+08	8.83E-05
S2_160538812	2	1.61E+08	8.83E-05
S2_160538843	2	1.61E+08	8.83E-05
S2_160539627	2	1.61E+08	8.83E-05
S2_160544169	2	1.61E+08	8.83E-05
S2_160544223	2	1.61E+08	8.83E-05
S2_160544232	2	1.61E+08	8.83E-05
S2_160544252	2	1.61E+08	8.83E-05
S2_160544322	2	1.61E+08	8.83E-05
S2_160544326	2	1.61E+08	8.83E-05
S2_160544333	2	1.61E+08	8.83E-05
S2_160544337	2	1.61E+08	8.83E-05
S2_160544441	2	1.61E+08	8.83E-05
S2_160543545	2	1.61E+08	8.83E-05
S2_160543715	2	1.61E+08	8.83E-05
S2_160543716	2	1.61E+08	8.83E-05
S2_160543874	2	1.61E+08	8.83E-05
S2_160543877	2	1.61E+08	8.83E-05
S2_160543955	2	1.61E+08	8.83E-05
S2_160543991	2	1.61E+08	8.83E-05
S2_160544054	2	1.61E+08	8.83E-05
S2_160544127	2	1.61E+08	8.83E-05
S2_160558282	2	1.61E+08	8.83E-05
S2_160558284	2	1.61E+08	8.83E-05
S2_160558509	2	1.61E+08	8.83E-05
S2_160558536	2	1.61E+08	8.83E-05
S2_160558706	2	1.61E+08	8.83E-05
S2_160558803	2	1.61E+08	8.83E-05
S2_160559449	2	1.61E+08	8.83E-05
S2_160560114	2	1.61E+08	8.83E-05
S2_160560290	2	1.61E+08	8.83E-05

S2_160544477	2	1.61E+08	8.83E-05
S2_160544478	2	1.61E+08	8.83E-05
S2_160544484	2	1.61E+08	8.83E-05
S2_160544505	2	1.61E+08	8.83E-05
S2_160544515	2	1.61E+08	8.83E-05
S2_160544553	2	1.61E+08	8.83E-05
S2_160544577	2	1.61E+08	8.83E-05
S2_160544722	2	1.61E+08	8.83E-05
S2_160544960	2	1.61E+08	8.83E-05
S2_160545176	2	1.61E+08	8.83E-05
S2_160545819	2	1.61E+08	8.83E-05
S2_160545933	2	1.61E+08	8.83E-05
S2_160546976	2	1.61E+08	8.83E-05
S2_160550401	2	1.61E+08	8.83E-05
S2_160556879	2	1.61E+08	8.83E-05
S2_160557103	2	1.61E+08	8.83E-05
S2_160558006	2	1.61E+08	8.83E-05
S2_160558011	2	1.61E+08	8.83E-05
S2_160560468	2	1.61E+08	8.83E-05
S2_160561186	2	1.61E+08	8.83E-05
S2_160561255	2	1.61E+08	8.83E-05
S2_160561502	2	1.61E+08	8.83E-05
S2_160561571	2	1.61E+08	8.83E-05
S2_160561787	2	1.61E+08	8.83E-05
S2_160561819	2	1.61E+08	8.83E-05
S2_160561998	2	1.61E+08	8.83E-05
S2_160562232	2	1.61E+08	8.83E-05
S2_160562279	2	1.61E+08	8.83E-05
S2_160562380	2	1.61E+08	8.83E-05
S2_160562705	2	1.61E+08	8.83E-05
S2_160562706	2	1.61E+08	8.83E-05
S2_160562728	2	1.61E+08	8.83E-05
S2_160562970	2	1.61E+08	8.83E-05
S2_160563003	2	1.61E+08	8.83E-05
S2_160563173	2	1.61E+08	8.83E-05
S2_160563362	2	1.61E+08	8.83E-05

S2_160558116	2	1.61E+08	8.83E-05	S2_160563457	2	1.61E+08	8.83E-05
S2_160563634	2	1.61E+08	8.83E-05	S2_160566274	2	1.61E+08	8.83E-05
S2_160563893	2	1.61E+08	8.83E-05	S2_160566324	2	1.61E+08	8.83E-05
S2_160563899	2	1.61E+08	8.83E-05	S2_160566431	2	1.61E+08	8.83E-05
S2_160563926	2	1.61E+08	8.83E-05	S2_160566454	2	1.61E+08	8.83E-05
S2_160565063	2	1.61E+08	8.83E-05	S2_160566458	2	1.61E+08	8.83E-05
S2_160565064	2	1.61E+08	8.83E-05	S2_160566570	2	1.61E+08	8.83E-05
S2_160565078	2	1.61E+08	8.83E-05	S2_160566676	2	1.61E+08	8.83E-05
S2_160565079	2	1.61E+08	8.83E-05	S2_160566945	2	1.61E+08	8.83E-05
S2_160565110	2	1.61E+08	8.83E-05	S2_160567367	2	1.61E+08	8.83E-05
S2_160565122	2	1.61E+08	8.83E-05	S2_160567952	2	1.61E+08	8.83E-05
S2_160565227	2	1.61E+08	8.83E-05	S2_160568346	2	1.61E+08	8.83E-05
S2_160565247	2	1.61E+08	8.83E-05	S2_160568485	2	1.61E+08	8.83E-05
S2_160565259	2	1.61E+08	8.83E-05	S2_160569088	2	1.61E+08	8.83E-05
S2_160565295	2	1.61E+08	8.83E-05	S2_160569241	2	1.61E+08	8.83E-05
S2_160565296	2	1.61E+08	8.83E-05	S2_160569409	2	1.61E+08	8.83E-05
S2_160565865	2	1.61E+08	8.83E-05	S2_160569423	2	1.61E+08	8.83E-05
S2_160565885	2	1.61E+08	8.83E-05	S2_160569482	2	1.61E+08	8.83E-05

S2_160565895	2	1.61E+08	8.83E-05	S2_160569821	2	1.61E+08	8.83E-05
S2_160565961	2	1.61E+08	8.83E-05	S2_160569957	2	1.61E+08	8.83E-05
S2_160566043	2	1.61E+08	8.83E-05	S2_160569998	2	1.61E+08	8.83E-05
S2_160566056	2	1.61E+08	8.83E-05	S2_160570072	2	1.61E+08	8.83E-05
S2_160566064	2	1.61E+08	8.83E-05	S2_160570115	2	1.61E+08	8.83E-05
S2_160566087	2	1.61E+08	8.83E-05	S2_160570337	2	1.61E+08	8.83E-05
S2_160566095	2	1.61E+08	8.83E-05	S2_160570584	2	1.61E+08	8.83E-05
S2_160566113	2	1.61E+08	8.83E-05	S2_160570649	2	1.61E+08	8.83E-05
S2_160566126	2	1.61E+08	8.83E-05	S2_160570660	2	1.61E+08	8.83E-05
S2_160566151	2	1.61E+08	8.83E-05	S2_160570740	2	1.61E+08	8.83E-05
S2_160566210	2	1.61E+08	8.83E-05	S2_160571225	2	1.61E+08	8.83E-05
S2_160571229	2	1.61E+08	8.83E-05	S2_161094567	2	1.61E+08	4.90E-05
S2_160571431	2	1.61E+08	8.83E-05	S2_161095209	2	1.61E+08	8.86E-05
S2_160571459	2	1.61E+08	8.83E-05	S2_161096097	2	1.61E+08	4.90E-05
S2_160571642	2	1.61E+08	8.83E-05	S2_161931043	2	1.62E+08	5.72E-05
S2_160571667	2	1.61E+08	8.83E-05	S2_162103141	2	1.62E+08	5.78E-05
S2_160571833	2	1.61E+08	8.83E-05	S2_162192875	2	1.62E+08	8.83E-05
S2_160572041	2	1.61E+08	8.83E-05	S2_162193076	2	1.62E+08	8.83E-05

S2_160572194	2	1.61E+08	8.83E-05
S2_160572204	2	1.61E+08	8.83E-05
S2_160572319	2	1.61E+08	8.83E-05
S2_160572375	2	1.61E+08	8.83E-05
S2_160572382	2	1.61E+08	8.83E-05
S2_160572476	2	1.61E+08	8.83E-05
S2_160572685	2	1.61E+08	8.83E-05
S2_160572787	2	1.61E+08	8.83E-05
S2_160578977	2	1.61E+08	8.83E-05
S2_160579124	2	1.61E+08	8.83E-05
S2_160579282	2	1.61E+08	8.83E-05
S2_160579511	2	1.61E+08	8.83E-05
S2_160579832	2	1.61E+08	8.83E-05
S2_160579837	2	1.61E+08	8.83E-05
S2_160580182	2	1.61E+08	8.83E-05
S2_160580550	2	1.61E+08	8.83E-05
S2_160580610	2	1.61E+08	8.83E-05
S2_160580766	2	1.61E+08	8.83E-05
S2_162193435	2	1.62E+08	8.83E-05
S2_162194291	2	1.62E+08	8.83E-05
S2_162194418	2	1.62E+08	8.83E-05
S2_162195023	2	1.62E+08	8.83E-05
S2_162195725	2	1.62E+08	8.83E-05
S2_162281264	2	1.62E+08	8.83E-05
S2_162399229	2	1.62E+08	8.83E-05
S2_162399310	2	1.62E+08	8.83E-05
S2_162399311	2	1.62E+08	8.83E-05
S2_162400969	2	1.62E+08	8.83E-05
S2_162400971	2	1.62E+08	8.83E-05
S2_162400978	2	1.62E+08	8.83E-05
S2_162400985	2	1.62E+08	8.83E-05
S2_162400991	2	1.62E+08	8.83E-05
S2_162401006	2	1.62E+08	8.83E-05
S2_162401010	2	1.62E+08	8.83E-05
S2_162401076	2	1.62E+08	8.83E-05
S2_162401087	2	1.62E+08	8.83E-05

S2_160580871	2	1.61E+08	8.83E-05
S2_160580961	2	1.61E+08	8.83E-05
S2_161094539	2	1.61E+08	4.90E-05
S2_162401336	2	1.62E+08	8.83E-05
S2_162401356	2	1.62E+08	8.83E-05
S2_162401378	2	1.62E+08	8.83E-05
S2_162401447	2	1.62E+08	8.83E-05
S2_162401671	2	1.62E+08	8.83E-05
S2_162401715	2	1.62E+08	8.83E-05
S2_162401740	2	1.62E+08	8.83E-05
S2_162401750	2	1.62E+08	8.83E-05
S2_162401756	2	1.62E+08	8.83E-05
S2_162401758	2	1.62E+08	8.83E-05
S2_162401759	2	1.62E+08	8.83E-05
S2_162401760	2	1.62E+08	8.83E-05
S2_162401761	2	1.62E+08	8.83E-05
S2_162401762	2	1.62E+08	8.83E-05
S2_162401765	2	1.62E+08	8.83E-05
S2_162401136	2	1.62E+08	8.83E-05
S2_162401194	2	1.62E+08	8.83E-05
S2_162401202	2	1.62E+08	8.83E-05
S2_162401844	2	1.62E+08	8.83E-05
S2_162401845	2	1.62E+08	8.83E-05
S2_162401852	2	1.62E+08	8.83E-05
S2_162401886	2	1.62E+08	8.83E-05
S2_162401907	2	1.62E+08	8.83E-05
S2_162401909	2	1.62E+08	8.83E-05
S2_162401915	2	1.62E+08	8.83E-05
S2_162401919	2	1.62E+08	8.83E-05
S2_162401944	2	1.62E+08	8.83E-05
S2_162401945	2	1.62E+08	8.83E-05
S2_162401982	2	1.62E+08	8.83E-05
S2_162401992	2	1.62E+08	8.83E-05
S2_162401996	2	1.62E+08	8.83E-05
S2_162402010	2	1.62E+08	8.83E-05
S2_162402026	2	1.62E+08	8.83E-05

S2_162401770	2	1.62E+08	8.83E-05
S2_162401773	2	1.62E+08	8.83E-05
S2_162401774	2	1.62E+08	8.83E-05
S2_162401776	2	1.62E+08	8.83E-05
S2_162401777	2	1.62E+08	8.83E-05
S2_162401778	2	1.62E+08	8.83E-05
S2_162401780	2	1.62E+08	8.83E-05
S2_162401783	2	1.62E+08	8.83E-05
S2_162401787	2	1.62E+08	8.83E-05
S2_162401788	2	1.62E+08	8.83E-05
S2_162401791	2	1.62E+08	8.83E-05
S2_162401805	2	1.62E+08	8.83E-05
S2_162401826	2	1.62E+08	8.83E-05
S2_162704136	2	1.63E+08	8.83E-05
S2_162704483	2	1.63E+08	8.83E-05
S2_162708524	2	1.63E+08	8.83E-05
S2_163003813	2	1.63E+08	8.83E-05
S2_163003845	2	1.63E+08	8.83E-05
S2_162402193	2	1.62E+08	8.83E-05
S2_162402736	2	1.62E+08	8.83E-05
S2_162402760	2	1.62E+08	8.83E-05
S2_162402779	2	1.62E+08	8.83E-05
S2_162537721	2	1.63E+08	8.83E-05
S2_162538122	2	1.63E+08	8.83E-05
S2_162538182	2	1.63E+08	8.83E-05
S2_162544136	2	1.63E+08	8.83E-05
S2_162544345	2	1.63E+08	8.83E-05
S2_162545694	2	1.63E+08	8.83E-05
S2_162545744	2	1.63E+08	8.83E-05
S2_162702878	2	1.63E+08	8.83E-05
S2_162702902	2	1.63E+08	8.83E-05
S2_163007852	2	1.63E+08	8.83E-05
S2_163007904	2	1.63E+08	8.83E-05
S2_163008015	2	1.63E+08	8.83E-05
S2_163008057	2	1.63E+08	8.83E-05
S2_163008069	2	1.63E+08	8.83E-05

S2_163004109	2	1.63E+08	8.83E-05
S2_163004676	2	1.63E+08	8.83E-05
S2_163004677	2	1.63E+08	8.83E-05
S2_163004752	2	1.63E+08	8.83E-05
S2_163004828	2	1.63E+08	8.83E-05
S2_163004895	2	1.63E+08	8.83E-05
S2_163005367	2	1.63E+08	8.83E-05
S2_163005746	2	1.63E+08	8.83E-05
S2_163005748	2	1.63E+08	8.83E-05
S2_163005853	2	1.63E+08	8.83E-05
S2_163005984	2	1.63E+08	8.83E-05
S2_163005991	2	1.63E+08	8.83E-05
S2_163006052	2	1.63E+08	8.83E-05
S2_163006174	2	1.63E+08	8.83E-05
S2_163006423	2	1.63E+08	8.83E-05
S2_163006431	2	1.63E+08	8.83E-05
S2_163006486	2	1.63E+08	8.83E-05
S2_163006676	2	1.63E+08	8.83E-05
S2_163008149	2	1.63E+08	8.83E-05
S2_163008243	2	1.63E+08	8.83E-05
S2_163008261	2	1.63E+08	8.83E-05
S2_163008339	2	1.63E+08	8.83E-05
S2_163008400	2	1.63E+08	8.83E-05
S2_163008458	2	1.63E+08	8.83E-05
S2_163008528	2	1.63E+08	8.83E-05
S2_163008534	2	1.63E+08	8.83E-05
S2_163009011	2	1.63E+08	8.83E-05
S2_163009167	2	1.63E+08	8.83E-05
S2_163009256	2	1.63E+08	8.83E-05
S2_163009296	2	1.63E+08	8.83E-05
S2_163009303	2	1.63E+08	8.83E-05
S2_163009307	2	1.63E+08	8.83E-05
S2_163009326	2	1.63E+08	8.83E-05
S2_163009328	2	1.63E+08	8.83E-05
S2_163009376	2	1.63E+08	8.83E-05
S2_163009540	2	1.63E+08	8.83E-05

S2_163006787	2	1.63E+08	8.83E-05	
S2_163007153	2	1.63E+08	8.83E-05	
S2_163007468	2	1.63E+08	8.83E-05	
S2_163007506	2	1.63E+08	8.83E-05	
S2_163007657	2	1.63E+08	8.83E-05	
S2_163010222	2	1.63E+08	8.83E-05	
S2_163010606	2	1.63E+08	8.83E-05	
S2_163010733	2	1.63E+08	8.83E-05	
S2_168535672	2	1.69E+08	9.82E-05	
S2_168536393	2	1.69E+08	9.82E-05	
S2_168536418	2	1.69E+08	9.82E-05	
S2_201332819	2	2.01E+08	6.95E-05	
S2_201333094	2	2.01E+08	6.95E-05	
S2_201333378	2	2.01E+08	6.95E-05	
S2_201333396	2	2.01E+08	6.95E-05	
S2_201333447	2	2.01E+08	6.95E-05	
S2_201333459	2	2.01E+08	6.95E-05	
S2_209823720	2	2.1E+08	6.01E-05	
S2_163009546	2	1.63E+08	8.83E-05	
S2_163009710	2	1.63E+08	8.83E-05	
S2_163009777	2	1.63E+08	8.83E-05	
S2_163010077	2	1.63E+08	8.83E-05	
S2_163010142	2	1.63E+08	8.83E-05	
S3_189707716	3	1.9E+08	9.40E-05	
S3_235222994	3	2.35E+08	1.87E-05	4.29E-05
S4_13223815	4	13223815	9.40E-05	
S4_13223865	4	13223865	9.40E-05	
S4_13223880	4	13223880	9.40E-05	
S4_15080055	4	15080055	9.40E-05	
S4_36264971	4	36264971	5.21E-05	
S4_36264975	4	36264975	5.21E-05	
S5_164452393	5	1.64E+08	4.69E-05	
S6_36325634	6	36325634	6.91E-05	
S7_129184316	7	1.29E+08	9.40E-05	
S8_73835890	8	73835890	9.40E-05	
S8_103506184	8	1.04E+08	3.79E-05	

S2_209823968	2	2.1E+08	6.01E-05	
S2_209823991	2	2.1E+08	6.01E-05	
S2_209824012	2	2.1E+08	6.01E-05	
S2_209824074	2	2.1E+08	6.01E-05	
S2_209824101	2	2.1E+08	6.01E-05	
S2_209824677	2	2.1E+08	6.01E-05	
S2_209824683	2	2.1E+08	6.01E-05	
S2_209824691	2	2.1E+08	6.01E-05	
S2_217207973	2	2.17E+08	9.59E-05	
S2_217207977	2	2.17E+08	9.59E-05	
S2_217208101	2	2.17E+08	9.59E-05	
S2_217208163	2	2.17E+08	9.16E-05	
S2_217208273	2	2.17E+08	9.16E-05	
S2_217208304	2	2.17E+08	9.59E-05	
S3_189694903	3	1.9E+08	9.40E-05	
S8_178636771	8	1.79E+08	9.40E-05	
S8_178637345	8	1.79E+08	9.40E-05	
S8_178637838	8	1.79E+08	9.40E-05	
S8_103506185	8	1.04E+08	3.79E-05	
S8_159082992	8	1.59E+08	6.52E-05	
S8_159082999	8	1.59E+08	6.52E-05	
S8_159083027	8	1.59E+08	6.52E-05	
S8_159083039	8	1.59E+08	6.52E-05	
S8_159083061	8	1.59E+08	6.52E-05	
S8_167028488	8	1.67E+08	9.40E-05	
S8_173699289	8	1.74E+08	9.75E-07	1.63E-06
S8_173699290	8	1.74E+08	9.75E-07	1.63E-06
S8_173699291	8	1.74E+08	9.75E-07	1.63E-06
S8_178635407	8	1.79E+08	9.40E-05	
S8_178635409	8	1.79E+08	9.40E-05	
S8_178636000	8	1.79E+08	9.40E-05	
S8_178636084	8	1.79E+08	9.40E-05	
S8_178636476	8	1.79E+08	9.40E-05	

S8_178638311	8	1.79E+08	9.40E-05
S8_178638815	8	1.79E+08	9.40E-05
S8_178639043	8	1.79E+08	9.40E-05
S8_178639049	8	1.79E+08	9.40E-05
S8_178639351	8	1.79E+08	9.40E-05
S8_178639802	8	1.79E+08	9.40E-05
S9_48368233	9	48368233	9.40E-05
S10_123911503	10	1.24E+08	9.40E-05