# Megabase-Scale Inversion Polymorphism in the Wild Ancestor of Maize

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**ABSTRACT** Chromosomal inversions are thought to play a special role in local adaptation, through dramatic suppression of recombination, which favors the maintenance of locally adapted alleles. However, relatively few inversions have been characterized in population genomic data. On the basis of single-nucleotide polymorphism (SNP) genotyping across a large panel of *Zea mays*, we have identified an ~50-Mb region on the short arm of chromosome 1 where patterns of polymorphism are highly consistent with a polymorphic paracentric inversion that captures >700 genes. Comparison to other taxa in *Zea* and *Tripsacum* suggests that the derived, inverted state is present only in the wild *Z. mays* subspecies *parviglumis* and *mexicana* and is completely absent in domesticated maize. Patterns of polymorphism suggest that the inversion is ancient and geographically widespread in *parviglumis*. Cytological screens find little evidence for inversion loops, suggesting that inversion heterozygotes may suffer few crossover-induced fitness consequences. The inversion polymorphism shows evidence of adaptive evolution, including a strong altitudinal cline, a statistical association with environmental variables and phenotypic traits, and a skewed haplotype frequency spectrum for inverted alleles.

THE evolutionary role of chromosomal inversions has been studied in a wide array of organisms, from insects (Ayala *et al.* 2011; Stevison *et al.* 2011) to birds (Huynh *et al.* 2011) and plants (Hoffmann and Rieseberg 2008; Lowry and Willis 2010). Examination of inversion polymorphism was fundamental to the early study of selection and adaptive diversity, as well as the basis for understanding the maintenance of neutral polymorphism within populations (Dobzhansky 1950; Hoffmann *et al.* 2004). Homologous pairing of an inverted and a noninverted chromosome in heterozygotes leads to the formation of an inversion loop, and crossing over in an inversion loop can cause the formation of a dicentric chromosome and an acentric fragment at meiosis I, resulting in terminal deletions of the affected chromosome and gamete death at frequencies that correlate with the size of the inversion (Burnham 1962). Because of the difficulty of homologous pairing and the deleterious effects of homologous crossing over in inversions, inversions are typically observed to disrupt recombination in heterozygous individuals, leading to measurable effects on nucleotide sequence polymorphism, including the generation of extended linkage disequilibrium (LD). Inversion-induced LD has been reported in a variety of organisms, including humans (Bansal *et al.* 2007), *Drosophila subobscura* (Munte *et al.* 2005), and several other species (reviewed in Hoffmann and Rieseberg 2008). Strong differentiation between chromosomal arrangements (as measured by $F_{ST}$) has also been used as evidence of inversions in *Drosophila* (Andolfatto *et al.* 1999; Depaulis *et al.* 1999; Nóbrega *et al.* 2008).

A variety of circumstances can favor the maintenance or spread of an inversion polymorphism. The inversion may be


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selected for if the structural rearrangement itself has fitness consequences (Castermans *et al.* 2007). Natural selection can also favor the spread of an inversion if it contains locally adapted alleles, because inversions can suppress recombination and thus protect adaptive alleles from gene flow (Kirkpatrick and Barton 2006; Machado *et al.* 2007). Some inversion polymorphisms display strong patterns of geographic structure, consistent with local adaptation to ecological factors such as temperature regimes or water availability (White *et al.* 2009; Lowry and Willis 2010; Ayala *et al.* 2011). For example, strong differentiation among ecological zones was observed for an inversion in the mosquito *Anopheles funestus* (Ayala *et al.* 2011). In the yellow monkeyflower, *Mimulus guttatus* (Lowry and Willis 2010), an inversion is involved in local adaptation to Mediterranean habitats through several morphological and phenological traits, while the standard arrangement appears in a perennial ecotype from habitats with high year-round soil moisture. In addition to selection, inversion polymorphisms without strong deleterious effects may also increase in frequency through genetic drift and migration, potentially resulting in fixation in small populations (Bengtsson and Bodmer 1976; Lande 1984).

Here we examine the population-level diversity of a newly discovered 50-Mb inversion found in the wild subspecies of *Zea mays* (known collectively as teosinte). Inversions in both wild and domesticated *Z. mays* and related taxa have been reported previously (McClintock 1931; Morgan 1950; Ting 1965, 1967; Kato 1975; Ting 1976), but these were detected cytologically and little is known about their evolution in natural populations. We examine genome-wide patterns of LD in *Z. mays*, using 941 single-nucleotide polymorphism (SNP) markers genotyped in a diverse sample of 2782 individuals, including representatives of three *Z. mays* subspecies: domesticated maize (*Z. mays* ssp. *mays*), its wild progenitor *Z. mays* ssp. *parviglumis*, and the weedy taxon *Z. mays* ssp. *mexicana* (hereafter *mays*, *parviglumis*, and *mexicana*, respectively). A region spanning ~50 Mb on the short arm of chromosome 1 in *parviglumis* and *mexicana* demonstrates the highest level of LD in the genome and coincides with a region of high differentiation between *mays* and *parviglumis* reported by Hufford *et al.* (2012). Comparison to other taxa in *Zea* and *Tripsacum* suggests that the inverted arrangement is derived. The inverted arrangement is present at population frequencies up to 90% in *parviglumis*, but completely absent in domesticated maize. We present evidence that the inversion is relatively ancient and has persisted in teosinte populations for sufficient time to permit its widespread occurrence in all 33 natural populations of subspecies *parviglumis* investigated. Our data further suggest the inversion may be adaptive, as the inverted arrangement shows a strong altitudinal cline and is associated with multiple environmental and phenotypic traits, and the haplotype frequency spectrum of inverted alleles appears inconsistent with neutral evolution.

## Materials and Methods

### *Plant materials and genetic data*

Plant materials (Supporting Information, Table S1) included accessions of all four subspecies of *Z. mays* (1573 ssp. *mays*, 975 ssp. *parviglumis*, 161 ssp. *mexicana*, and 10 ssp. *huehuetenangensis*), as well as *Z. luxurians* (17), *Z. diploperennis* (15), and *Z. perennis* (9). The panel also included 22 *Tripsacum* accessions used as outgroups. The 975 *parviglumis* accessions include 33 populations with at least 10 individuals in each population. The *mays* samples include 1283 accessions representing ~250 traditional open-pollinated landraces (including 27 inbred landraces) and 290 modern inbred lines (Table S1).

Genotyping for the genome-wide set of 959 SNPs followed previously described methods (Weber *et al.* 2007; van Heerwaarden *et al.* 2010). The SNP discovery panel consisted of 14 *mays* inbred lines and 16 teosinte partial inbreds (Wright *et al.* 2005; Weber *et al.* 2007). We excluded accessions (7 *parviglumis*, 1 *mexicana*, and 20 *mays*) and loci (3 SNPs) with >15% missing data. We also removed SNPs where BLAST searches of context sequence identified multiple locations in the *mays* reference genome (Release 5a.59) (Schnable *et al.* 2009). This resulted in a final panel of 941 SNPs (Table S2) from 542 mapped genes. SNP genotypes and their contextual sequences are available at http://www.panzea.org and http://www.rilab.org. A subset of these data has been published elsewhere, including 706 SNPs from 584 *parviglumis* accessions in Weber *et al.* (2007); 123 SNPs from 817 *parviglumis* in Weber *et al.* (2008); and 468 SNPs from 1127 *mays*, 100 *parviglumis*, and 96 *mexicana* in van Heerwaarden *et al.* (2011).

The majority of the accessions represent open-pollinated populations that are highly heterozygous, resulting in genotypic data of unknown phase. We computationally phased each of the three subspecies separately using the software fastPHASE (Scheet and Stephens 2006) with 20 random starts and 25 iterations of the expectation-maximization algorithm. For each subspecies, inbred lines (Table S1) were used as training data.

We made use of published Sanger resequencing data from Wright *et al.* (2005). Wright and coauthors sequenced PCR products from teosinte accessions that had been inbred for two generations. Within the inversion, two individuals with a sequence from one arrangement at one locus and the alternate arrangement at a different locus were deemed heterozygous and removed from the analysis. We limited our analyses to reliably aligned loci on chromosome 1 with $n \geq 10$ total sequences and $n \geq 3$ of each arrangement. In total, we analyzed 95 loci, including 7 inside the inversion (Table S3; data available at www.panzea.org). We used the top BLAST hit from the *Sorghum* genome (Paterson *et al.* 2009) as an outgroup for each locus. Loci were annotated by BLAST comparison to the *mays* reference genome (Release 5a.59) (Schnable *et al.* 2009).

### Data analysis and divergence time

Summary statistics of the SNP genotyping data and the resequencing data were calculated using the analysis package of the libsequence library (Thornton 2003). Although the absolute values of some summary statistics of the SNP genotyping data may be affected by ascertainment bias (Clark *et al.* 2005a), the relative values of these statistics are expected to be more robust.

We tested for Hardy–Weinberg equilibrium by treating the inversion as a single biallelic locus. LD (as measured by $r^2$) was calculated for SNPs with a minor allele frequency (MAF) >5%, using the LDheatmap package (Shin *et al.* 2006) in R (R Development Core Team 2011). To assign individuals to haplotype clusters at the inversion, we used the genetic assignment software STRUCTURE (Pritchard *et al.* 2000; Falush *et al.* 2003). We estimated haplotype clusters for values of $K$ ranging from 1 to 5. For each value of $K$, we used 10 replicate runs of the admixture model, with a burn-in of 100,000 iterations and a run length of 100,000 steps. To compare differentiation inside and outside of the inversion, we divided the sample of *parviglumis* into the two clusters identified by STRUCTURE and calculated $F_{ST}$ (Weir and Cockerham 1984) between these two groups along chromosome 1.

Genetic (Manhattan) distance among inbred *parviglumis* lines was estimated with the software TASSEL (Bradbury *et al.* 2007) and calculated separately for SNPs inside and outside of the inversion. We used a Fitch–Margoliash least-squares approach (Fitch and Margoliash 1967) as implemented in the software package PHYLIP (Felsenstein 2005) to estimate a dendrogram for all taxa using the 17 SNPs inside the inversion.

We applied two common tests of neutrality (Hudson *et al.* 1987; McDonald and Kreitman 1991) to the Sanger resequencing data. For the McDonald–Kreitman (MK) test we used the seven resequenced loci inside the inversion and compared polymorphism at the inverted arrangement to divergence between the inverted arrangement and a *Sorghum* outgroup. For the Hudson–Kreitman–Aguade (HKA) test, we used 74 loci with ancestral information. HKA tests were performed both for the combined set of sequences and for sequences from each of the chromosomal arrangements separately. Because loci within the inversion are unlikely to be independent, we summed polymorphism and divergence data across loci within the inversion. We used the maximum-likelihood approach of Wright and Charlesworth (2004), running 100,000 Markov chain Monte Carlo (MCMC) iterations, and a starting *parviglumis–Sorghum* divergence of 60$N$ generations.

We estimated divergence time between the arrangements, using sequences at seven loci from the two observed haplotype groups inside the inversion. We treated samples of the two chromosomal arrangements as distinct populations and estimated divergence time under an isolation-with-migration model as implemented in the software MIMAR (Becquet and Przeworski 2007). We set the inheritance and the mutation rate variation scalars both to 1 and the recombination inheritance and rate variation scalar to $(Z_{ri} - 1)/(Z_i - 1)$, where $Z_{ri}$ is the initial length of locus $i$ and $Z_i$ corresponds to the number of base pairs in locus $i$ after filtering out indels and missing data. The mutation rate per generation per base pair was assumed constant across loci and set to $3 \times 10^{-8}$ (Clark *et al.* 2005b). The population mutation rate per base pair, divergence time, and the natural logarithm of the population migration parameter were sampled from the uniform distributions $U(0, 0.08)$, $U(0, 10^6)$, and $U(-2, 1)$, respectively. The exponential growth parameter was set to 6 (other values did not change results considerably). We ran the Markov chain for 5000 burn-in steps followed by 10,000 steps for parameter estimation, repeating our analysis with two independent seeds. Three hundred genealogies were generated per locus for each step of the MCMC. We inferred that convergence was reached when the posterior distributions of both runs were very similar; results reported are the average of both runs.

### Association analyses

We used a Bayesian approach (Coop *et al.* 2010) to test for associations between the inversion and 22 geographical (altitude, latitude, and longitude) and bioclimatic (worldclim.org) variables in the 33 *parviglumis* populations with ≥10 samples (Table S4). The analysis explicitly accounts for population structure, using a covariance matrix of allele frequencies estimated by 50,000 MCMC steps using all SNPs. We assessed association genome-wide using all SNPs and using a single-marker test, treating the inversion as a single locus. In each case, five separate runs with 50,000 iterations were performed to control for differences among MCMC runs.

To examine whether the inverted arrangement was associated with phenotypic variation, we used phenotype data from Weber *et al.* (2008). Both phenotype and genotype data were available for 811 individuals. A kinship matrix was estimated from all 941 SNPs, using the options "all" and "additive" in the EMMA R package (Kang *et al.* 2008). Both genome-wide association and single-marker association (treating the inversion as a single locus) were performed for each of 37 phenotypes. Associations were tested using a mixed linear model as implemented in the software TASSEL (Bradbury *et al.* 2007). The R package qvalue was used to estimate the false discovery rate (FDR) and identify SNPs that were significant at an FDR of 5% (Storey and Tibshirani 2003).

### Cytology

To assess the potential cytological impacts of the inversion, we screened 174 meiocytes from immature tassels of six *parviglumis/mays* $F_1$ progeny resulting from the cross of two inbred *parviglumis* each with a single *mays* inbred line. Meiocytes were collected and staged following Li *et al.* (2010) and the chromosomes stained with either 1% aceto-orcein or DAPI. Recombination within the inversion was scored as previously described, noting chromosome

bridges and acentric fragments at anaphase I (Dawe and Cande 1996).

## Results

We examined the level of LD in each of the three subspecies of *Z. mays* with a genome-wide set of 941 SNPs from 2782 samples. Using computationally phased genotypic data, we searched for pairs of markers in high LD ($r^2 > 0.6$) and separated by >1 Mb. Our scan identified two such regions, an ~50-Mb region on chromosome 1 and an ~15-Mb span of chromosome 8. Because the region on chromosome 8 is near a likely assembly error in the reference genome (J. Glaubitz, unpublished data), we focused our analysis on chromosome 1. The region of high LD on chromosome 1 in our data corresponds closely to the 65- to 115-Mb region on the physical map of the reference *mays* genome (B73 RefGen v2, release 5a.59, 2010–2011) recently reported by Hufford *et al.* (2012) as a putative inversion. Our data reveal high LD (mean $r^2 = 0.24$) among the 17 SNPs from Mb 65.09 to 106.16 (Figure 1), compared to a genome-wide average of 0.004. Gametic disequilibrium, as estimated from unphased SNP genotyping data, also demonstrates this excess of LD (data not shown). Finally, high levels of LD are also evident in genotypic data from a panel of 13 individuals of *parviglumis* genotyped using the 55,000 SNPs on the MaizeSNP50 Illumina Infinium Assay (Hufford *et al.* 2012), suggesting that the LD observed is not an artifact of the genotyping platform used.

### *The extended region of high LD on chromosome 1 is a putative inversion*

Because *mays* and the teosintes are outcrossing taxa with large effective population sizes, LD in the genome generally declines rapidly with distance ($r^2 < 0.1$ within 1500 bp in domesticated *mays*) (Remington *et al.* 2001). The region of high LD is distinct from both the centromere (Wolfgruber *et al.* 2009) and known heterochromatic knobs (Buckler *et al.* 1999) and exhibits relatively low recombination (Figure 1). An ~50-Mb span of high LD is unexpected, and while *parviglumis* and *mexicana* show evidence of high LD in this chromosomal region, levels of LD in our large sample of domesticated *mays* are similar to genome-wide averages (Figure 1). Other wild taxa also do not show an excess of LD on the short arm of chromosome 1, although our power to measure LD in these samples is likely hampered by smaller sample size and SNP ascertainment bias. Finally, a recent genetic map from a BC2S3 population derived from a cross between a *mays* line and a *parviglumis* line with the putatively inverted arrangement shows no crossovers inside the ~50-Mb span in the 881 progeny genotyped, consistent with the putative inversion suppressing recombination in heterozygotes (L. Shannon and J. Doebley, unpublished data). Although final validation will require demonstrating differential marker order in the progeny of self-fertilized individuals

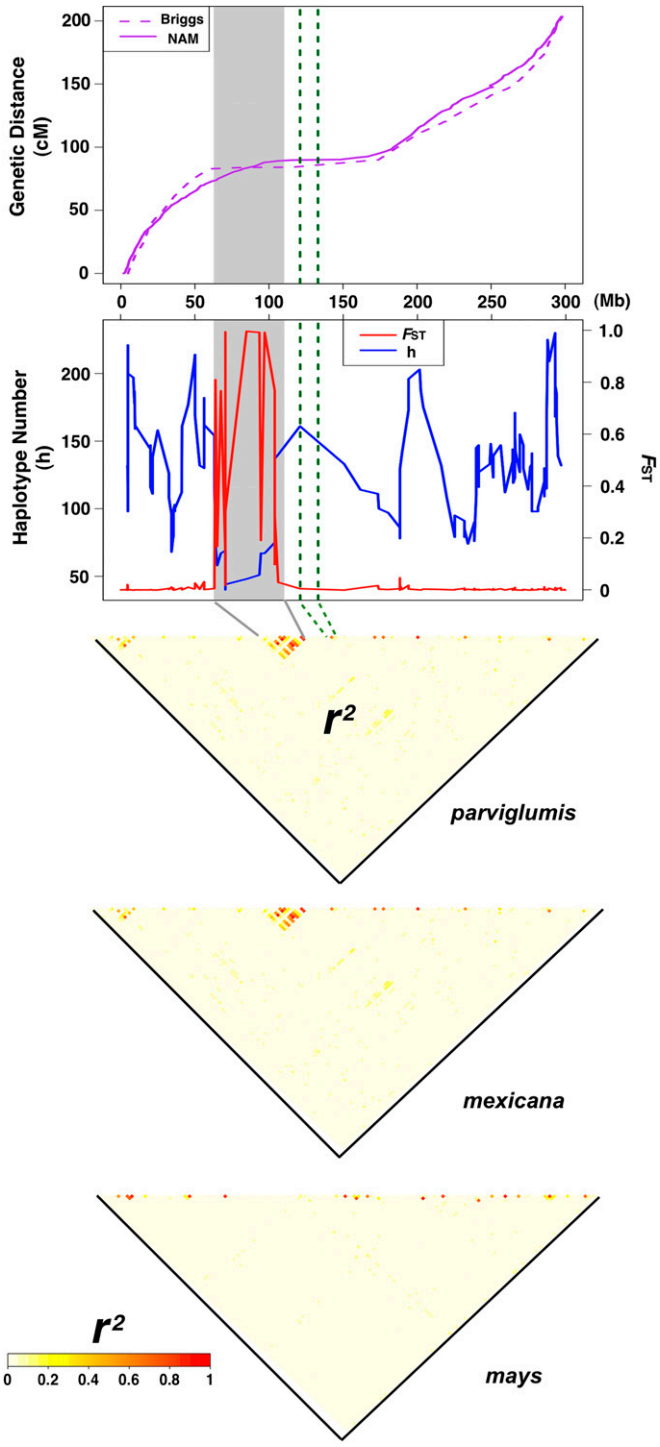


**Figure 1** Population genetic evidence for the *Inv1n* inversion. Top, cumulative genetic distance by physical position along chromosome 1. The dashed curve is based on the teosinte–maize backcross map of Briggs *et al.* (2007) and the solid curve is from the maize nested association-mapping (NAM) population (Yu *et al.* 2008). Bottom, haplotype number (blue curve) and $F_{ST}$ between the inverted and standard arrangements (red curve). The number of haplotypes present across chromosome 1 was calculated in overlapping 10-SNP windows with 1-SNP increments. The inverted region is marked in gray and the centromere in green dashed lines. Below, LD ($r^2$) is plotted across the chromosome for *parviglumis*, *mexicana*, and *mays*.

homozygous for alternate arrangements (Mano *et al.* 2012), we view these multiple lines of evidence as a strong case that recombination is suppressed due to an inversion in this region, henceforth identified as *Inv1n*.

To test for evidence of pairing and recombination within the large *Inv1n* region, we examined male meiocytes from six $F_1$ plants derived from two crosses between *mays* and an inbred *parviglumis* line containing *Inv1n*. Both hybrids revealed a low frequency of dicentric bridge formation at ~4% (7/167), but no acentric fragments were observed (Table S5). Although such bridges were rare, an anaphase I bridge in a plant heterozygous for *Inv1n* was observed (Figure S1). In addition, we observed no obvious reduction in pollen viability or seed set in a total of five $F_1$ plants (data not shown).

### *Haplotype variation and divergence time*

STRUCTURE (Pritchard *et al.* 2000; Falush *et al.* 2003) analysis of SNPs on all 1936 *parviglumis* chromosomes inside *Inv1n* shows the highest likelihood for $K = 2$ clusters, a pattern not seen from the full set of genome-wide SNPs (data not shown). These groups are hereafter referred to as *Inv1n-I* and *Inv1n-S* for the inverted and standard arrangements, respectively (Figure 2). Recombination among loci within a chromosomal arrangement should be unaffected, and levels of LD within *Inv1n-I* (mean $r^2 = 0.11$) and *Inv1n-S* arrangements (mean $r^2 = 0.07$) are indeed low and similar to background levels (Figure S2). Average $F_{ST}$ between chromosomes with alternate arrangements is notably higher inside the *Inv1n* region (0.54) than across the rest of the genome (0.01) (Figure 1). Genetic distance among accessions for SNPs along chromosome 1 outside the *Inv1n* region shows little evidence of haplotype structure (Figure 3A), while genetic distance for SNPs inside *Inv1n* divides *parviglumis* into two clear haplotypic groups representing *Inv1n-I* and *Inv1n-S* (Figure 3B). The *Inv1n-S* cluster includes all taxa of *Zea* and *Tripsacum* investigated, and it is parsimonious to assume that the *Inv1n-I* cluster, present only in *parviglumis* and *mexicana*, represents the derived inverted arrangement (Figure 3C). Despite strong differentiation, the two arrangements share polymorphic SNPs (Figure 2), even in homozygous individuals unaffected by haplotype phasing (data not shown). Among the 968 *parviglumis* samples, 345 (35.6%) are heterozygous at *Inv1n*, while 369 (38.1%) and 254 (26.3%) are homozygous for the *Inv1n-I* and *Inv1n-S* arrangements, respectively. *Inv1n-I* consists of a smaller number of distinct haplotypes and shows a paucity of rare haplotype variants compared to *Inv1n-S* (Figure 2).

Resequencing data from seven loci within *Inv1n* mirror these results (Table 1). Four loci (PZA00692, PZA00593, PZA03014, and PZA00146) show distinct haplotype clusters consistent with the SNP genotyping data (data not shown), dividing *parviglumis* into two groups representing *Inv1n-I* and *Inv1n-S*. A comparison of the two groups reveals a higher number of fixed differences, fewer shared derived SNPs, and higher average $F_{ST}$ (0.53 *vs.* 0.05) inside the *Inv1n* region than outside. Average Tajima's *D* of the entire sample is higher inside *Inv1n* (0.58 *vs.* −0.29), and the lack of rare haplotypes on the *Inv1n-I* background observed in the SNP data is reflected in the positive Tajima's *D* at sequences from these chromosomes (Table 1). All alleles private to *Inv1n-I* are derived on the basis of the *Sorghum* outgroup sequence, but 30% of the alleles private to *Inv1n-S* are ancestral.

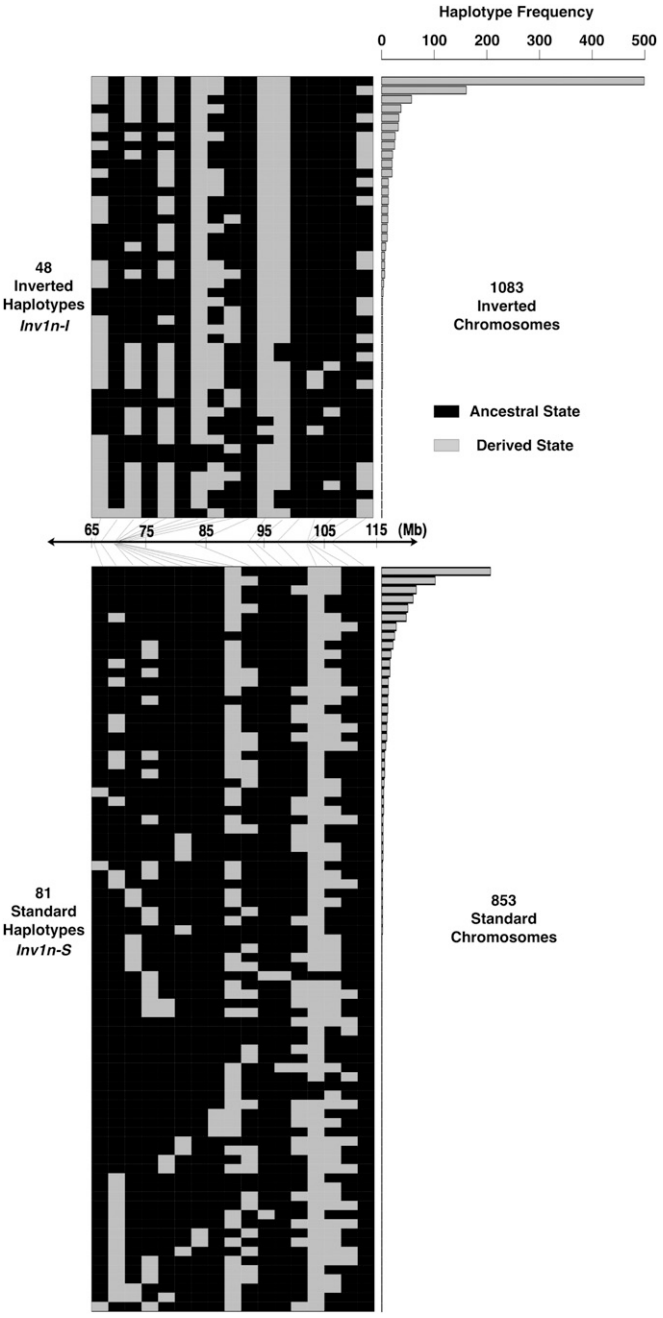


**Figure 2** Diagram of haplotype diversity in *parviglumis* based on the 17 SNPs within *Inv1n*. Haplotypes are divided into the two clusters identified by STRUCTURE. Each SNP is represented by either the ancestral state (solid) or the derived state (shaded). The frequency of each of the haplotypes from the inverted (top) and standard (bottom) arrangements is shown on the right. The middle bar shows the physical position of each of the 17 SNPs inside *Inv1n*.

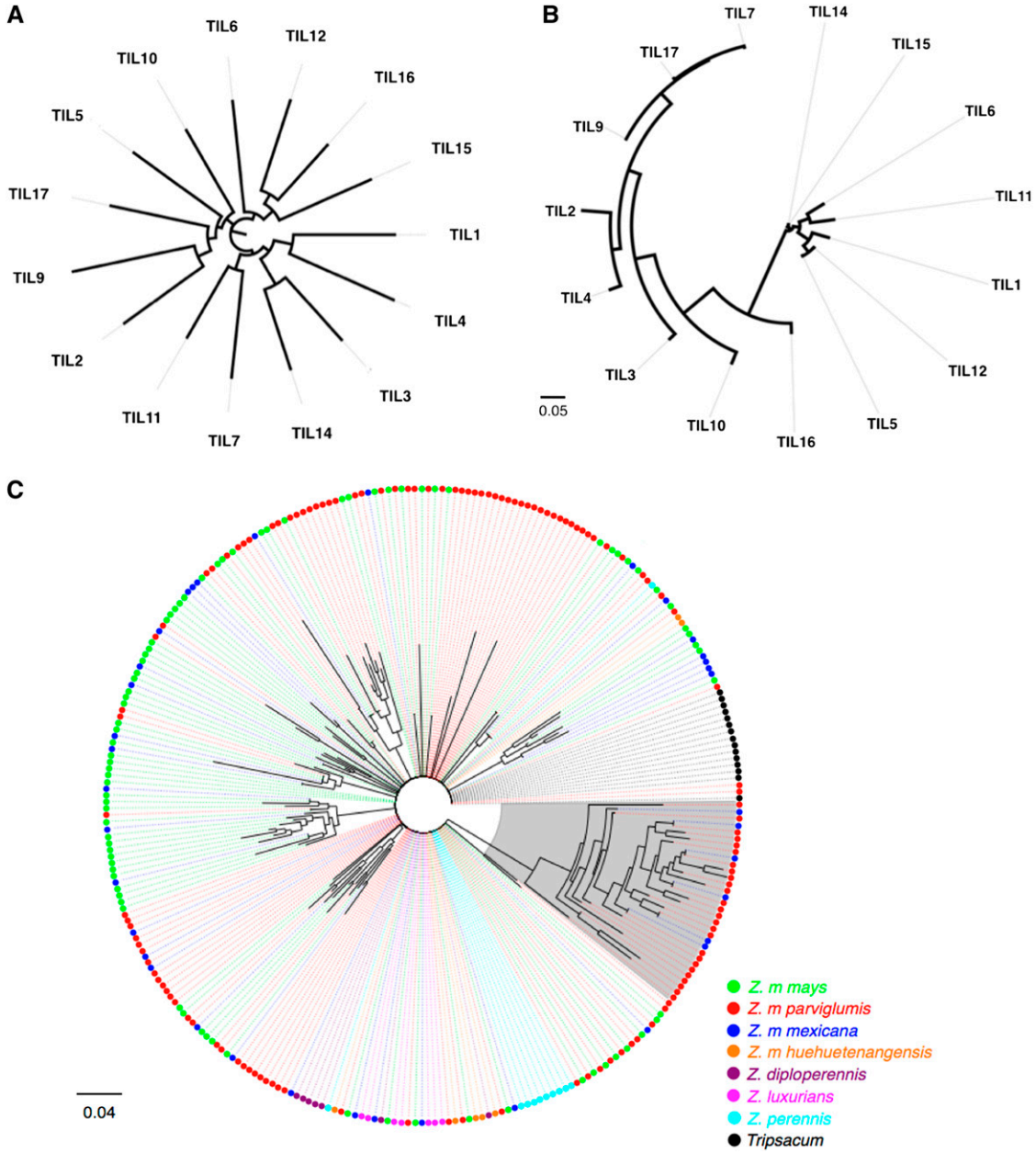


**Figure 3** (A) Neighbor-joining tree for all SNPs outside *Inv1n*, using 15 *parviglumis* inbred lines. (B) Neighbor-joining tree for all SNPs inside *Inv1n*, using 15 *parviglumis* inbred lines. (C) Neighbor-joining tree for all unique haplotypes in each taxon, using all SNPs inside *Inv1n*. The haplotypes in the gray region represent the *Inv1n-I* arrangement.

We used multiple approaches to estimate the age of *Inv1n-I* from the resequencing data. Using the MCMC approach of Becquet and Przeworski (2007), which estimates divergence time from patterns of shared polymorphism under an isolation model, divergence was estimated to be ~296,000 generations, with a 95% confidence interval

**Table 1 Mean (and standard deviation) of summary statistics for 7 resequenced loci inside and 88 loci outside *Inv1n***

| | No. loci | *n* | *L* | $S_{sh}$ | $S_f$ | $S_p$ | *h* | *H* | $\theta_\pi$ | Taj *D* | Fay and Wu's *H* |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Inside (*Inv1n-I*) | 7 (6) | 14.6 (1.5) | 307 (88) | 0.3 (0.8) | 4.3 (3.1) | 2.9 (3.2) | 2.3 (1.4) | 0.49 (0.41) | 0.004 (0.004) | 0.37 (1.21) | −0.001 (0.003) |
| Inside (*Inv1n-S*) | 7 (6) | 14.6 (1.5) | 307 (88) | 0.3 (0.8) | 4.3 (3.1) | 2.9 (2.5) | 3.3 (1.7) | 0.59 (0.36) | 0.004 (0.003) | −0.70 (0.56) | 0 (0.003) |
| Outside (*Inv1n-I*) | 88 (68) | 13.5 (1.9) | 414 (107) | 4.7 (4.6) | 0.1 (0.9) | 4.1 (4.1) | 3.9 (1.2) | 0.89 (0.21) | 0.011 (0.009) | −0.22 (0.65) | −0.003 (0.017) |
| Outside (*Inv1n-S*) | 88 (68) | 13.5 (1.9) | 414 (107) | 4.7 (4.6) | 0.1 (0.9) | 4.7 (3.6) | 4.7 (1.8) | 0.88 (0.21) | 0.010 (0.007) | −0.34 (0.62) | −0.008 (0.029) |

The number of loci with an outgroup is listed in parentheses in the "No. loci" column. The numbers in parentheses in other columns are standard deviations: *n*, number of samples; *L*, length of the locus; $S_{sh}$, number of shared SNPs between *Inv1n-I* and *Inv1n-S*; $S_f$, number of fixed SNPs; $S_p$, number of private SNPs; *h*, number of haplotypes; *H*, haplotype diversity; $\theta_\pi$, pairwise difference per base pair.

(C.I.) between 221,000 and 398,000 generations. Assuming a constant rate of substitution of $3 \times 10^{-8}$ per generation (Clark *et al.* 2005b), we can also calculate divergence time from net differences in nucleotide diversity (Nei and Li 1979) between *Inv1n-I* and *Inv1n-S*, which gives an estimate of 260,000 generations. Finally, estimates of the time to the most recent common ancestor (TMRCA) (Thomson *et al.* 2000; Hudson 2007) of the complete sample inside *Inv1n* (308,100 generations, 95% C.I. of 272,800–345,600 generations) and of *Inv1n-I* alone (133,200 generations, 95% C.I. of 96,500–175,800 generations) are consistent with other methods.

### *Neutrality tests*

On the basis of standard tests of neutrality, there is limited evidence of selection on *Inv1n*. HKA tests on *Inv1n* did not detect evidence of balancing selection caused by environmental heterogeneity (*P*-value = 0.46, divergence to diversity ratio = 2.58). MK (*P*-value = 0.65) and HKA (*P*-value = 0.15) tests on resequencing data from the *Inv1n-I* arrangement failed to reject a neutral model, and Fay and Wu's *H* (Fay and Wu 2000) did not differ markedly between the *Inv1n-I* arrangements or compared to loci outside of *Inv1n* (Table 1).

### *Population frequencies and association analyses*

All 33 *parviglumis* populations sampled were polymorphic for both arrangements at the *Inv1n* locus, with a mean *Inv1n-I* frequency of 55%. The frequency of *Inv1n-I* is negatively correlated with altitude ($r^2$ = 0.34) (Figure 4, Figure S3, and Table S4), ranging from 90% in the Quenchendio population at an altitude of 653 m to 18.4% in Ahuacatitlan at 1528 m. Consistent with this, *Inv1n-I* occurs at a frequency of only 9.7% in subspecies *mexicana*, which is found at higher altitudes than subspecies *parviglumis* (mean altitude of 2091 m *vs.* 1087 m for our *mexicana* and *parviglumis* samples). The most common *Inv1n-I* haplotype makes up 46% (499/1083) of *parviglumis* chromosomes with the *Inv1n-I* variant and does not vary significantly in frequency among populations ($\chi^2$ = 2.27, d.f. = 32, *P*-value = 1).

Using a model-based approach (Coop *et al.* 2010) to control for population structure, we examined the association between *Inv1n-I* frequency and 22 environmental variables (Table S6). Among environmental variables, altitude was most strongly correlated with *Inv1n-I* frequency and consistently obtained the highest Bayes factors among runs (mean 136). High Bayes factors were also observed for other bioclimatic variables, including temperature (mean temperature of driest quarter, mean Bayes factor = 49) and precipitation (precipitation of driest month, mean Bayes factor = 48). Genome-wide analysis of all SNPs produced mean Bayes factors for association with altitude ranging from 0.29 to 1048 (Table S6). SNPs in the inversion are 10-fold enriched in the top 5% tail of Bayes factors for altitude and >20-fold enriched in the top 1% tail, strongly suggesting a link between *Inv1n* and altitude (Figure 5).

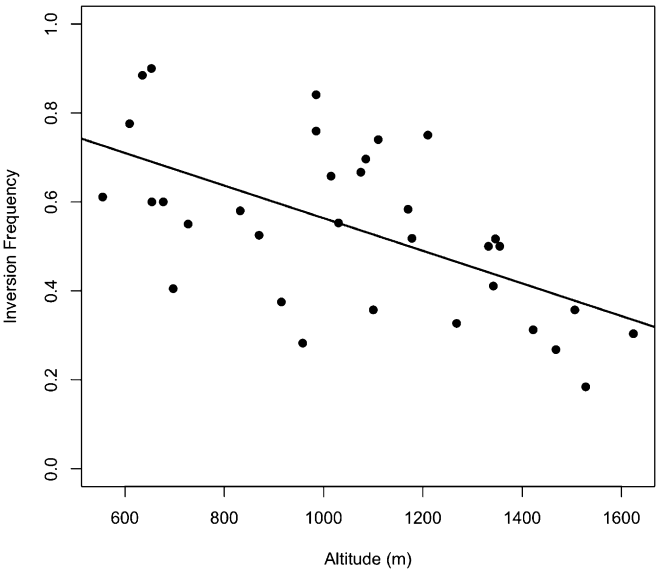


**Figure 4** *Inv1n-I* frequency in *parviglumis* populations is negatively correlated with altitude. Each point corresponds to a population, with its altitude on the *x*-axis and *Inv1n-I* frequency on the *y*-axis.

We also used a mixed linear model analysis to test for associations between *Inv1n-I* and phenotypic data from the same populations (Weber *et al.* 2008). *Inv1n-I* appears to be associated with the percentage of male internodes (PSIN) (*P*-value = 0.0055, $r^2$ = 0.024), percentage of staminate spikelets (STAM) (*P*-value = 0.0069, $r^2$ = 0.023), culm diameter (CULM) (*P*-value = 0.0137, $r^2$ = 0.011), and leaf number (LFNM) (*P*-value = 0.0232, $r^2$ = 0.010) (Table S7), but none of the associations are significant after Bonferroni correction for phenotypes tested and effect sizes for all phenotypes are very small. In addition to testing the inversion as a single locus, we also investigated associations between individual SNPs and phenotypes. For both PSIN and STAM, none of the 17 SNPs in *Inv1n* were among the 1% of SNPs most strongly associated with the two phenotypes. However, SNPs in *Inv1n* were enriched in the 1% tail of *P*-values for both CULM (15× enrichment) and LFNM (3×). None of the SNPs were significantly associated with PSIN or LFNM at a FDR of 5%, while four SNPs outside of the inversion were significantly associated with STAM. Of the seven SNPs significantly associated with CULM at an FDR of 5%, four (PZA00263.14, PZD00077.7, PZA00692.5, and PZA03014.24) are inside *Inv1n*.

## Discussion

Using a genome-wide set of SNPs in a large panel of wild and domesticated *Zea*, we provide evidence of an ~50-Mb inversion on the short arm of chromosome 1 of subspecies *parviglumis* and *mexicana*. While our cytological data are not directly diagnostic for an inversion, population genetic data preclude alternative explanations. For example, the dramatic reduction in haplotype number in the *Inv1n* region (Figure 1) could be indicative of a selective sweep (Kim and

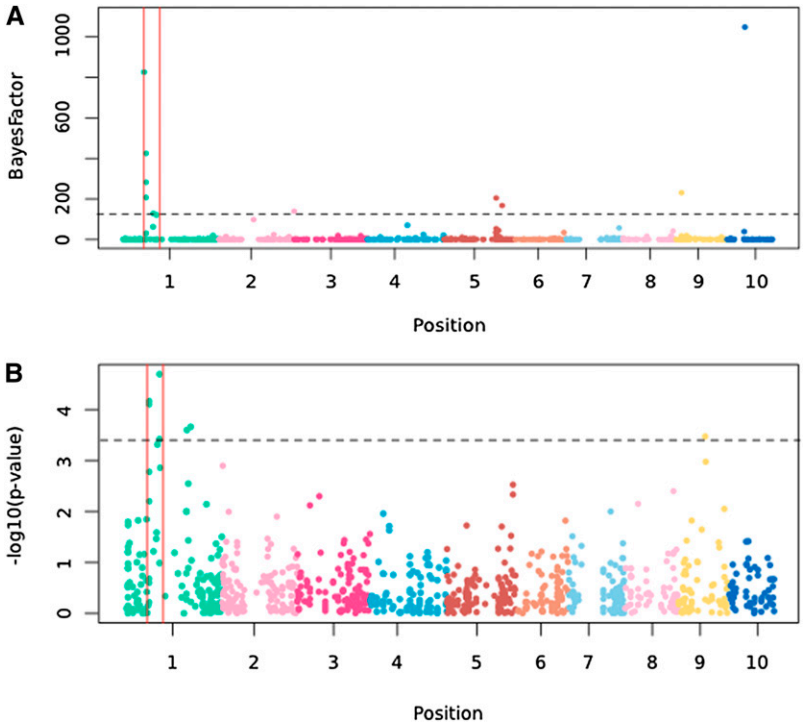


**Figure 5** (A) Bayes factors for correlation between allele frequencies and altitude in 33 natural *parviglumis* populations. *Inv1n* is indicated by red vertical lines. The 99th percentile of the distribution of Bayes factors is indicated by a horizontal dashed line. Chromosomes 1–10 are plotted in order and in different colors. (B) Association between all SNPs and culm diameter. SNPs significant at 5% FDR are above the dashed line.

Nielsen 2004; Nielsen *et al.* 2005; McVean 2007). However, the largest sweep identified in maize to date is only 1.1 Mb (Tian *et al.* 2009), and both the age of the inversion and common tests for departures from neutrality do not provide evidence of strong selection. Another alternative explanation would be the presence of strong negative interactions between distantly linked loci, potentially due to synthetic lethality (Boone *et al.* 2007). Such interactions should not generate extended patterns of elevated LD among intervening SNPs, as crossing over among haplotypes not carrying alleles involved in the negative interaction should not be affected. Both selective sweeps and negative interactions are inconsistent with the presence of only two major haplotypes in the *Inv1n* region and fail to explain the clinal variation in haplotype frequencies seen at *Inv1n-I*.

To our knowledge, the only prior evidence for *Inv1n* is a report of high LD and high $F_{ST}$ from a much smaller sample of *parviglumis* (Hufford *et al.* 2012), but a number of other large inversions have been previously reported in *mays* and its wild relatives (Ting 1965, 1967, 1976; Maguire 1966; Kato 1975). These include an ~50-Mb inversion on the long arm of chromosome 3 in *Z. luxurians* (Ting 1965) and an ~35-Mb inversion that covers most of the short arm of chromosome 8 in both *mays* (McClintock 1960) and *mexicana* (Ting 1976). While some of these inversions were experimentally induced (McClintock 1931; Morgan 1950), several have also been identified in natural populations of multiple taxa (Kato 1975; Ting 1976).

One of the factors that may limit the geographic spread of large inversions is the potential fitness cost of crossing over. The frequency of chromosome loss is dependent on the inversion size and efficiency of synapsis over the inverted region (Burnham 1962; Maguire and Riess 1994; Lamb *et al.* 2007). When gene density is low, such as in pericentromeric regions, or there is a lack of continuous homology, chromosomes will often synapse in a nonhomologous manner without recombination (McClintock 1933). In maize, for example, an inversion on the long arm of chromosome 1 similar in size to *Inv1n* (19 cM) was seen to undergo homologous pairing in only about one-third of cases (Maguire 1966). Since *Inv1n* is located in a pericentromeric region with low gene density and covers a short genetic distance (2–13 cM), we anticipated that it would rarely pair and recombine with a noninverted chromosome. Our data are consistent with these arguments. We observed repressed recombination around *Inv1n* and no cytological evidence of crossing over in inversion heterozygotes. SNP data indicate no deviations from expected Hardy–Weinberg genotype frequencies at *Inv1n*, and we see no obvious evidence of effects on fertility. Given these observations, we suspect that inversion polymorphisms may be relatively common in natural plant populations, especially in regions of the genome with low recombination rates such as pericentromeres. Low recombination has also been offered as an explanation for the lack of underdominance in many pericentromeric inversions in *Drosophila* (Coyne *et al.* 1993). As dense genotyping becomes more cost effective, we predict that numerous common inversions will be identified in natural populations of *Zea* and other organisms.

### *Origin and age of Inv1n*

Our evidence suggests that *Inv1n-I* is the derived, inverted arrangement. *Inv1n-I* is not found in *Tripsacum* or *Zea* taxa except for *parviglumis* and *mexicana* (Figure 3C), and, unlike in *Inv1n-S*, all SNPs private to *Inv1n-I* are derived in

resequencing data. Both SNP and resequencing data show strong differentiation between the two arrangements (Figure 1 and Table 1). Multiple methods of estimating the age of the *Inv1n-I* haplotype point to an origin ~300,000 generations ago. This predates both the split between *mexicana* and *parviglumis* and the split between *Z. luxurians* and *Z. mays* and is similar to the estimated age of divergence of most species in the genus *Zea* (Ross-Ibarra *et al.* 2009). Several considerations suggest that these numbers are plausible. First, the proportion of SNPs shared between *parviglumis* and *mexicana* on chromosome 1 does not differ inside or outside of *Inv1n* (15/17 *vs.* 134/139, Fisher's exact test *P*-value = 0.48), suggesting that the presence of the inversion in both subspecies is likely due to shared ancestral polymorphism rather than recent gene flow. Second, while the estimated age of *Inv1n-I* is similar to the estimated divergence of species, other species in *Zea* have narrow distributions (Fukunaga *et al.* 2005) and presumably small effective population sizes, increasing the potential for loss of variants at low frequency in the ancestral population. Third, *Inv1n-I* could consist of multiple independent inversions, similar to the inversion polymorphisms identified in the white-throated sparrow (Thomas *et al.* 2008). In this case, estimates of the age of the inversion would be biased upward, as each inversion would have arisen independently on distinct backgrounds. Such a scenario might also explain the observation of shared polymorphisms between *Inv1n-I* and *Inv1n-S*. Our data cannot distinguish the number of independent inversions in the region, however, which would instead require analysis of progeny derived from crosses of multiple individuals homozygous for different haplotypes of *Inv1n-I* and a more dense set of markers.

While small effective population size may explain the absence of *Inv1n-I* from other taxa in *Zea*, its complete absence in our sample of 1573 *mays* requires additional explanation. Sampling alone is unlikely to play a role, as the vast majority of our *mays* accessions are landraces, collected from across the Americas, including accessions collected within the range of *parviglumis* and *mexicana*. Estimates of the domestication bottleneck and observed levels of diversity in domesticated *mays* (Tenaillon *et al.* 2004; Wright *et al.* 2005) also suggest that drift during domestication is not a compelling explanation, especially given that *Inv1n-I* occurs at frequencies of up to 90% in the lowland areas where domestication is thought to have occurred (Matsuoka *et al.* 2002; Piperno *et al.* 2009; van Heerwaarden *et al.* 2011). We speculate instead that *Inv1n-I* may have been selected against in domesticated *mays*. Our association analysis provides limited evidence in support of this idea, as *Inv1n-I* is negatively associated with culm width in *parviglumis*, while domesticated *mays* has more robust culms than its wild progenitor (Briggs *et al.* 2007).

### *Selection on Inv1n*

While standard tests of neutrality do not provide evidence for selection, there is reason to believe that *Inv1n* is not evolving neutrally. First, the *Inv1n-I* arrangement is widely distributed, segregating in all 33 populations investigated; only two SNPs on chromosome 1 are also polymorphic in all populations. Second, pairwise $F_{ST}$ inside *Inv1n* appears uncorrelated to pairwise $F_{ST}$ genome-wide ($r^2 = 0.04$; Figure S4), suggesting that the frequency of *Inv1n* is not entirely due to isolation by distance. Third, even after correcting for population structure, *Inv1n-I* frequency is associated with a number of environmental variables (Table S6), including a strong altitudinal cline (Figure 4 and Figure S3). Latitudinal (Anderson *et al.* 2005; Santos *et al.* 2005; Umina *et al.* 2005) and altitudinal clines (Levitan 2001) are commonly observed for inversion polymorphisms and are often thought to be related to temperature adaptation (Levitan 2001; Umina *et al.* 2005; Balanyá *et al.* 2006). Fourth, the *Inv1n-I* arrangement is, to our knowledge, the first inversion in *Zea* shown to be associated with phenotypic differences (Table S7). These include culm diameter, a trait that differentiates maize from teosinte (Briggs *et al.* 2007), and tassel morphology (Table S7), which is known to differ between *parviglumis* and *mexicana* (Doebley 1983) and between lowland and highland maize (Anderson 1946; Bretting and Goodman 1989). Fifth, the lack of rare variants and the high frequency of the most common *Inv1n-I* haplotype (Figure 2) suggest that this haplotype may have recently risen to high frequency due to a partial sweep. The observed lack of rare variants is especially striking given the genome-wide pattern of an excess of low-frequency variants (Table 1), an observation reported in multiple studies (Tenaillon *et al.* 2004; Wright *et al.* 2005; Moeller *et al.* 2007; Ross-Ibarra *et al.* 2009). While the most common haplotype at *Inv1n-I* does not show signs of extended homozygosity beyond the borders of the inversion (Figure S5) as might be expected if it has been recently swept to higher frequency, the nearest flanking SNPs are 1.1 and 14.6 Mb distant and our power to detect an extended haplotype is low. Sixth, the absence of *Inv1n-I* from domesticated maize, in spite of recurrent gene flow from both *parviglumis* and *mexicana* (Wilkes 1967; Fukunaga *et al.* 2005; Ross-Ibarra *et al.* 2009; van Heerwaarden *et al.* 2011), suggests that the inverted arrangement was selected against at some point during *mays* domestication or breeding. Finally, we note that, aside from strong divergence between chromosomes of different arrangements, selection may be difficult to detect in diversity data from inversions of an age similar to ours (Guerrero *et al.* 2012).

Selection may act on inversions because of the fitness consequences of the structural rearrangement itself or of adaptive alleles at loci inside the inversion (Kirkpatrick and Barton 2006). While these scenarios predict somewhat different patterns of diversity (Guerrero *et al.* 2012), our SNP genotyping data are of insufficient density to distinguish between them. Regardless of the mechanism of selection, the observed altitudinal cline and absence in domesticated *mays* suggest that *Inv1n-I* is not ubiquitously adaptive. Even in low-altitude populations where it seems to be favored, a large inversion such as *Inv1n* may have captured several

recessive deleterious alleles, effectively preventing its fixation (Kirkpatrick and Barton 2006).

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GENETICS

**Supporting Information**
http://www.genetics.org/content/suppl/2012/04/27/genetics.112.138578.DC1

# Megabase-Scale Inversion Polymorphism in the Wild Ancestor of Maize

**Zhou Fang, Tanja Pyhäjärvi, Allison L. Weber, R. Kelly Dawe, Jeffrey C. Glaubitz, José de Jesus Sánchez González, Claudia Ross-Ibarra, John Doebley, Peter L. Morrell, and Jeffrey Ross-Ibarra**


DOI: 10.1534/genetics.112.138578

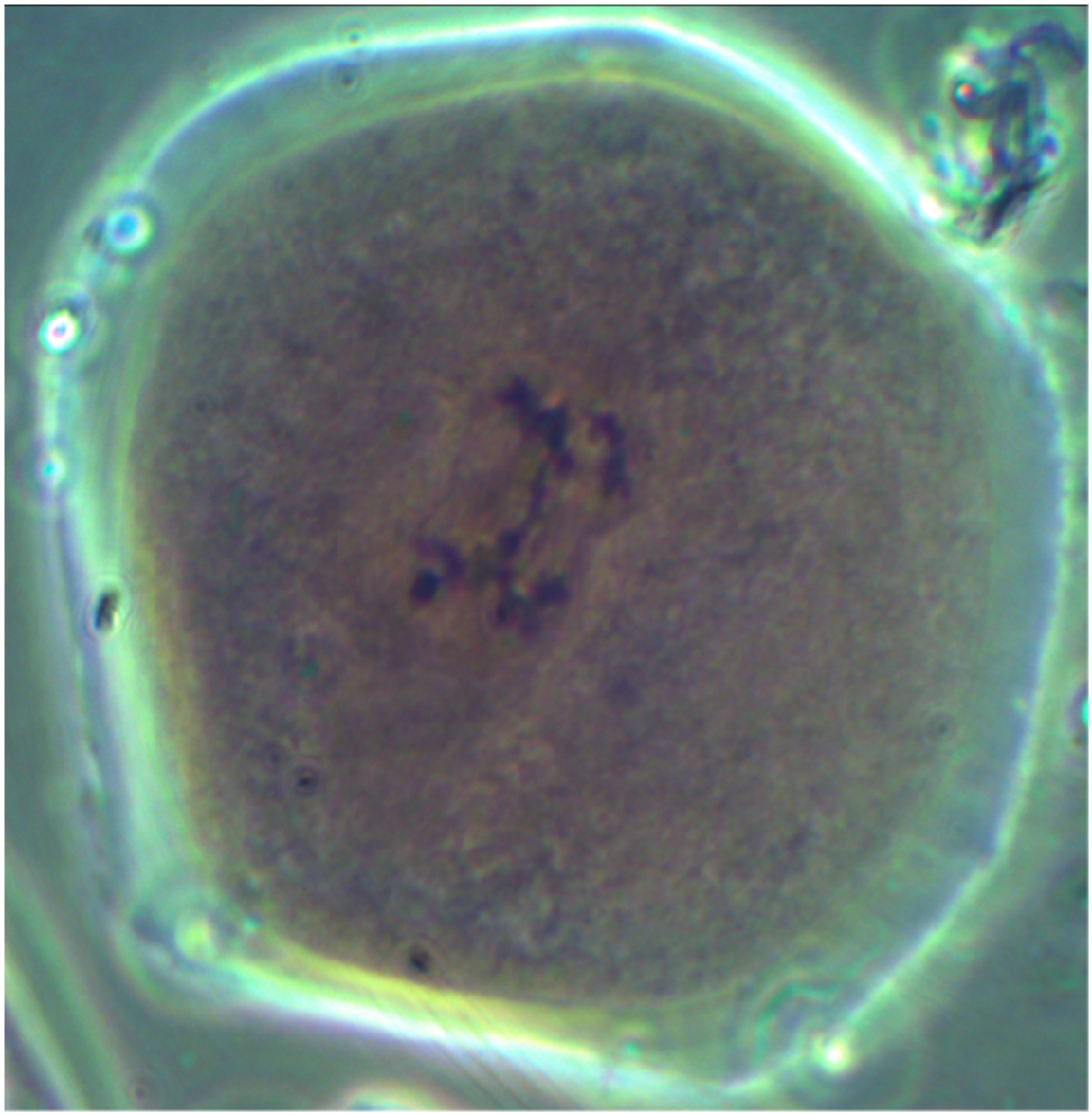

**Figure S1** An anaphase I bridge in a plant heterozygous for *Inv1n*. Such bridges were rare, observed in only ~4% of the meiocytes undergoing anaphase I.

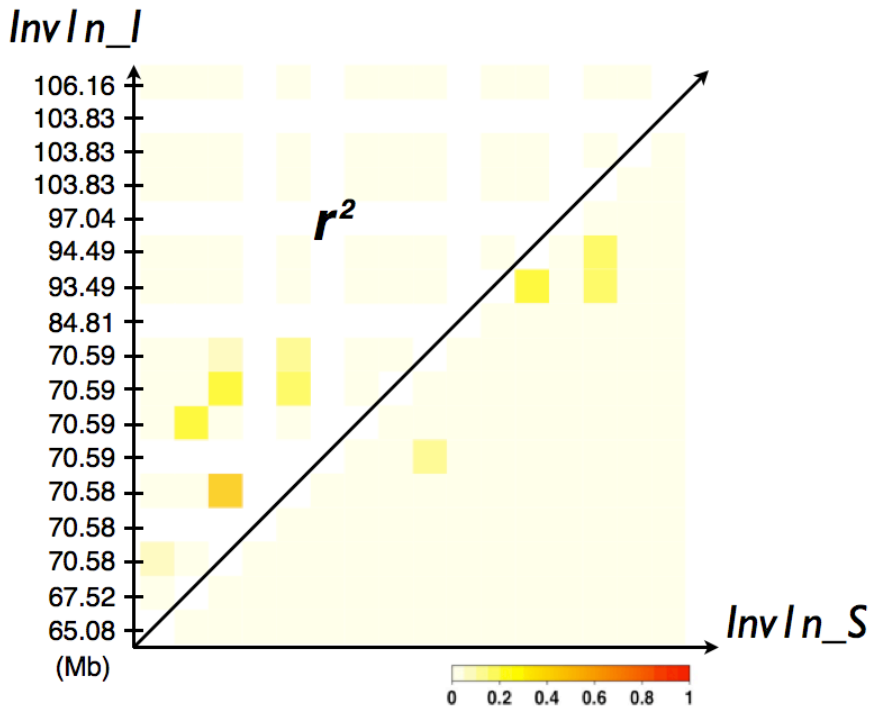


**Figure S2** LD ($r^2$) among the 17 SNPs inside *Inv1n* in *parviglumis.* The physical positions of the 17 SNPs are shown on the left. The upper triangle represents LD in *Inv1n-I*, and *Inv1n-S* is shown in the lower triangle.

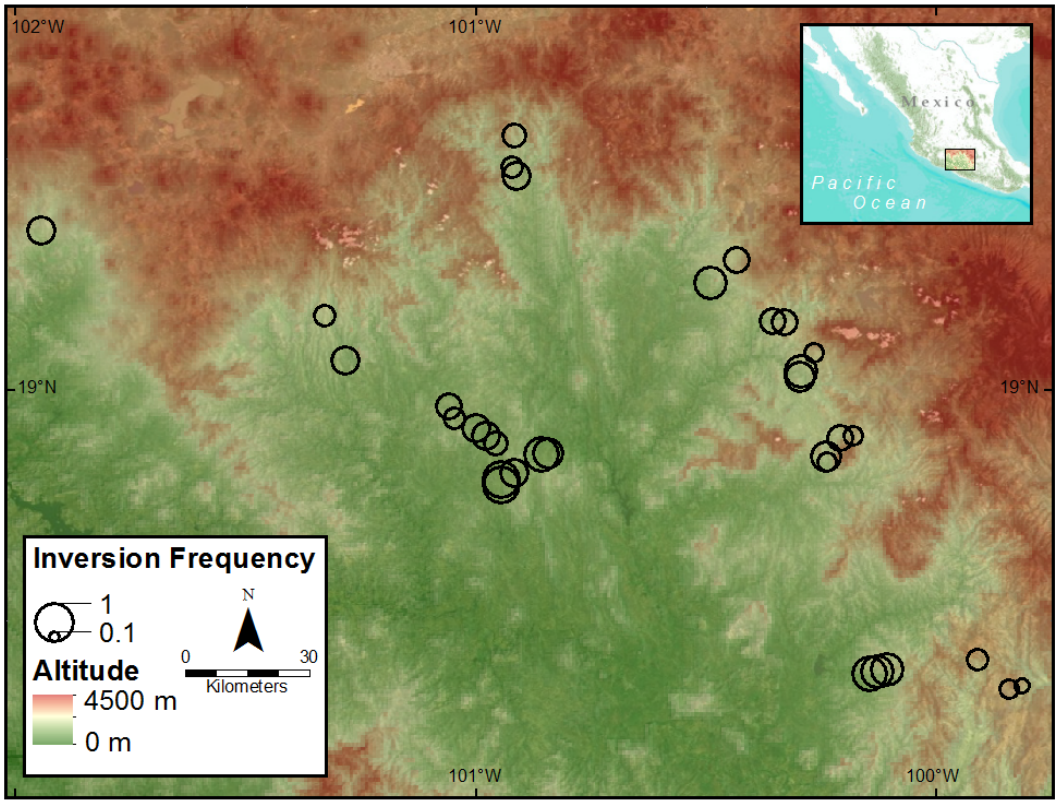


**Figure S3** Geographic distribution of the 33 *parviglumis* populations. The size of the circle is proportional to the *Inv1n* frequency, and color represents elevation. The study area in Mexico is shown in the inset.

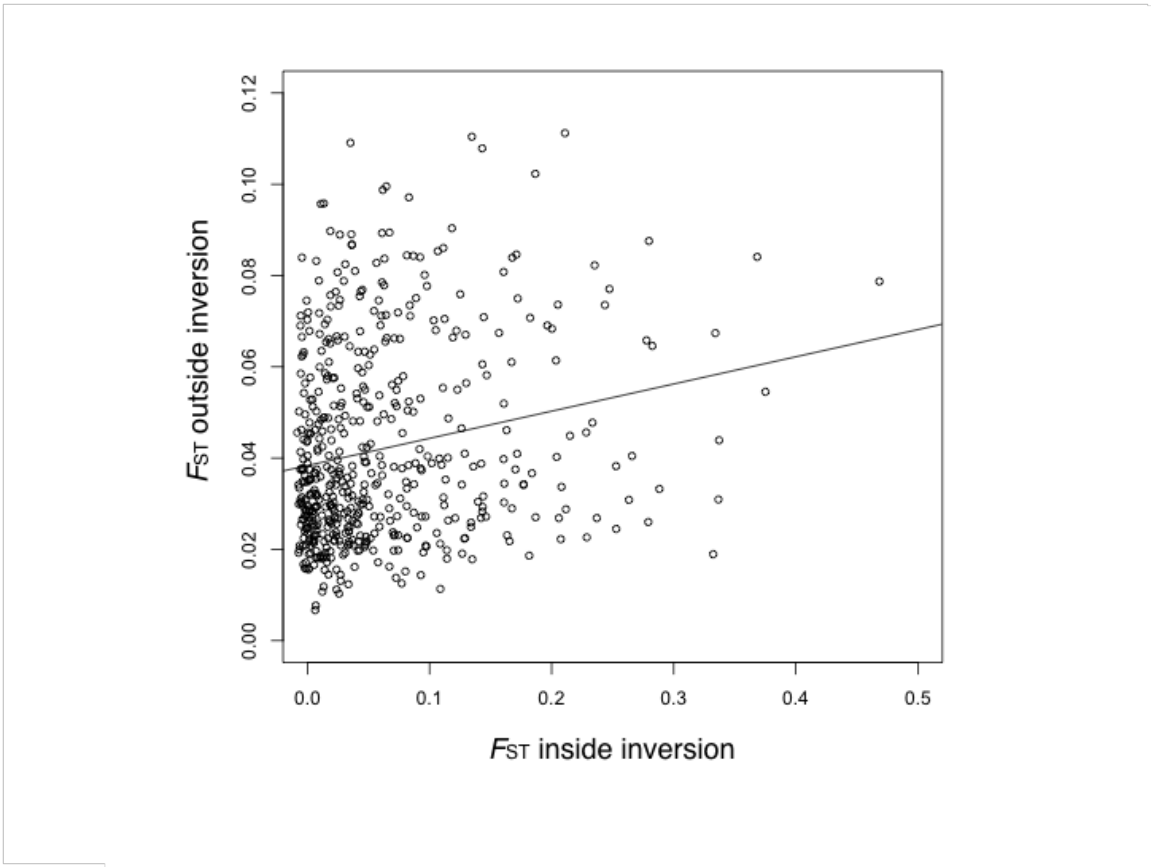


**Figure S4** Pairwise $F_{ST}$ among 33 *parviglumis* natural populations at SNPs inside *Inv1n* compared to SNPs outside *Inv1n.*

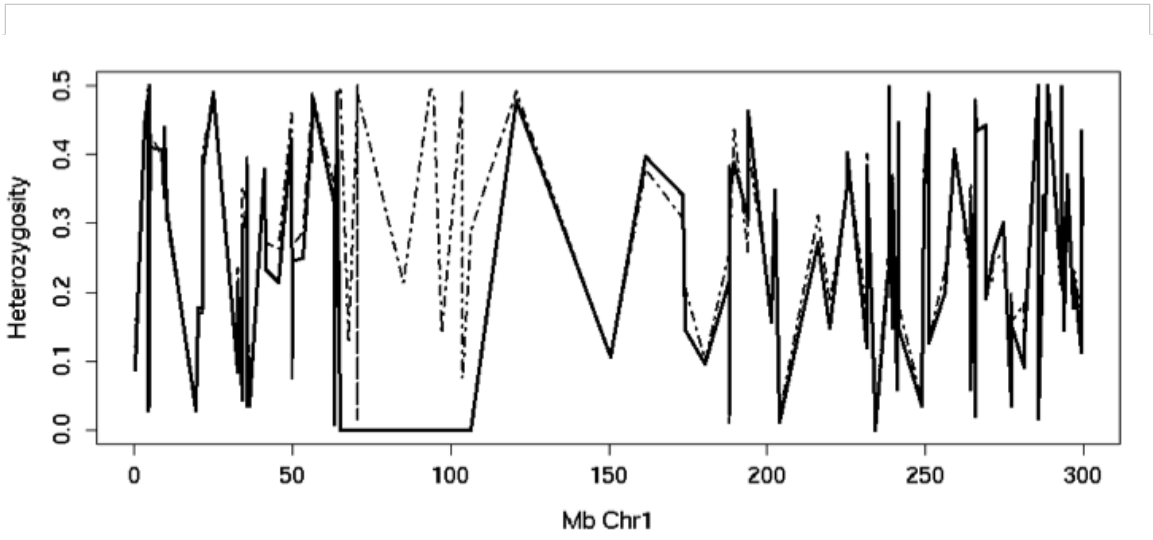


**Figure S5** Expected SNP heterozygosity across chromosome 1 for all *parviglumis* (dashed line) and the most common *Inv1n-I* haplotype (solid line).

**Table S1 Sample locality including germplasm type (in a separate file).**

Table S1 is available for download at http://www.genetics.org/content/suppl/2012/04/27/genetics.112.138578.DC1 as an Excel file.

**Table S2 Data on 941 SNPs used in this paper**

| SNP | Chr | RefGen v2 Position |
|---|---|---|
| abph1.20 | 2 | 27,482,289 |
| abph1.22 | 2 | 27,482,777 |
| ae1.3 | 5 | 168,468,441 |
| ae1.4 | 5 | 168,468,333 |
| ae1.5 | 5 | 168,468,472 |
| an1.4 | 1 | 241,222,410 |
| ba1.6 | 3 | 183,084,850 |
| ba1.9 | 3 | 183,085,136 |
| bt2.5 | 4 | 58,957,188 |
| bt2.7 | 4 | 58,956,243 |
| bt2.8 | 4 | 58,956,482 |
| Fea2.1 | 4 | 133,663,613 |
| Fea2.5 | 4 | 133,663,191 |
| id1.3 | 1 | 239,609,554 |
| lg2.11 | 3 | 176,805,886 |
| lg2.2 | 3 | 176,805,320 |
| pbf1.1 | 2 | 153,513,462 |
| pbf1.2 | 2 | 153,513,364 |
| pbf1.3 | 2 | 153,512,659 |
| pbf1.5 | 2 | 153,512,386 |
| pbf1.6 | 2 | 153,511,544 |
| pbf1.7 | 2 | 153,510,870 |
| pbf1.8 | 2 | 153,510,843 |
| PZA00003.11 | 6 | 121,697,500 |
| PZA00004.2 | 5 | 13,621,123 |
| PZA00005.8 | 4 | 237,391,332 |
| PZA00005.9 | 4 | 237,391,476 |
| PZA00006.13 | 6 | 86,257,528 |
| PZA00006.14 | 6 | 86,257,555 |
| PZA00008.1 | 2 | 12,024,277 |
| PZA00010.5 | 1 | 120,848,790 |
| PZA00013.10 | 1 | 264,163,949 |
| PZA00013.11 | 1 | 264,163,707 |
| PZA00013.9 | 1 | 264,164,037 |
| PZA00015.4 | 9 | 113,420,505 |
| PZA00017.1 | 1 | 35,578,083 |
| PZA00018.5 | 8 | 156,627,475 |

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| PZA00029.11 | 2 | 147,311,129 |
| PZA00029.12 | 2 | 147,311,042 |
| PZA00031.5 | 5 | 123,964,207 |
| PZA00041.3 | 6 | 122,710,163 |
| PZA00042.2 | 6 | 156,981,860 |
| PZA00042.5 | 6 | 156,981,744 |
| PZA00043.7 | 7 | 172,926,856 |
| PZA00045.1 | 8 | 118,191,980 |
| PZA00049.12 | 8 | 134,066,246 |
| PZA00050.9 | 1 | 296,575,998 |
| PZA00051.2 | 4 | 239,429,365 |
| PZA00058.5 | 8 | 6,023,537 |
| PZA00058.6 | 8 | 6,023,577 |
| PZA00060.2 | 9 | 129,011,584 |
| PZA00061.1 | 2 | 33,346,033 |
| PZA00065.2 | 1 | 49,621,367 |
| PZA00069.4 | 5 | 215,340,163 |
| PZA00070.5 | 9 | 88,242,881 |
| PZA00078.2 | 4 | 18,682,174 |
| PZA00079.1 | 10 | 18,859,495 |
| PZA00081.17 | 1 | 45,513,286 |
| PZA00084.2 | 7 | 41,732,007 |
| PZA00084.3 | 7 | 41,731,951 |
| PZA00088.3 | 3 | 230,181,537 |
| PZA00090.2 | 8 | 138,794,764 |
| PZA00092.1 | 4 | 114,693,724 |
| PZA00092.5 | 4 | 114,693,700 |
| PZA00093.2 | 8 | 124,657,588 |
| PZA00096.26 | 7 | 149,603,394 |
| PZA00097.13 | 8 | 146,033,256 |
| PZA00098.14 | 1 | 161,615,948 |
| PZA00100.10 | 3 | 5,673,891 |
| PZA00100.12 | 3 | 5,673,605 |
| PZA00100.14 | 3 | 5,673,926 |
| PZA00100.9 | 3 | 5,673,572 |
| PZA00106.9 | 1 | 10,096,325 |
| PZA00107.18 | 3 | 182,088,854 |
| PZA00108.12 | 2 | 13,851,566 |
| PZA00108.14 | 2 | 13,851,376 |
| PZA00108.15 | 2 | 13,851,427 |
| PZA00109.3 | 3 | 113,066,409 |
| PZA00109.5 | 3 | 113,066,444 |
| PZA00111.2 | 7 | 139,366,525 |

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| PZA00111.4 | 7 | 139,366,225 |
| PZA00111.5 | 7 | 139,366,472 |
| PZA00111.6 | 7 | 139,366,469 |
| PZA00111.8 | 7 | 139,366,372 |
| PZA00114.3 | 3 | 146,252,963 |
| PZA00116.2 | 9 | 129,409,633 |
| PZA00119.4 | 1 | 84,814,783 |
| PZA00120.4 | 8 | 148,515,290 |
| PZA00123.1 | 9 | 153,738,351 |
| PZA00125.2 | 4 | 36,210,500 |
| PZA00131.14 | 1 | 203,947,049 |
| PZA00132.17 | 7 | 31,773,777 |
| PZA00132.18 | 7 | 31,773,878 |
| PZA00132.3 | 7 | 31,773,709 |
| PZA00135.6 | 10 | 109,712,602 |
| PZA00137.2 | 1 | 248,738,069 |
| PZA00139.14 | 4 | 20,200,937 |
| PZA00140.10 | 2 | 143,045,557 |
| PZA00140.6 | 2 | 143,045,483 |
| PZA00140.9 | 2 | 143,045,604 |
| PZA00142.6 | 8 | 144,271,083 |
| PZA00163.4 | 2 | 223,310,842 |
| PZA00164.1 | 2 | 220,832,970 |
| PZA00164.2 | 2 | 220,833,009 |
| PZA00164.3 | 2 | 220,832,898 |
| PZA00166.1 | 3 | 173,587,461 |
| PZA00166.3 | 3 | 173,587,211 |
| PZA00170.1 | 2 | 69,704,230 |
| PZA00170.3 | 2 | 69,704,287 |
| PZA00170.4 | 2 | 69,704,335 |
| PZA00174.1 | 10 | 66,638,175 |
| PZA00174.2 | 10 | 66,638,311 |
| PZA00175.2 | 1 | 8,558,256 |
| PZA00176.8 | 2 | 10,624,968 |
| PZA00177.4 | 8 | 156,772,795 |
| PZA00178.3 | 7 | 170,990,302 |
| PZA00182.3 | 6 | 113,558,220 |
| PZA00182.4 | 6 | 113,558,165 |
| PZA00184.1 | 9 | 155,683,609 |
| PZA00184.4 | 9 | 155,683,487 |
| PZA00188.1 | 7 | 2,998,218 |
| PZA00188.3 | 7 | 2,998,557 |
| PZA00191.5 | 5 | 2,120,221 |

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| PZA00192.7 | 1 | 35,579,161 |
| PZA00193.2 | 4 | 192,205,587 |
| PZA00198.39 | 6 | 164,372,830 |
| PZA00200.11 | 2 | 5,819,590 |
| PZA00200.17 | 2 | 5,820,190 |
| PZA00200.9 | 2 | 5,819,731 |
| PZA00201.2 | 3 | 199,274,401 |
| PZA00204.1 | 10 | 127,348,939 |
| PZA00210.1 | 3 | 30,057,289 |
| PZA00210.6 | 3 | 30,057,176 |
| PZA00211.7 | 7 | 131,186,613 |
| PZA00212.1 | 6 | 72,869,016 |
| PZA00213.19 | 9 | 130,918,999 |
| PZA00214.1 | 6 | 92,813,618 |
| PZA00216.9 | 4 | 2,999,034 |
| PZA00218.1 | 4 | 71,640,363 |
| PZA00218.6 | 4 | 71,640,430 |
| PZA00219.7 | 3 | 220,883,383 |
| PZA00220.11 | 3 | 208,344,179 |
| PZA00220.12 | 3 | 208,344,329 |
| PZA00221.7 | 1 | 173,317,166 |
| PZA00225.8 | 9 | 107,625,055 |
| PZA00226.7 | 2 | 42,792,015 |
| PZA00227.8 | 7 | 167,241,354 |
| PZA00230.5 | 1 | 299,528,078 |
| PZA00232.24 | 3 | 174,582,549 |
| PZA00234.21 | 3 | 223,307,712 |
| PZA00235.6 | 1 | 293,795,824 |
| PZA00235.8 | 1 | 293,795,893 |
| PZA00237.2 | 2 | 6,049,080 |
| PZA00237.7 | 2 | 6,048,795 |
| PZA00237.8 | 2 | 6,048,913 |
| PZA00238.3 | 2 | 197,595,234 |
| PZA00240.9 | 1 | 41,104,364 |
| PZA00241.6 | 6 | 150,304,658 |
| PZA00243.27 | 1 | 296,891,619 |
| PZA00245.14 | 1 | 285,522,115 |
| PZA00245.16 | 1 | 285,522,140 |
| PZA00245.17 | 1 | 285,521,947 |
| PZA00245.18 | 1 | 285,521,975 |
| PZA00245.19 | 1 | 285,522,004 |
| PZA00249.2 | 5 | 100,929,495 |

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| PZA00251.1 | 10 | 122,801,848 |
| PZA00254.3 | 3 | 143,488,417 |
| PZA00255.15 | 5 | 170,416,067 |
| PZA00255.17 | 5 | 170,416,167 |
| PZA00256.16 | 7 | 17,520,123 |
| PZA00256.21 | 7 | 17,520,225 |
| PZA00256.23 | 7 | 17,520,294 |
| PZA00257.11 | 10 | 10,882,576 |
| PZA00257.22 | 10 | 10,882,651 |
| PZA00261.6 | 5 | 75,935,660 |
| PZA00263.14 | 1 | 65,086,477 |
| PZA00266.5 | 6 | 161,454,751 |
| PZA00273.1 | 5 | 84,064,839 |
| PZA00274.7 | 1 | 41,377,563 |
| PZA00277.17 | 2 | 144,729,592 |
| PZA00277.9 | 2 | 144,729,626 |
| PZA00280.14 | 2 | 62,991,918 |
| PZA00287.1 | 9 | 75,780,129 |
| PZA00289.11 | 1 | 216,050,825 |
| PZA00294.20 | 1 | 63,891,664 |
| PZA00297.2 | 3 | 40,322,808 |
| PZA00297.3 | 3 | 40,322,831 |
| PZA00297.4 | 3 | 40,322,907 |
| PZA00298.4 | 8 | 168,273,519 |
| PZA00298.5 | 8 | 168,273,438 |
| PZA00299.2 | 8 | 79,007,430 |
| PZA00300.12 | 5 | 172,395,470 |
| PZA00300.13 | 5 | 172,395,364 |
| PZA00300.14 | 5 | 172,395,199 |
| PZA00300.16 | 5 | 172,395,504 |
| PZA00301.3 | 1 | 106,159,660 |
| PZA00303.19 | 3 | 189,347,439 |
| PZA00303.21 | 3 | 189,347,297 |
| PZA00307.12 | 1 | 293,041,636 |
| PZA00307.14 | 1 | 293,041,693 |
| PZA00309.2 | 3 | 1,298,636 |
| PZA00310.5 | 10 | 20,409,576 |
| PZA00314.6 | 8 | 154,651,600 |
| PZA00314.8 | 8 | 154,651,315 |
| PZA00315.1 | 4 | 40,157,629 |
| PZA00315.6 | 4 | 40,157,532 |
| PZA00318.2 | 1 | 256,084,651 |

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| PZA00323.3 | 9 | 146,915,036 |
| PZA00323.4 | 9 | 146,915,233 |
| PZA00326.16 | 7 | 159,131,005 |
| PZA00326.18 | 7 | 159,131,080 |
| PZA00326.19 | 7 | 159,131,038 |
| PZA00332.8 | 4 | 189,042,100 |
| PZA00332.9 | 4 | 189,042,120 |
| PZA00334.2 | 8 | 155,483,084 |
| PZA00337.3 | 10 | 86,424,870 |
| PZA00337.4 | 10 | 86,424,768 |
| PZA00337.5 | 10 | 86,424,803 |
| PZA00342.9 | 10 | 130,512,105 |
| PZA00344.10 | 4 | 187,355,764 |
| PZA00345.15 | 5 | 62,595,345 |
| PZA00346.1 | 7 | 145,729,154 |
| PZA00346.2 | 7 | 145,729,102 |
| PZA00346.3 | 7 | 145,729,100 |
| PZA00349.3 | 2 | 21,283,667 |
| PZA00349.5 | 2 | 21,283,640 |
| PZA00350.2 | 7 | 152,832,335 |
| PZA00352.22 | 5 | 191,590,886 |
| PZA00355.1 | 6 | 79,915,144 |
| PZA00355.2 | 6 | 79,915,132 |
| PZA00356.9 | 1 | 264,533,418 |
| PZA00364.5 | 1 | 269,025,539 |
| PZA00364.6 | 1 | 269,025,550 |
| PZA00367.2 | 2 | 164,723,975 |
| PZA00369.1 | 1 | 219,807,376 |
| PZA00370.1 | 7 | 128,121,229 |
| PZA00370.5 | 7 | 128,121,322 |
| PZA00380.5 | 3 | 39,822,327 |
| PZA00380.7 | 3 | 39,822,411 |
| PZA00381.3 | 1 | 238,343,204 |
| PZA00381.4 | 1 | 238,343,143 |
| PZA00381.5 | 1 | 238,343,616 |
| PZA00382.17 | 6 | 118,604,616 |
| PZA00385.3 | 1 | 292,796,839 |
| PZA00386.3 | 7 | 170,656,392 |
| PZA00390.6 | 2 | 209,927,372 |
| PZA00391.2 | 3 | 158,354,531 |
| PZA00392.3 | 7 | 144,981,423 |
| PZA00392.4 | 7 | 144,981,553 |
| PZA00393.1 | 1 | 4,193,258 |

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| PZA00393.4 | 1 | 4,193,538 |
| PZA00394.11 | 2 | 56,966,318 |
| PZA00395.1 | 5 | 203,679,356 |
| PZA00395.2 | 5 | 203,679,327 |
| PZA00396.12 | 2 | 4,692,070 |
| PZA00401.11 | 5 | 56,019,395 |
| PZA00401.6 | 5 | 56,019,323 |
| PZA00406.1 | 5 | 92,183,810 |
| PZA00407.9 | 5 | 49,522,205 |
| PZA00408.7 | 5 | 215,357,992 |
| PZA00409.3 | 10 | 62,249,775 |
| PZA00411.1 | 1 | 251,088,838 |
| PZA00411.4 | 1 | 251,088,969 |
| PZA00411.5 | 1 | 251,088,935 |
| PZA00413.17 | 3 | 128,907,269 |
| PZA00413.18 | 3 | 128,907,125 |
| PZA00413.21 | 3 | 128,907,248 |
| PZA00417.2 | 8 | 45,262,229 |
| PZA00417.3 | 8 | 45,262,014 |
| PZA00419.1 | 8 | 126,550,861 |
| PZA00420.4 | 3 | 228,448,528 |
| PZA00422.2 | 8 | 154,682,448 |
| PZA00422.5 | 8 | 154,682,386 |
| PZA00422.6 | 8 | 154,682,317 |
| PZA00423.16 | 7 | 172,769,215 |
| PZA00423.17 | 7 | 172,769,301 |
| PZA00424.1 | 7 | 174,785,900 |
| PZA00425.4 | 1 | 21,468,390 |
| PZA00425.9 | 1 | 21,468,287 |
| PZA00429.1 | 8 | 145,842,587 |
| PZA00433.5 | 5 | 214,074,969 |
| PZA00436.7 | 4 | 6,408,499 |
| PZA00439.6 | 6 | 141,610,864 |
| PZA00440.1 | 6 | 32,969,931 |
| PZA00442.3 | 2 | 63,668,565 |
| PZA00442.4 | 2 | 63,668,537 |
| PZA00442.5 | 2 | 63,668,622 |
| PZA00442.6 | 2 | 63,668,616 |
| PZA00444.1 | 10 | 106,952,925 |
| PZA00444.5 | 10 | 106,952,878 |
| PZA00445.18 | 4 | 49,917,528 |
| PZA00449.2 | 5 | 38,201,854 |
| PZA00458.6 | 3 | 5,674,594 |

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| PZA00459.5 | 2 | 17,094,806 |
| PZA00460.3 | 8 | 164,859,711 |
| PZA00460.5 | 8 | 164,859,744 |
| PZA00460.7 | 8 | 164,859,811 |
| PZA00462.2 | 6 | 44,008,563 |
| PZA00463.3 | 10 | 13,493,461 |
| PZA00466.1 | 9 | 12,104,064 |
| PZA00468.11 | 1 | 50,096,641 |
| PZA00468.7 | 1 | 50,096,930 |
| PZA00470.1 | 5 | 170,023,744 |
| PZA00471.2 | 2 | 22,504,931 |
| PZA00471.3 | 2 | 22,505,161 |
| PZA00471.4 | 2 | 22,505,011 |
| PZA00472.2 | 5 | 63,229,797 |
| PZA00477.10 | 1 | 299,197,598 |
| PZA00477.11 | 1 | 299,197,721 |
| PZA00477.5 | 1 | 299,197,562 |
| PZA00477.9 | 1 | 299,197,628 |
| PZA00478.10 | 2 | 165,667,714 |
| PZA00478.11 | 2 | 165,667,750 |
| PZA00478.7 | 2 | 165,668,066 |
| PZA00478.9 | 2 | 165,667,779 |
| PZA00480.10 | 3 | 23,306,494 |
| PZA00481.7 | 8 | 24,530,674 |
| PZA00484.5 | 1 | 180,308,158 |
| PZA00485.2 | 2 | 124,057,780 |
| PZA00487.16 | 2 | 225,160,494 |
| PZA00487.24 | 2 | 225,160,213 |
| PZA00487.26 | 2 | 225,160,158 |
| PZA00489.1 | 6 | 51,226,441 |
| PZA00495.3 | 2 | 173,250,676 |
| PZA00495.4 | 2 | 173,250,689 |
| PZA00495.6 | 2 | 173,250,638 |
| PZA00496.1 | 7 | 167,915,230 |
| PZA00497.1 | 2 | 19,918,031 |
| PZA00497.4 | 2 | 19,917,977 |
| PZA00498.4 | 8 | 52,299,554 |
| PZA00499.10 | 5 | 35,276,873 |
| PZA00499.12 | 5 | 35,276,915 |
| PZA00499.3 | 5 | 35,276,907 |
| PZA00501.12 | 6 | 34,440,016 |
| PZA00501.14 | 6 | 34,440,097 |
| PZA00502.5 | 9 | 143,803,192 |

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| PZA00503.5 | 6 | 22,667,086 |
| PZA00504.1 | 7 | 147,716,994 |
| PZA00504.2 | 7 | 147,716,948 |
| PZA00505.4 | 7 | 168,254,993 |
| PZA00505.8 | 7 | 168,255,179 |
| PZA00510.2 | 6 | 131,323,502 |
| PZA00510.3 | 6 | 131,323,440 |
| PZA00514.1 | 9 | 107,313,968 |
| PZA00514.6 | 9 | 107,313,892 |
| PZA00514.7 | 9 | 107,314,063 |
| PZA00515.14 | 2 | 172,144,187 |
| PZA00516.3 | 8 | 164,866,616 |
| PZA00517.6 | 5 | 18,348,509 |
| PZA00522.12 | 5 | 58,603,542 |
| PZA00523.2 | 4 | 149,284,134 |
| PZA00525.16 | 2 | 2,539,802 |
| PZA00525.2 | 2 | 2,539,982 |
| PZA00527.6 | 2 | 219,860,018 |
| PZA00527.9 | 2 | 219,860,155 |
| PZA00529.3 | 4 | 235,165,818 |
| PZA00531.1 | 8 | 125,316,626 |
| PZA00533.3 | 2 | 190,430,209 |
| PZA00533.4 | 2 | 190,430,143 |
| PZA00533.5 | 2 | 190,430,284 |
| PZA00533.6 | 2 | 190,430,239 |
| PZA00534.2 | 7 | 21,636,438 |
| PZA00536.2 | 6 | 123,777,598 |
| PZA00538.12 | 3 | 208,472,870 |
| PZA00538.16 | 3 | 208,473,135 |
| PZA00538.8 | 3 | 208,472,941 |
| PZA00543.2 | 6 | 81,692,897 |
| PZA00543.4 | 6 | 81,693,175 |
| PZA00543.5 | 6 | 81,693,243 |
| PZA00545.21 | 5 | 207,708,730 |
| PZA00545.22 | 5 | 207,708,616 |
| PZA00545.4 | 5 | 207,708,479 |
| PZA00547.13 | 5 | 93,579,904 |
| PZA00547.18 | 5 | 93,579,495 |
| PZA00552.4 | 10 | 26,987,438 |
| PZA00562.4 | 10 | 61,954,391 |
| PZA00565.3 | 3 | 73,964,566 |
| PZA00568.19 | 9 | 133,422,395 |
| PZA00573.3 | 5 | 160,830,866 |

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| PZA00579.6 | 9 | 151,724,182 |
| PZA00582.4 | 6 | 62,187,756 |
| PZA00586.1 | 3 | 187,713,152 |
| PZA00587.3 | 10 | 84,610,447 |
| PZA00587.6 | 10 | 84,610,480 |
| PZA00588.2 | 9 | 61,356,589 |
| PZA00588.4 | 9 | 61,356,555 |
| PZA00589.10 | 9 | 43,679,421 |
| PZA00589.8 | 9 | 43,679,500 |
| PZA00589.9 | 9 | 43,679,530 |
| PZA00593.2 | 1 | 93,492,705 |
| PZA00595.3 | 5 | 165,658,227 |
| PZA00600.11 | 8 | 85,123,811 |
| PZA00603.1 | 5 | 184,494,852 |
| PZA00608.1 | 3 | 68,056,795 |
| PZA00608.5 | 3 | 68,056,885 |
| PZA00610.18 | 1 | 281,206,778 |
| PZA00610.9 | 1 | 281,206,931 |
| PZA00613.22 | 2 | 4,193,245 |
| PZA00614.12 | 7 | 151,523,785 |
| PZA00615.3 | 3 | 1,885,957 |
| PZA00615.6 | 3 | 1,885,816 |
| PZA00615.8 | 3 | 1,885,793 |
| PZA00617.16 | 1 | 53,270,492 |
| PZA00618.22 | 3 | 190,889,590 |
| PZA00620.2 | 2 | 10,516,860 |
| PZA00621.2 | 3 | 69,856,000 |
| PZA00622.1 | 6 | 114,439,165 |
| PZA00622.2 | 6 | 114,438,752 |
| PZA00623.2 | 1 | 294,729,591 |
| PZA00626.3 | 5 | 66,831,722 |
| PZA00626.4 | 5 | 66,831,656 |
| PZA00630.9 | 4 | 96,312,649 |
| PZA00637.4 | 2 | 172,403,167 |
| PZA00639.12 | 2 | 210,078,347 |
| PZA00639.13 | 2 | 210,078,538 |
| PZA00639.15 | 2 | 210,078,233 |
| PZA00641.7 | 8 | 167,465,970 |
| PZA00641.8 | 8 | 167,465,876 |
| PZA00644.11 | 4 | 25,326,089 |
| PZA00647.9 | 10 | 130,080,970 |
| PZA00650.8 | 1 | 189,588,779 |

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| PZA00654.12 | 1 | 32,543,175 |
| PZA00655.1 | 7 | 139,358,571 |
| PZA00656.15 | 10 | 17,602,152 |
| PZA00656.16 | 10 | 17,602,091 |
| PZA00656.18 | 10 | 17,601,973 |
| PZA00656.4 | 10 | 17,601,894 |
| PZA00658.19 | 1 | 225,130,798 |
| PZA00658.23 | 1 | 225,131,040 |
| PZA00662.3 | 4 | 124,359,583 |
| PZA00665.6 | 10 | 69,031,285 |
| PZA00667.1 | 3 | 162,743,710 |
| PZA00672.6 | 2 | 232,004,707 |
| PZA00672.8 | 2 | 232,004,713 |
| PZA00673.2 | 1 | 259,012,580 |
| PZA00674.3 | 5 | 169,236,723 |
| PZA00676.2 | 2 | 217,281,403 |
| PZA00680.1 | 2 | 1,094,384 |
| PZA00680.3 | 2 | 1,094,394 |
| PZA00682.2 | 4 | 239,370,840 |
| PZA00684.12 | 5 | 920,922 |
| PZA00686.8 | 8 | 148,078,863 |
| PZA00692.5 | 1 | 94,489,227 |
| PZA00693.3 | 9 | 28,399,313 |
| PZA00695.1 | 7 | 171,232,753 |
| PZA00698.4 | 1 | 274,531,768 |
| PZA00700.3 | 4 | 3,262,444 |
| PZA00704.11 | 4 | 129,738,534 |
| PZA00705.5 | 1 | 97,038,983 |
| PZA00706.16 | 8 | 161,188,592 |
| PZA00710.1 | 5 | 62,200,260 |
| PZA00710.16 | 5 | 62,200,400 |
| PZA00712.4 | 10 | 117,991,835 |
| PZA00715.3 | 5 | 193,301,336 |
| PZA00717.14 | 8 | 70,199,281 |
| PZA00719.1 | 3 | 144,344,237 |
| PZA00719.2 | 3 | 144,344,055 |
| PZA00719.3 | 3 | 144,343,938 |
| PZA00720.2 | 2 | 153,510,503 |
| PZA00720.3 | 2 | 153,510,547 |
| PZA00721.4 | 6 | 147,137,475 |
| PZA00721.5 | 6 | 147,137,547 |
| PZA00725.4 | 2 | 204,879,868 |

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| PZA00726.7 | 4 | 91,996,159 |
| PZA00726.9 | 4 | 91,996,053 |
| PZA00727.11 | 10 | 143,259,325 |
| PZA00727.12 | 10 | 143,259,404 |
| PZA00729.18 | 2 | 188,980,715 |
| PZA00729.19 | 2 | 188,980,910 |
| PZA00730.2 | 2 | 37,867,237 |
| PZA00731.6 | 1 | 9,304,156 |
| PZA00731.7 | 1 | 9,304,303 |
| PZA01104.1 | 6 | 126,148,975 |
| PZA01149.1 | 9 | 34,845,337 |
| PZA01149.3 | 9 | 34,845,357 |
| PZA01182.1 | 5 | 162,837,167 |
| PZA01240.1 | 4 | 19,597,341 |
| PZA01240.2 | 4 | 19,597,206 |
| PZA01420.1 | 3 | 88,528,316 |
| PZA01420.2 | 3 | 88,528,312 |
| PZA01420.3 | 3 | 88,528,283 |
| PZA01474.2 | 2 | 47,506,839 |
| PZA01637.2 | 4 | 181,187,885 |
| PZA01637.3 | 4 | 181,187,743 |
| PZA01637.4 | 4 | 181,187,733 |
| PZA01725.1 | 1 | 20,115,876 |
| PZA01725.2 | 1 | 20,115,867 |
| PZA01782.2 | 9 | 19,325,456 |
| PZA01782.3 | 9 | 19,325,169 |
| PZA01782.4 | 9 | 19,325,560 |
| PZA02789.31 | 3 | 223,691,724 |
| PZA02789.36 | 3 | 223,691,657 |
| PZA02791.6 | 1 | 67,524,140 |
| PZA02792.16 | 5 | 21,893,193 |
| PZA02792.9 | 5 | 21,893,329 |
| PZA02806.4 | 1 | 34,255,672 |
| PZA02806.9 | 1 | 34,255,898 |
| PZA02807.5 | 5 | 168,532,545 |
| PZA02808.12 | 2 | 44,168,169 |
| PZA02808.16 | 2 | 44,168,094 |
| PZA02819.35 | 4 | 173,601,472 |
| PZA02820.6 | 5 | 201,667,378 |
| PZA02822.2 | 5 | 149,459,255 |
| PZA02824.1 | 3 | 218,898,837 |
| PZA02824.3 | 3 | 218,898,805 |

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| PZA02831.5 | 2 | 133,841,755 |
| PZA02837.5 | 1 | 288,742,212 |
| PZA02844.1 | 9 | 17,751,142 |
| PZA02850.18 | 7 | 174,836,174 |
| PZA02850.4 | 7 | 174,836,372 |
| PZA02853.10 | 10 | 25,976,137 |
| PZA02853.7 | 10 | 25,976,183 |
| PZA02856.1 | 3 | 156,482,524 |
| PZA02865.11 | 4 | 215,239,863 |
| PZA02869.2 | 1 | 4,608,173 |
| PZA02869.8 | 1 | 4,608,015 |
| PZA02872.1 | 7 | 13,174,365 |
| PZA02872.3 | 7 | 13,174,261 |
| PZA02878.12 | 9 | 37,409,502 |
| PZA02888.3 | 3 | 138,624,226 |
| PZA02890.3 | 2 | 190,160,002 |
| PZA02890.4 | 2 | 190,159,942 |
| PZA02890.5 | 2 | 190,159,924 |
| PZA02894.1 | 5 | 945,545 |
| PZA02897.12 | 9 | 97,246,219 |
| PZA02906.12 | 3 | 148,289,175 |
| PZA02906.7 | 3 | 148,289,102 |
| PZA02921.9 | 1 | 24,941,000 |
| PZA02923.7 | 3 | 161,729,466 |
| PZA02927.1 | 8 | 34,033,391 |
| PZA02938.5 | 4 | 68,402,538 |
| PZA02939.6 | 2 | 159,987,717 |
| PZA02940.3 | 7 | 150,550,725 |
| PZA02941.3 | 10 | 71,361,885 |
| PZA02941.6 | 10 | 71,361,989 |
| PZA02941.8 | 10 | 71,362,041 |
| PZA02947.2 | 6 | 56,218,574 |
| PZA02949.22 | 4 | 186,040,517 |
| PZA02949.26 | 4 | 186,040,520 |
| PZA02952.10 | 3 | 196,048,525 |
| PZA02954.2 | 1 | 19,460,965 |
| PZA02955.3 | 8 | 14,778,018 |
| PZA02958.17 | 6 | 151,822,737 |
| PZA02959.7 | 7 | 157,280,779 |
| PZA02961.1 | 10 | 16,212,441 |
| PZA02962.13 | 1 | 3,274,647 |
| PZA02963.5 | 1 | 173,991,765 |

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| PZA02966.11 | 2 | 130,956,103 |
| PZA02968.4 | 4 | 39,092,497 |
| PZA02969.11 | 10 | 144,061,127 |
| PZA02970.9 | 6 | 98,315,872 |
| PZA02972.1 | 4 | 3,257,744 |
| PZA02982.5 | 4 | 149,276,720 |
| PZA02982.6 | 4 | 149,276,909 |
| PZA02983.38 | 7 | 4,238,932 |
| PZA02988.2 | 4 | 134,622,435 |
| PZA02993.5 | 10 | 106,792,585 |
| PZA02997.16 | 9 | 150,813,060 |
| PZA02997.19 | 9 | 150,813,124 |
| PZA03001.15 | 1 | 231,701,106 |
| PZA03001.18 | 1 | 231,701,045 |
| PZA03001.9 | 1 | 231,701,259 |
| PZA03009.5 | 3 | 11,649,287 |
| PZA03009.6 | 3 | 11,649,362 |
| PZA03009.7 | 3 | 11,649,402 |
| PZA03009.8 | 3 | 11,649,449 |
| PZA03011.6 | 3 | 203,579,387 |
| PZA03012.10 | 8 | 116,625,263 |
| PZA03013.7 | 4 | 139,753 |
| PZA03013.8 | 4 | 139,810 |
| PZA03014.10 | 1 | 103,826,380 |
| PZA03014.21 | 1 | 103,826,237 |
| PZA03014.24 | 1 | 103,826,094 |
| PZA03017.10 | 4 | 237,610,824 |
| PZA03017.11 | 4 | 237,610,827 |
| PZA03024.16 | 5 | 199,380,293 |
| PZA03024.18 | 5 | 199,380,332 |
| PZA03024.7 | 5 | 199,380,207 |
| PZA03028.5 | 1 | 150,682,455 |
| PZA03032.16 | 3 | 173,016,042 |
| PZA03034.1 | 5 | 6,823,291 |
| PZA03035.5 | 8 | 77,590,436 |
| PZA03037.8 | 1 | 287,063,325 |
| PZA03037.9 | 1 | 287,063,398 |
| PZA03041.8 | 6 | 115,129,610 |
| PZA03042.1 | 5 | 65,114,161 |
| PZA03042.5 | 5 | 65,114,362 |
| PZA03046.2 | 5 | 3,206,772 |
| PZA03046.3 | 5 | 3,206,775 |
| PZA03047.12 | 6 | 31,412,258 |

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| PZA03047.20 | 6 | 31,412,046 |
| PZA03047.22 | 6 | 31,412,177 |
| PZA03049.23 | 5 | 89,317,871 |
| PZA03051.1 | 10 | 96,330,328 |
| PZA03051.3 | 10 | 96,330,666 |
| PZA03052.15 | 8 | 130,730,669 |
| PZA03054.3 | 3 | 32,026,203 |
| PZA03054.5 | 3 | 32,026,168 |
| PZA03058.17 | 9 | 19,393,926 |
| PZA03062.15 | 9 | 3,927,674 |
| PZA03062.7 | 9 | 3,927,845 |
| PZA03063.17 | 6 | 35,896,303 |
| PZA03063.18 | 6 | 35,896,343 |
| PZA03064.6 | 1 | 249,417,407 |
| PZA03067.17 | 7 | 14,460,265 |
| PZA03067.20 | 7 | 14,460,194 |
| PZA03068.11 | 6 | 140,409,576 |
| PZA03068.13 | 6 | 140,409,675 |
| PZA03069.6 | 6 | 82,967,424 |
| PZA03073.23 | 3 | 170,110,501 |
| PZA03073.24 | 3 | 170,110,525 |
| PZA03074.24 | 1 | 201,486,818 |
| PZA03078.33 | 10 | 6,594,010 |
| PZA03081.1 | 4 | 209,799,999 |
| PZA03081.10 | 4 | 209,800,055 |
| PZA03081.11 | 4 | 209,800,051 |
| PZA03081.13 | 4 | 209,800,213 |
| PZA03081.6 | 4 | 209,800,094 |
| PZA03083.7 | 2 | 162,471,818 |
| PZA03089.12 | 6 | 165,631,271 |
| PZA03090.31 | 6 | 71,014,658 |
| PZA03092.7 | 5 | 12,038,114 |
| PZA03094.18 | 5 | 173,805,293 |
| PZA03094.6 | 5 | 173,805,347 |
| PZA03095.1 | 5 | 66,432,514 |
| PZA03095.2 | 5 | 66,432,703 |
| PZA03095.3 | 5 | 66,432,443 |
| PZA03097.4 | 9 | 44,336,288 |
| PZA03097.7 | 9 | 44,336,417 |
| PZA03097.9 | 9 | 44,336,534 |
| PZA03102.10 | 6 | 145,649,127 |
| PZA03102.2 | 6 | 145,649,201 |
| PZA03102.9 | 6 | 145,649,075 |

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| PZA03137.1 | 10 | 28,603,151 |
| PZA03172.2 | 5 | 188,967,385 |
| PZA03223.3 | 7 | 143,204,647 |
| PZA03258.2 | 7 | 143,203,880 |
| PZA03283.2 | 3 | 7,774,330 |
| PZA03284.3 | 5 | 92,369,229 |
| PZA03290.1 | 6 | 9,144,627 |
| PZA03290.2 | 6 | 9,144,765 |
| PZA03295.4 | 7 | 172,723,384 |
| PZA03296.6 | 6 | 84,226,532 |
| PZA03296.7 | 6 | 84,226,556 |
| PZA03298.1 | 5 | 21,933,689 |
| PZA03298.2 | 5 | 21,933,666 |
| PZA03301.2 | 1 | 241,298,148 |
| PZA03301.4 | 1 | 241,298,319 |
| PZA03302.1 | 3 | 119,175,697 |
| PZA03305.6 | 1 | 287,728,642 |
| PZA03305.7 | 1 | 287,728,786 |
| PZA03311.2 | 4 | 154,166,345 |
| PZA03311.3 | 4 | 154,166,386 |
| PZA03311.4 | 4 | 154,166,658 |
| PZA03311.5 | 4 | 154,166,660 |
| PZA03312.1 | 5 | 193,819,059 |
| PZA03312.2 | 5 | 193,819,018 |
| PZA03316.2 | 8 | 4,792,016 |
| PZA03319.3 | 2 | 31,493,278 |
| PZA03319.4 | 2 | 31,493,137 |
| PZA03320.3 | 5 | 190,746,629 |
| PZA03320.4 | 5 | 190,746,566 |
| PZA03328.5 | 2 | 36,843,149 |
| PZA03329.1 | 7 | 158,299,030 |
| PZA03329.2 | 7 | 158,298,929 |
| PZA03333.3 | 6 | 143,961,781 |
| PZA03335.2 | 5 | 211,666,584 |
| PZA03335.3 | 5 | 211,666,758 |
| PZA03337.1 | 4 | 47,242,400 |
| PZA03340.2 | 5 | 20,310,727 |
| PZA03342.2 | 10 | 59,878,382 |
| PZA03344.4 | 7 | 22,014,951 |
| PZA03344.5 | 7 | 22,015,062 |
| PZA03344.6 | 7 | 22,015,028 |
| PZA03345.1 | 1 | 36,509,795 |
| PZA03345.2 | 1 | 36,509,841 |

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| PZA03345.4 | 1 | 36,509,719 |
| PZA03347.1 | 4 | 154,166,530 |
| PZA03348.1 | 6 | 159,694,555 |
| PZA03349.1 | 3 | 211,536,618 |
| PZA03349.9 | 3 | 211,536,839 |
| PZA03767.1 | 1 | 56,289,498 |
| PZA03767.4 | 1 | 56,289,530 |
| PZA03767.5 | 1 | 56,289,258 |
| PZA03773.2 | 3 | 88,529,456 |
| PZA03773.3 | 3 | 88,529,363 |
| PZA03774.1 | 5 | 181,588,954 |
| PZA03774.10 | 5 | 181,591,578 |
| PZA03774.2 | 5 | 181,589,966 |
| PZA03774.4 | 5 | 181,590,507 |
| PZA03774.5 | 5 | 181,590,649 |
| PZA03774.6 | 5 | 181,590,922 |
| PZA03774.8 | 5 | 181,591,195 |
| PZA03774.9 | 5 | 181,591,369 |
| PZA03775.1 | 2 | 47,509,672 |
| PZA03775.11 | 2 | 47,507,587 |
| PZA03775.2 | 2 | 47,509,355 |
| PZA03775.3 | 2 | 47,509,287 |
| PZA03775.4 | 2 | 47,508,979 |
| PZA03775.6 | 2 | 47,508,409 |
| PZA03775.7 | 2 | 47,508,297 |
| PZA03775.8 | 2 | 47,508,224 |
| PZA03775.9 | 2 | 47,508,186 |
| PZA03781.1 | 5 | 162,834,983 |
| PZA03781.2 | 5 | 162,835,430 |
| PZA03781.3 | 5 | 162,835,530 |
| PZA03781.4 | 5 | 162,835,750 |
| PZA03781.5 | 5 | 162,835,982 |
| PZA03781.6 | 5 | 162,836,268 |
| PZA03781.7 | 5 | 162,836,471 |
| PZA03781.8 | 5 | 162,836,647 |
| PZA03782.1 | 5 | 80,719,678 |
| PZA03782.3 | 5 | 80,720,324 |
| PZA03786.1 | 9 | 34,845,691 |
| PZA03786.2 | 9 | 34,845,657 |
| PZA03789.1 | 8 | 70,201,052 |
| PZA03789.2 | 8 | 70,201,552 |
| PZA03789.4 | 8 | 70,201,822 |
| PZB00011.4 | 1 | 234,058,603 |

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| PZB00011.5 | 1 | 234,058,440 |
| PZB00041.2 | 8 | 44,554,499 |
| PZB00041.4 | 8 | 44,554,252 |
| PZB00049.2 | 8 | 21,102,553 |
| PZB00049.4 | 8 | 21,102,159 |
| PZB00049.7 | 8 | 21,102,626 |
| PZB00055.1 | 10 | 140,854,286 |
| PZB00060.4 | 3 | 133,090,703 |
| PZB00062.6 | 7 | 150,661,551 |
| PZB00062.7 | 7 | 150,661,408 |
| PZB00062.8 | 7 | 150,661,711 |
| PZB00067.2 | 1 | 277,152,522 |
| PZB00067.3 | 1 | 277,152,084 |
| PZB00067.4 | 1 | 277,152,753 |
| PZB00067.5 | 1 | 277,152,107 |
| PZB00078.1 | 2 | 32,588,115 |
| PZB00081.2 | 5 | 7,001,502 |
| PZB00081.4 | 5 | 7,001,339 |
| PZB00081.5 | 5 | 7,002,138 |
| PZB00081.7 | 5 | 7,001,555 |
| PZB00092.1 | 4 | 157,210,342 |
| PZB00092.4 | 4 | 157,210,317 |
| PZB00093.3 | 4 | 123,980,253 |
| PZB00093.4 | 4 | 123,980,408 |
| PZB00093.6 | 4 | 123,980,230 |
| PZB00096.2 | 8 | 21,100,594 |
| PZB00096.3 | 8 | 21,100,482 |
| PZB00136.3 | 5 | 5,886,221 |
| PZB00140.1 | 7 | 2,062,178 |
| PZB00145.2 | 8 | 44,553,085 |
| PZB00149.2 | 1 | 188,182,081 |
| PZB00149.4 | 1 | 188,182,112 |
| PZB00153.1 | 4 | 123,979,525 |
| PZB00153.2 | 4 | 123,979,477 |
| PZB00153.3 | 4 | 123,979,555 |
| PZB00153.5 | 4 | 123,979,344 |
| PZB00160.1 | 8 | 158,759,297 |
| PZB00160.2 | 8 | 158,759,347 |
| PZB00160.4 | 8 | 158,759,510 |
| PZB00165.2 | 2 | 43,558,423 |
| PZB00165.6 | 2 | 43,558,519 |
| PZB00169.4 | 7 | 133,170,656 |
| PZB00169.6 | 7 | 133,170,485 |

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| PZB00175.1 | 7 | 110,332,040 |
| PZB00175.2 | 7 | 110,331,886 |
| PZB00175.3 | 7 | 110,332,043 |
| PZB00175.4 | 7 | 110,332,075 |
| PZB00175.5 | 7 | 110,331,867 |
| PZB00180.1 | 5 | 80,718,715 |
| PZB00180.2 | 5 | 80,719,063 |
| PZB00183.3 | 2 | 43,558,626 |
| PZB00207.3 | 9 | 135,803,288 |
| PZB00221.3 | 9 | 146,686,210 |
| PZB00221.8 | 9 | 146,686,602 |
| PZB00229.3 | 4 | 157,210,028 |
| PZB00232.1 | 5 | 64,118,796 |
| PZB00232.2 | 5 | 64,119,272 |
| PZB00232.4 | 5 | 64,119,116 |
| PZB00232.5 | 5 | 64,119,253 |
| PZB00379.3 | 9 | 26,715,605 |
| PZB00379.4 | 9 | 26,715,588 |
| PZB00379.5 | 9 | 26,715,442 |
| PZB00393.7 | 1 | 202,305,125 |
| PZB00409.3 | 10 | 84,096,438 |
| PZB00416.2 | 6 | 131,158,004 |
| PZB00416.5 | 6 | 131,157,450 |
| PZB00454.2 | 1 | 188,182,192 |
| PZB00454.3 | 1 | 188,182,145 |
| PZB00454.4 | 1 | 188,182,274 |
| PZB00454.5 | 1 | 188,182,373 |
| PZB00498.2 | 5 | 88,793,779 |
| PZB00498.4 | 5 | 88,793,994 |
| PZB00598.1 | 7 | 167,238,971 |
| PZB00598.2 | 7 | 167,238,920 |
| PZB00603.3 | 7 | 171,703,464 |
| PZB00603.4 | 7 | 171,703,461 |
| PZB00603.5 | 7 | 171,703,857 |
| PZB00607.2 | 2 | 108,634,037 |
| PZB00761.1 | 9 | 86,863,679 |
| PZB00761.2 | 9 | 86,864,051 |
| PZB00849.2 | 10 | 59,516,563 |
| PZB00849.3 | 10 | 59,516,587 |
| PZB00849.4 | 10 | 59,516,627 |
| PZB00859.1 | 1 | 157,104 |
| PZB01109.2 | 3 | 196,440,909 |
| PZB01109.3 | 3 | 196,441,027 |

| | | |
|---|---|---|
| PZB01110.1 | 9 | 24,069,690 |
| PZB01110.2 | 9 | 24,069,762 |
| PZB01110.3 | 9 | 24,069,506 |
| PZB01111.6 | 10 | 134,413,629 |
| PZB01111.7 | 10 | 134,413,440 |
| PZB01111.8 | 10 | 134,413,161 |
| PZB01112.3 | 5 | 69,120,089 |
| PZB01112.4 | 5 | 69,119,579 |
| PZB01112.5 | 5 | 69,119,926 |
| PZB01112.6 | 5 | 69,119,810 |
| PZB01113.4 | 4 | 147,122,242 |
| PZB01114.1 | 9 | 63,685,643 |
| PZB01114.3 | 9 | 63,685,291 |
| PZB01115.1 | 5 | 61,672,319 |
| PZB01115.5 | 5 | 61,672,126 |
| PZB01115.6 | 5 | 61,672,027 |
| PZB01116.2 | 5 | 120,484,698 |
| PZB01221.1 | 6 | 83,673,652 |
| PZB01222.1 | 6 | 164,321,896 |
| PZB01222.3 | 6 | 164,321,834 |
| PZB01223.3 | 3 | 194,674,364 |
| PZB01223.7 | 3 | 194,674,207 |
| PZB01225.1 | 1 | 63,212,578 |
| PZB01225.2 | 1 | 63,212,688 |
| PZB01225.4 | 1 | 63,212,638 |
| PZB01228.1 | 7 | 15,457,461 |
| PZB01228.3 | 7 | 15,457,543 |
| PZB01228.4 | 7 | 15,457,589 |
| PZB01233.2 | 2 | 3,388,933 |
| PZB01233.3 | 2 | 3,388,514 |
| PZB01238.5 | 7 | 166,860,469 |
| PZB01238.6 | 7 | 166,860,367 |
| PZB01427.1 | 1 | 271,346,409 |
| PZB01427.3 | 1 | 271,346,495 |
| PZB01463.2 | 3 | 158,567,940 |
| PZB01463.3 | 3 | 158,568,190 |
| PZB01463.4 | 3 | 158,568,045 |
| PZD00003.1 | 3 | 162,800,088 |
| PZD00003.3 | 3 | 162,800,459 |
| PZD00007.1 | 3 | 165,178,026 |
| PZD00008.3 | 3 | 165,176,818 |
| PZD00011.1 | 6 | 131,832,400 |
| PZD00011.3 | 6 | 131,831,855 |

| | | |
|---|---|---|
| PZD00011.4 | 6 | 131,831,919 |
| PZD00012.1 | 6 | 131,825,470 |
| PZD00012.2 | 6 | 131,826,708 |
| PZD00012.3 | 6 | 131,826,731 |
| PZD00012.4 | 6 | 131,826,486 |
| PZD00012.5 | 6 | 131,826,355 |
| PZD00013.3 | 3 | 137,233,322 |
| PZD00013.4 | 3 | 137,233,307 |
| PZD00014.3 | 3 | 137,230,750 |
| PZD00017.1 | 5 | 196,556,802 |
| PZD00019.1 | 1 | 4,877,306 |
| PZD00020.2 | 1 | 4,862,839 |
| PZD00020.3 | 1 | 4,863,420 |
| PZD00020.4 | 1 | 4,863,098 |
| PZD00020.6 | 1 | 4,863,339 |
| PZD00021.2 | 1 | 4,862,689 |
| PZD00021.4 | 1 | 4,862,621 |
| PZD00021.5 | 1 | 4,862,745 |
| PZD00022.1 | 2 | 235,853,547 |
| PZD00022.3 | 2 | 235,853,500 |
| PZD00022.4 | 2 | 235,852,911 |
| PZD00024.2 | 8 | 22,248,100 |
| PZD00025.1 | 8 | 22,245,644 |
| PZD00025.2 | 8 | 22,246,020 |
| PZD00030.1 | 4 | 178,888,718 |
| PZD00030.4 | 4 | 178,889,674 |
| PZD00030.5 | 4 | 178,889,949 |
| PZD00030.6 | 4 | 178,889,456 |
| PZD00034.3 | 8 | 22,978,660 |
| PZD00043.1 | 7 | 164,417,453 |
| PZD00043.2 | 7 | 164,417,394 |
| PZD00043.3 | 7 | 164,417,373 |
| PZD00043.4 | 7 | 164,417,293 |
| PZD00044.2 | 7 | 164,412,086 |
| PZD00044.3 | 7 | 164,412,214 |
| PZD00044.4 | 7 | 164,412,165 |
| PZD00045.1 | 7 | 164,413,574 |
| PZD00045.2 | 7 | 164,413,483 |
| PZD00045.3 | 7 | 164,413,785 |
| PZD00045.4 | 7 | 164,413,134 |
| PZD00049.3 | 9 | 17,019,874 |
| PZD00049.4 | 9 | 17,019,800 |
| PZD00049.5 | 9 | 17,019,677 |

| | | |
|---|---|---|
| PZD00051.1 | 1 | 194,013,409 |
| PZD00052.3 | 1 | 194,021,359 |
| PZD00052.4 | 1 | 194,021,224 |
| PZD00062.2 | 1 | 265,690,409 |
| PZD00066.1 | 1 | 266,095,785 |
| PZD00067.1 | 4 | 133,663,998 |
| PZD00067.2 | 4 | 133,663,533 |
| PZD00067.3 | 4 | 133,663,860 |
| PZD00068.1 | 1 | 239,609,530 |
| PZD00069.2 | 1 | 292,891,821 |
| PZD00069.3 | 1 | 292,891,218 |
| PZD00069.4 | 1 | 292,892,381 |
| PZD00069.5 | 1 | 292,891,797 |
| PZD00073.1 | 7 | 110,331,963 |
| PZD00073.2 | 7 | 110,331,259 |
| PZD00073.6 | 7 | 110,331,230 |
| PZD00074.1 | 2 | 3,387,857 |
| PZD00075.1 | 10 | 147,059,868 |
| PZD00075.2 | 10 | 147,060,198 |
| PZD00076.1 | 1 | 70,581,280 |
| PZD00076.2 | 1 | 70,581,470 |
| PZD00076.4 | 1 | 70,581,587 |
| PZD00077.10 | 1 | 70,592,301 |
| PZD00077.5 | 1 | 70,593,006 |
| PZD00077.7 | 1 | 70,592,373 |
| PZD00077.8 | 1 | 70,592,832 |
| sh2.5 | 3 | 216,418,060 |
| sh2.6 | 3 | 216,418,000 |
| sh2.7 | 3 | 216,417,426 |
| sh2.9 | 3 | 216,418,124 |
| su1.4 | 4 | 41,369,511 |
| su1.5 | 4 | 41,378,878 |
| su1.7 | 4 | 41,376,540 |
| tb1.17 | 1 | 265,747,286 |
| tb1.18 | 1 | 265,747,334 |
| tb1.19 | 1 | 265,747,374 |
| tb1.5 | 1 | 265,745,267 |
| te1.3 | 3 | 165,177,210 |
| te1.4 | 3 | 165,176,963 |
| zagl1.1 | 1 | 4,877,511 |
| zagl1.6 | 1 | 4,862,498 |
| zap1.2 | 2 | 235,852,993 |
| zfl2.6 | 2 | 12,642,670 |

| | | |
|---|---|---|
| zmm3.4 | 9 | 17,013,962 |

**Table S3 Data on 95 resequencing loci used**

| Locus | Length | Sample size | RefGen v2 position |
|---|---|---|---|
| PZA00624 | 519 | 15 | 1,177,470 |
| PZA02851 | 347 | 16 | 3,834,244 |
| PZA02869 | 360 | 12 | 4,607,915 |
| PZA00181 | 271 | 15 | 8,351,398 |
| PZA00528 | 577 | 15 | 8,352,809 |
| PZA00175 | 329 | 14 | 8,558,092 |
| PZA00447 | 398 | 15 | 9,052,384 |
| PZA00106 | 369 | 16 | 10,096,199 |
| PZA00697 | 433 | 16 | 17,856,957 |
| PZA00358 | 546 | 14 | 18,980,277 |
| PZA00631 | 554 | 13 | 20,113,871 |
| PZA00491 | 372 | 14 | 20,419,065 |
| PZA00688 | 290 | 16 | 21,461,304 |
| PZA00425 | 296 | 14 | 21,468,171 |
| PZA02921 | 450 | 14 | 24,940,726 |
| PZA00691 | 323 | 11 | 25,415,740 |
| PZA03004 | 359 | 16 | 26,434,743 |
| PZA00021 | 373 | 16 | 28,799,398 |
| PZA00654 | 328 | 15 | 32,543,070 |
| PZA02790 | 420 | 15 | 33,722,666 |
| PZA00017 | 547 | 16 | 35,577,839 |
| PZA00192 | 542 | 13 | 35,579,032 |
| PZA00240 | 487 | 16 | 41,104,182 |
| PZA00014 | 363 | 13 | 41,278,262 |
| PZA00605 | 544 | 15 | 42,476,893 |
| PZA00661 | 267 | 15 | 47,506,412 |
| PZA00065 | 459 | 12 | 49,621,287 |
| PZA00468 | 597 | 16 | 50,096,486 |
| PZA00617 | 397 | 14 | 53,270,379 |
| PZA02826 | 355 | 11 | 56,220,687 |
| PZA00328 | 633 | 10 | 59,581,784 |
| PZA00378 | 685 | 13 | 63,008,454 |
| PZA00263 | 249 | 13 | 65,086,382 |
| PZA02791 | 233 | 13 | 67,523,911 |
| PZA00593 | 357 | 16 | 93,492,381 |
| PZA00692 | 233 | 15 | 94,489,012 |
| PZA00146 | 249 | 16 | 100,583,349 |
| PZA03014 | 477 | 13 | 103,826,023 |
| PZA00301 | 323 | 16 | 106,159,360 |
| PZA00205 | 331 | 12 | 119,652,952 |
| PZA00010 | 426 | 14 | 120,848,690 |
| PZA03086 | 722 | 14 | 125,074,531 |
| PZA00075 | 307 | 16 | 138,146,925 |
| PZA00083 | 391 | 16 | 151,738,698 |
| PZA00098 | 396 | 12 | 161,615,693 |
| PZA03101 | 359 | 12 | 161,775,074 |
| PZA00660 | 420 | 13 | 170,476,533 |

| | | | |
|---|---|---|---|
| PZA02963 | 476 | 12 | 173,991,638 |
| PZA00455 | 377 | 12 | 179,989,018 |
| PZA00484 | 272 | 12 | 180,308,017 |
| PZA00375 | 312 | 16 | 181,496,388 |
| PZA00421 | 453 | 11 | 182,092,438 |
| PZA00068 | 559 | 10 | 183,985,724 |
| PZA00544 | 383 | 12 | 188,182,045 |
| PZA00650 | 305 | 11 | 189,588,623 |
| PZA00469 | 494 | 12 | 195,187,825 |
| PZA00435 | 317 | 15 | 199,902,446 |
| PZA03074 | 497 | 13 | 201,486,648 |
| PZA00131 | 324 | 13 | 203,947,004 |
| PZA00369 | 383 | 15 | 219,807,209 |
| PZA02960 | 310 | 15 | 223,825,184 |
| PZA00403 | 276 | 16 | 224,079,008 |
| PZA03091 | 376 | 15 | 224,522,055 |
| PZA02823 | 346 | 15 | 226,625,187 |
| PZA00664 | 247 | 12 | 228,194,890 |
| PZA03001 | 639 | 10 | 231,700,907 |
| PZA00137 | 327 | 11 | 248,737,932 |
| PZA00411 | 447 | 15 | 251,088,838 |
| PZA00318 | 306 | 16 | 256,084,575 |
| PZA00035 | 380 | 16 | 260,619,385 |
| PZA00339 | 348 | 11 | 261,177,655 |
| PZA00709 | 562 | 15 | 262,720,110 |
| PZA02985 | 368 | 14 | 263,200,608 |
| PZA00013 | 566 | 15 | 264,163,639 |
| PZA00364 | 328 | 13 | 269,025,379 |
| PZA00698 | 327 | 13 | 274,531,678 |
| PZA00036 | 350 | 13 | 275,249,952 |
| PZA02957 | 383 | 14 | 282,796,262 |
| PZA02837 | 303 | 11 | 288,742,129 |
| PZA02935 | 409 | 13 | 289,217,209 |
| PZA00150 | 240 | 13 | 289,336,993 |
| PZA00313 | 517 | 13 | 289,566,801 |
| PZA00520 | 379 | 14 | 291,254,752 |
| PZA00242 | 341 | 11 | 292,089,628 |
| PZA03033 | 355 | 11 | 292,875,379 |
| PZA00235 | 415 | 10 | 293,795,684 |
| PZA00623 | 535 | 10 | 294,729,356 |
| PZA00343 | 563 | 12 | 295,762,441 |
| PZA00703 | 582 | 10 | 295,790,731 |
| PZA03018 | 431 | 12 | 296,020,928 |
| PZA00050 | 403 | 13 | 296,575,866 |
| PZA00243 | 528 | 14 | 296,891,356 |
| PZA03006 | 501 | 12 | 298,408,692 |
| PZA00477 | 411 | 14 | 299,197,483 |
| PZA00230 | 323 | 15 | 299,527,976 |

**Table S4 Location of the 33 *parviglumis* study populations with mean per-SNP values of summary statistics**

| Population | State/ Province | Latitude | Longitude | Altit-ude | N | F | HWE_ P-value | θH | π | Taj*D* | Fay/ Wu H |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Crustel | Guererro | 18.383 | -100.145 | 985 | 22 | 0.84 | 0.48 | 0.32 | 0.26 | 1.31 | -0.06 |
| Amates 1 | Guererro | 18.388 | -100.128 | 1110 | 25 | 0.74 | 0.47 | 0.31 | 0.28 | 1.36 | -0.03 |
| Amates 2 | Guererro | 18.394 | -100.108 | 1210 | 24 | 0.75 | 0.39 | 0.30 | 0.28 | 1.31 | -0.02 |
| Iguala | Guererro | 18.414 | -99.909 | 1506 | 28 | 0.36 | 0.96 | 0.31 | 0.28 | 1.51 | -0.03 |
| Rincon | Guererro | 18.350 | -99.841 | 1624 | 28 | 0.30 | 0.20 | 0.31 | 0.27 | 1.68 | -0.04 |
| Ahuacatitlan | Guererro | 18.356 | -99.814 | 1528 | 19 | 0.18 | 0.59 | 0.29 | 0.27 | 1.43 | -0.02 |
| Huetamo 1 | Michoacan | 19.063 | -101.283 | 832 | 25 | 0.58 | 0.63 | 0.31 | 0.25 | 1.28 | -0.06 |
| Puerto 1 | Michoacan | 18.963 | -101.058 | 870 | 20 | 0.53 | 0.66 | 0.32 | 0.26 | 1.26 | -0.06 |
| Zapote | Michoacan | 18.938 | -101.048 | 915 | 24 | 0.38 | 0.59 | 0.31 | 0.26 | 1.33 | -0.05 |
| Puerto 2 | Michoacan | 18.916 | -101.000 | 727 | 20 | 0.56 | 0.58 | 0.31 | 0.24 | 1.12 | -0.07 |
| Huetamo 2 | Michoacan | 18.900 | -100.979 | 677 | 20 | 0.60 | 0.46 | 0.30 | 0.25 | 1.09 | -0.05 |
| Cuirindalillo | Michoacan | 18.883 | -100.957 | 697 | 21 | 0.40 | 0.69 | 0.31 | 0.25 | 1.03 | -0.06 |
| Crucero | Michoacan | 18.794 | -100.946 | 653 | 25 | 0.90 | 0.02 | 0.30 | 0.23 | 1.17 | -0.07 |
| Quenchendio | Michoacan | 18.805 | -100.946 | 635 | 26 | 0.88 | 0.51 | 0.31 | 0.25 | 1.09 | -0.06 |
| Potrero | Michoacan | 18.820 | -100.916 | 654 | 20 | 0.60 | 0.85 | 0.30 | 0.26 | 1.12 | -0.04 |
| Crucita | Michoacan | 18.858 | -100.857 | 609 | 29 | 0.78 | 0.56 | 0.31 | 0.25 | 1.25 | -0.06 |
| Guayabo | Michoacan | 18.862 | -100.844 | 555 | 27 | 0.61 | 0.12 | 0.31 | 0.25 | 1.23 | -0.06 |
| Toluca 1 | Mexico | 18.899 | -100.181 | 1422 | 24 | 0.31 | 0.74 | 0.31 | 0.27 | 1.33 | -0.04 |
| Toluca 2 | Mexico | 18.895 | -100.209 | 1355 | 23 | 0.50 | 0.86 | 0.31 | 0.28 | 1.22 | -0.03 |
| Toluca 3 | Mexico | 18.854 | -100.239 | 1015 | 19 | 0.66 | 0.82 | 0.32 | 0.27 | 1.06 | -0.05 |
| Salitre-Monte | Mexico | 18.842 | -100.238 | 958 | 23 | 0.28 | 0.23 | 0.31 | 0.27 | 1.17 | -0.04 |
| Taretan | Michoacan | 19.344 | -101.944 | 1170 | 18 | 0.58 | 0.90 | 0.29 | 0.21 | 0.98 | -0.08 |
| Los Guajes | Michoacan | 19.231 | -100.491 | 985 | 27 | 0.76 | 0.65 | 0.31 | 0.27 | 1.36 | -0.04 |
| Norte | Michoacan | 19.281 | -100.434 | 1332 | 27 | 0.50 | 0.85 | 0.30 | 0.27 | 1.33 | -0.03 |
| Zuluapan 1 | Mexico | 19.148 | -100.355 | 1178 | 28 | 0.53 | 0.46 | 0.31 | 0.28 | 1.33 | -0.03 |
| Zuluapan 2 | Mexico | 19.146 | -100.329 | 1346 | 30 | 0.52 | 0.73 | 0.31 | 0.27 | 1.30 | -0.04 |
| Zacazonapan 1 | Mexico | 19.079 | -100.266 | 1468 | 28 | 0.27 | 0.99 | 0.30 | 0.26 | 1.33 | -0.04 |
| Zacazonapan 2 | Mexico | 19.039 | -100.295 | 1085 | 28 | 0.70 | 0.71 | 0.32 | 0.27 | 1.38 | -0.05 |
| El Puente | Mexico | 19.029 | -100.296 | 1075 | 24 | 0.67 | 0.76 | 0.31 | 0.27 | 1.30 | -0.04 |
| Queretanillo | Michoacan | 19.551 | -100.918 | 1342 | 28 | 0.41 | 0.32 | 0.32 | 0.26 | 1.33 | -0.06 |
| Temascal 1 | Michoacan | 19.483 | -100.921 | 1100 | 28 | 0.36 | 0.80 | 0.32 | 0.27 | 1.33 | -0.05 |
| Temascal 2 | Michoacan | 19.464 | -100.912 | 1030 | 19 | 0.55 | 0.27 | 0.31 | 0.27 | 1.18 | -0.04 |
| Casa Blanca | Michoacan | 19.161 | -101.329 | 1268 | 26 | 0.33 | 0.00 | 0.33 | 0.26 | 1.40 | -0.07 |

N: sample size; F: frequency of *Inv1n-I*.

**Table S5 Counts of anaphase and telophase pollen meiocytes showing dicentric bridges or normal segregation during meiosis**

| | Line | Normal | Bridge | **Sum** |
|---|---|---|---|---|
| 1 | B73 x TIL5 | 17 | 0 | **17** |
| 2 | B73 x TIL5 | 45 | 3 | **48** |
| 3 | OH43 x TIL11 | 48 | 2 | **50** |
| 4 | OH43 x TIL11 | 36 | 1 | **37** |
| 5 | OH43 x TIL11 | 4 | 0 | **4** |
| 6 | OH43 x TIL11 | 17 | 1 | **18** |

**Table S6 Mean Bayes factors for all environmental variables and inversion as single marker, all the SNPs in *Inv1n* and all SNPs. T: temperature.**

| | Inversion | SNPs in *Inv1n* | All SNPs |
|---|---|---|---|
| Longitude | 0.36 | 0.69 | 1020.37 |
| Latitude | 1.64 | 0.87 | 34.59 |
| Altitude | 136.37 | 124.63 | 5.86 |
| Annual Mean T | 18.93 | 12.57 | 5.75 |
| Mean Diurnal T Range | 0.82 | 4.35 | 28.61 |
| Isothermality | 1.26 | 0.84 | 2.77 |
| T Seasonality | 0.92 | 0.87 | 2.15 |
| Max T of Warmest Month | 22.46 | 16.42 | 5.76 |
| Min T of Coldest Month | 11.47 | 5.69 | 7.43 |
| T Annual Range | 1.90 | 9.75 | 28.75 |
| Mean T of Wettest Quarter | 21.04 | 17.20 | 9.33 |
| Mean T of Driest Quarter | 48.98 | 26.87 | 3.35 |
| Mean T of Warmest Quarter | 21.27 | 13.83 | 5.30 |
| Mean T of Coldest Quarter | 17.19 | 10.34 | 6.66 |
| Annual Precipitation | 0.88 | 1.26 | 2.69 |
| Precipitation of Wettest Month | 0.33 | 0.53 | 19.25 |
| Precipitation of Driest Month | 47.29 | 17.46 | 2.40 |
| Precipitation Seasonality | 10.54 | 3.67 | 2.24 |
| Precipitation of Wettest Quarter | 0.46 | 0.70 | 2.89 |
| Precipitation of Driest Quarter | 34.48 | 17.86 | 4.53 |
| Precipitation of Warmest Quarter | 0.44 | 0.51 | 1.73 |
| Precipitation of Coldest Quarter | 5.21 | 2.45 | 1.43 |

**Table S7 Results of association analysis.** P-value, marker $r^2$, *a* (genotypic value of inversion homozygote) and *d* (genotypic value of heterozygote) are based on analysis of *Inv1n* as single marker. Number of significant SNPs at FDR 5% is reported separately for all SNPs and for SNPs inside *Inv1n*.

| | Inversion as single marker | | | | Association analysis for all SNPs | |
|---|---|---|---|---|---|---|
| Trait | p | marker $r^2$ | a | d | Significant SNPs at FDR 5% | Significant SNPs in inversion at FDR 5% |
| Blade Length[a] | 0.7065 | 0.001 | -0.33 | 0.15 | 0 | 0 |
| Culm diameter | 0.0137 | 0.011 | -0.55 | 0.54 | 7 | 4 |
| Days to Pollen | 0.2595 | 0.004 | -0.50 | 0.69 | 0 | 0 |
| Days to Silk | 0.4831 | 0.002 | -0.33 | 0.54 | 0 | 0 |
| Female ear length[b] | 0.3304 | 0.005 | 1.18 | -0.80 | 0 | 0 |
| Fruitcase compression[b] | 0.0662 | 0.007 | -0.11 | 0.03 | 0 | 0 |
| Fruitcase length[b] | 0.1393 | 0.008 | 0.12 | -0.03 | 0 | 0 |
| Fruitcase weight | 0.5961 | 0.001 | 0.00 | 0.00 | 0 | 0 |
| Lateral branch internode number[a] | 0.663 | 0.001 | -1.05 | 0.56 | 0 | 0 |
| Lateral Branch Length[a] | 0.8508 | 0.001 | -0.02 | -0.06 | 0 | 0 |
| Lateral inflorescence branch number[a] | 0.5653 | 0.002 | -0.62 | 0.42 | 0 | 0 |
| Lateral inflorescence length | 0.3641 | 0.005 | -0.65 | 0.94 | 0 | 0 |
| Leaf Number | 0.0232 | 0.01 | -0.12 | 0.68 | 0 | 0 |
| Leaf Width | 0.1243 | 0.005 | -0.13 | 0.11 | 2 | 0 |
| Maize Introgressed | 0.5062 | 0.002 | -0.01 | 0.00 | 4 | 0 |
| Mean lateral branch internode length[a] | 0.7455 | 0.001 | -0.27 | 0.32 | 0 | 0 |
| Number of Barren nodes | 0.7907 | 0.001 | 0.00 | 0.01 | 0 | 0 |
| Number of female cupules[b] | 0.7164 | 0.001 | 0.03 | -0.13 | 0 | 0 |
| Number of female internodes[b] | 0.8604 | 0.001 | 0.06 | -0.09 | 0 | 0 |
| Oil Content, Wet | 0.7653 | 0.001 | 0.01 | 0.04 | 0 | 0 |
| Paired Spikelets | 0.5523 | 0.002 | 0.00 | 0.00 | 5 | 0 |
| Pedicellate Spikelet | 0.1717 | 0.006 | 0.00 | 0.01 | 15 | 1 |
| Percent of Male Internodes in the lateral inflorescence | 0.0069 | 0.023 | -2.62 | 2.75 | 0 | 0 |
| Percent staminate spikelets in the lateral inflorescence | 0.0055 | 0.024 | -1.96 | 2.08 | 4 | 0 |

| | | | | | | |
|---|---|---|---|---|---|---|
| Plant Height | 0.1175 | 0.005 | -1.21 | 6.42 | 0 | 0 |
| Polystichous | 0.1162 | 0.007 | -0.01 | 0.02 | 2 | 0 |
| Prolificacy[a] | 0.3762 | 0.002 | -0.41 | 0.28 | 0 | 0 |
| Proportion of female cupules[b] | 0.2483 | 0.007 | 0.02 | -0.01 | 0 | 0 |
| Proportion of female ear length[b] | 0.3717 | 0.005 | 0.02 | -0.01 | 0 | 0 |
| Proportion of female internodes[b] | 0.2604 | 0.007 | 0.02 | -0.01 | 0 | 0 |
| Protein Content | 0.5198 | 0.002 | -0.22 | 0.07 | 0 | 0 |
| Sexual Identity of the Lateral Inflorescence | 0.294 | 0.003 | -0.02 | 0.05 | 0 | 0 |
| Sheath Length | 0.9239 | 0 | -0.03 | 0.04 | 0 | 0 |
| Starch Content[c] | 0.4999 | 0.002 | 0.21 | -0.12 | 0 | 0 |
| Tassel branch number | 0.1425 | 0.01 | -5.80 | 0.64 | 0 | 0 |
| Tiller number | 0.2321 | 0.004 | 0.55 | 0.58 | 0 | 0 |
| Yoked Cupules | 0.7034 | 0.001 | 0.00 | 0.00 | 21 | 0 |

[a] On the second lateral branch from the top of the plant
[b] In the basal ear
[c] Adjusted to percent dry matter using a pooled moisture content estimate