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Exploring the many facets of phenotypic changes after 13 years of divergent selection for flowering time in maize



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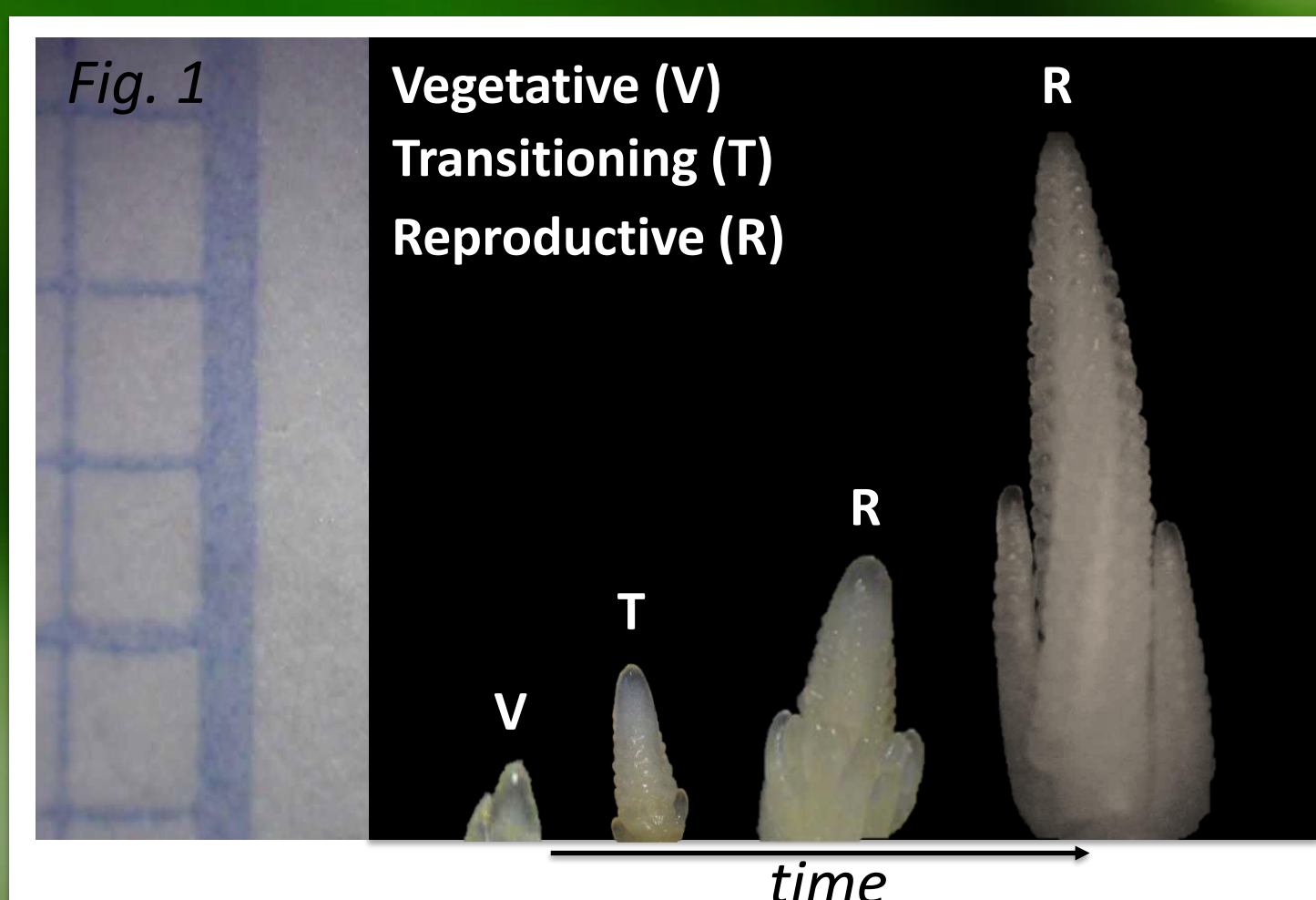
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Two seed lots from maize inbred lines, F252 (F) and MBS (M), were chosen as initial populations for a divergent selection experiment for flowering time. After 13 generations (G13) within each line, we obtained two to three populations of genotypes - Early (E), Late (L) and Very Late (VL) for F, Early and Late for M - that display major differences in flowering time. We observed a significant response to selection in most populations, indicating a significant heritability for different traits related to flowering time despite strong genetic drift [1, 2]. Both standing variation and new mutations have contributed to this response [3]. Here, we aimed at exploring convergence (within Early/Late) and divergence (between Early and Late) among genotypes.

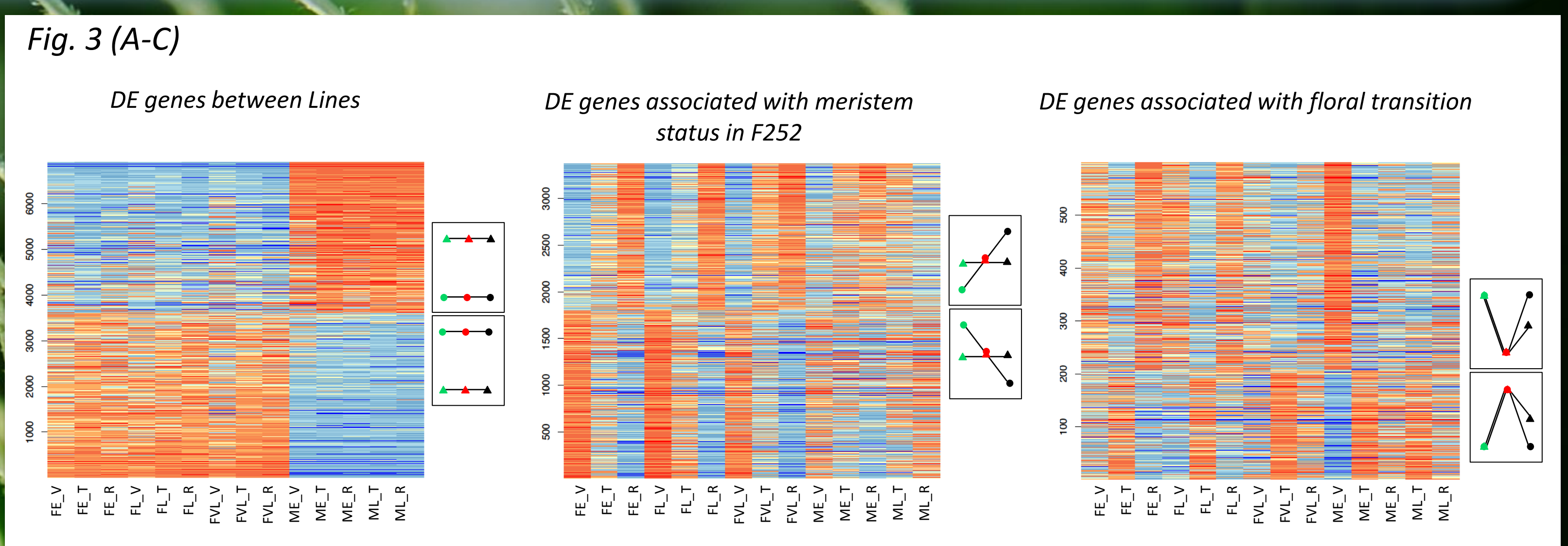
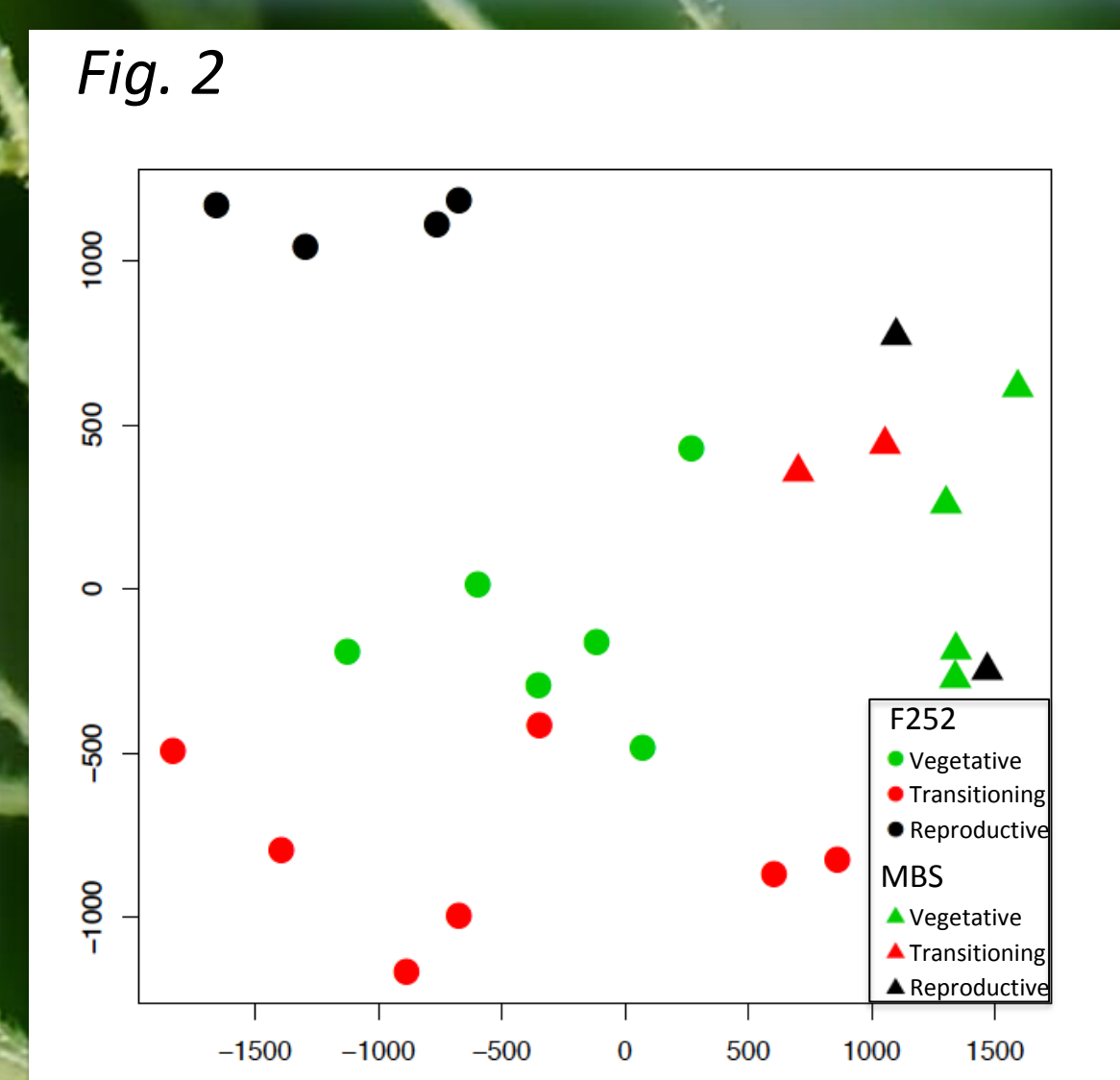
Characterization of evolved inbred populations during floral transition

RNASeq snapshots of the Shoot Apical Meristem (SAM)



Reads were aligned filtered for rRNAs, trimmed for quality, and aligned to the maize reference genome V3 [3] using Tophat v2 [4]. Only uniquely mapped reads to exons were subsequently used. We determined the number of raw counts for the longest transcript of each of the 39,787 annotated maize genes. We further filtered and normalised counts and performed a multidimensional scaling plot (Fig. 2). We identified Differentially Expressed (DE) genes using DESeq2 [5]. We computed a series of contrasts between Inbreds, Genotypes, Meristem status, and determined significance after correcting for multiple testing. Our list of DE genes contain DE genes significant in at least one contrast. Average expression for 21,696 DE genes was determined from normalized counts after correcting for Year effect. These values were used to compute a Principal Component analysis and we obtained 3 heatmaps corresponding to sets of DE genes correlated to 3 PCs (Fig. 3).

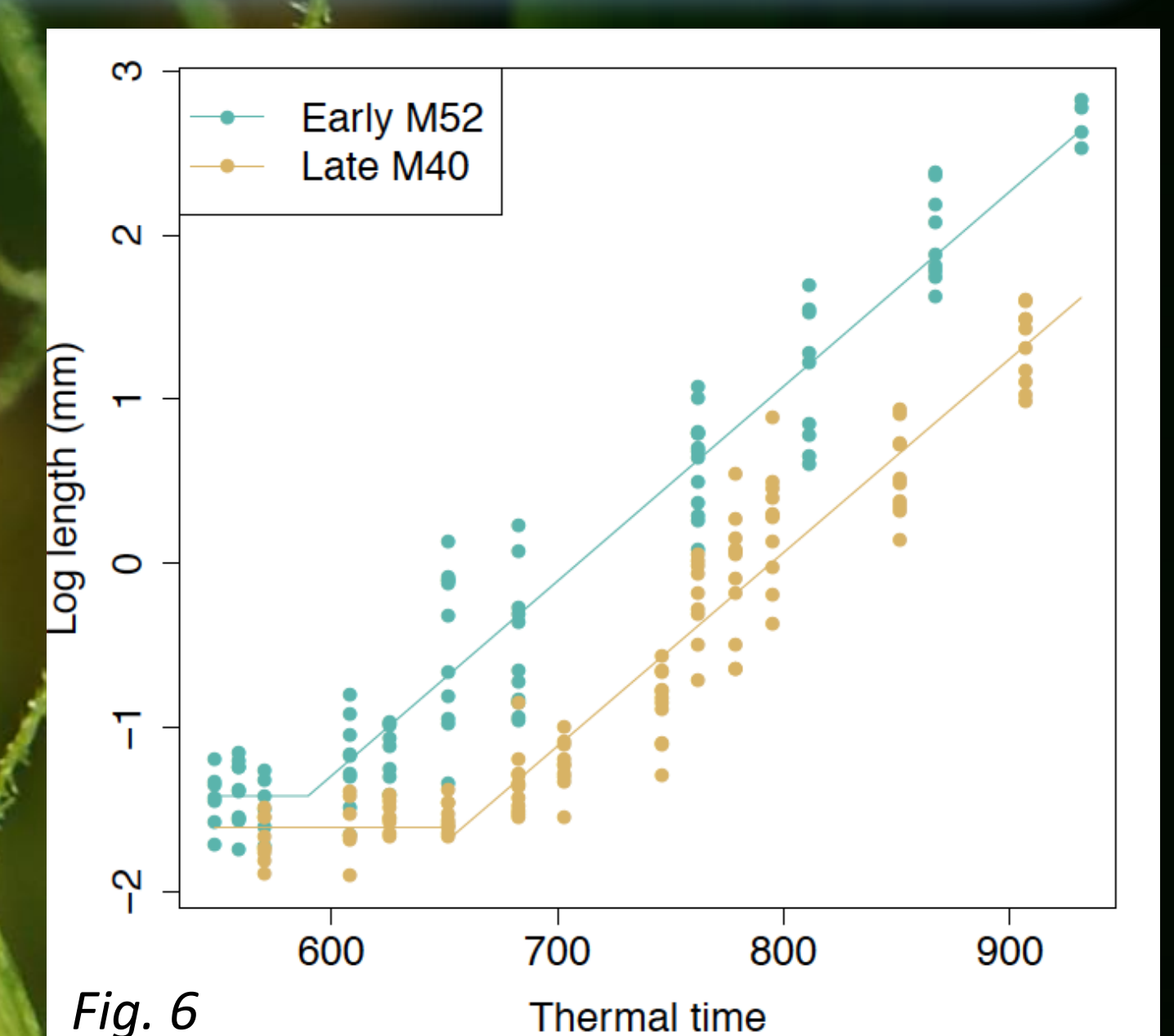
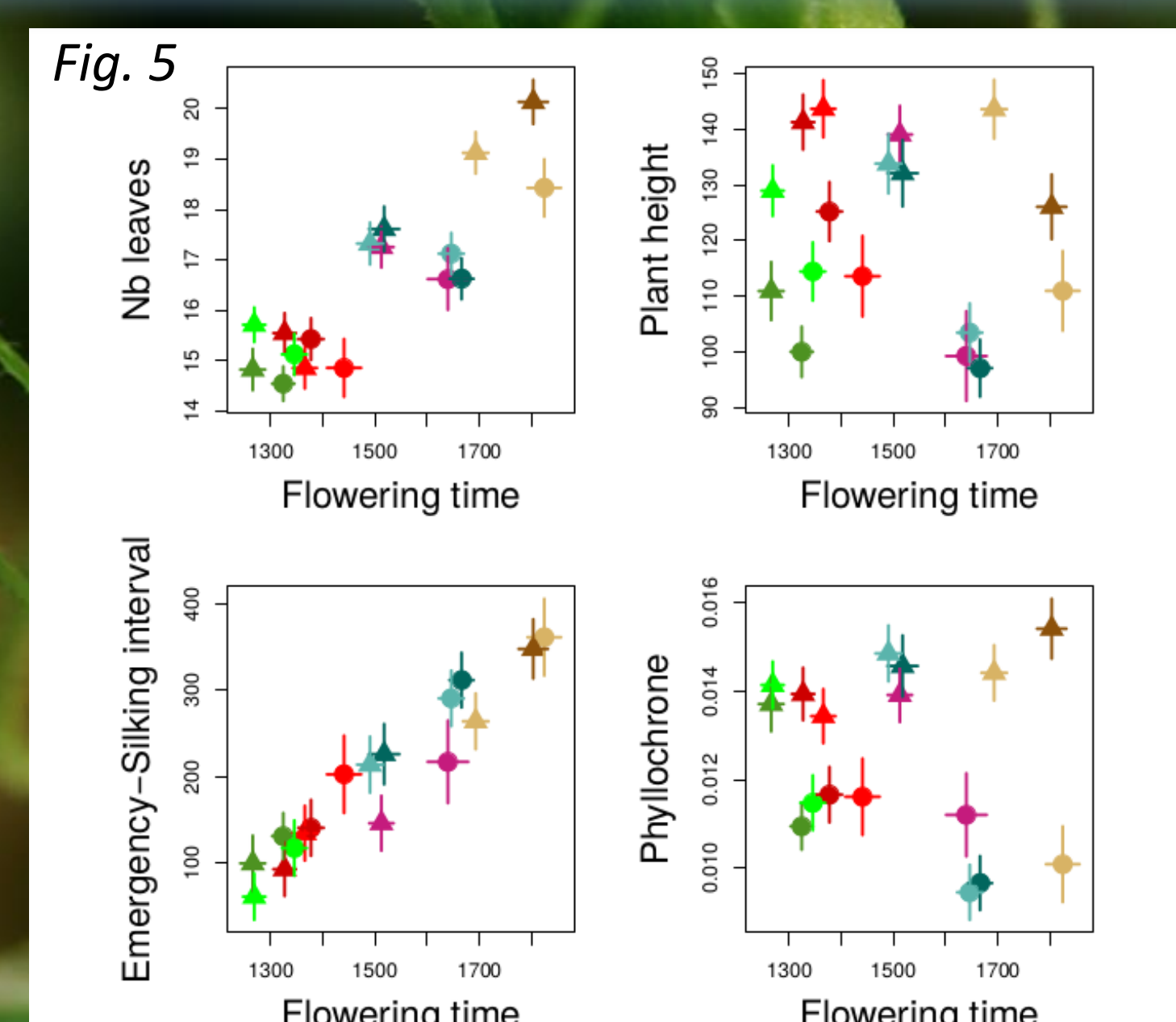
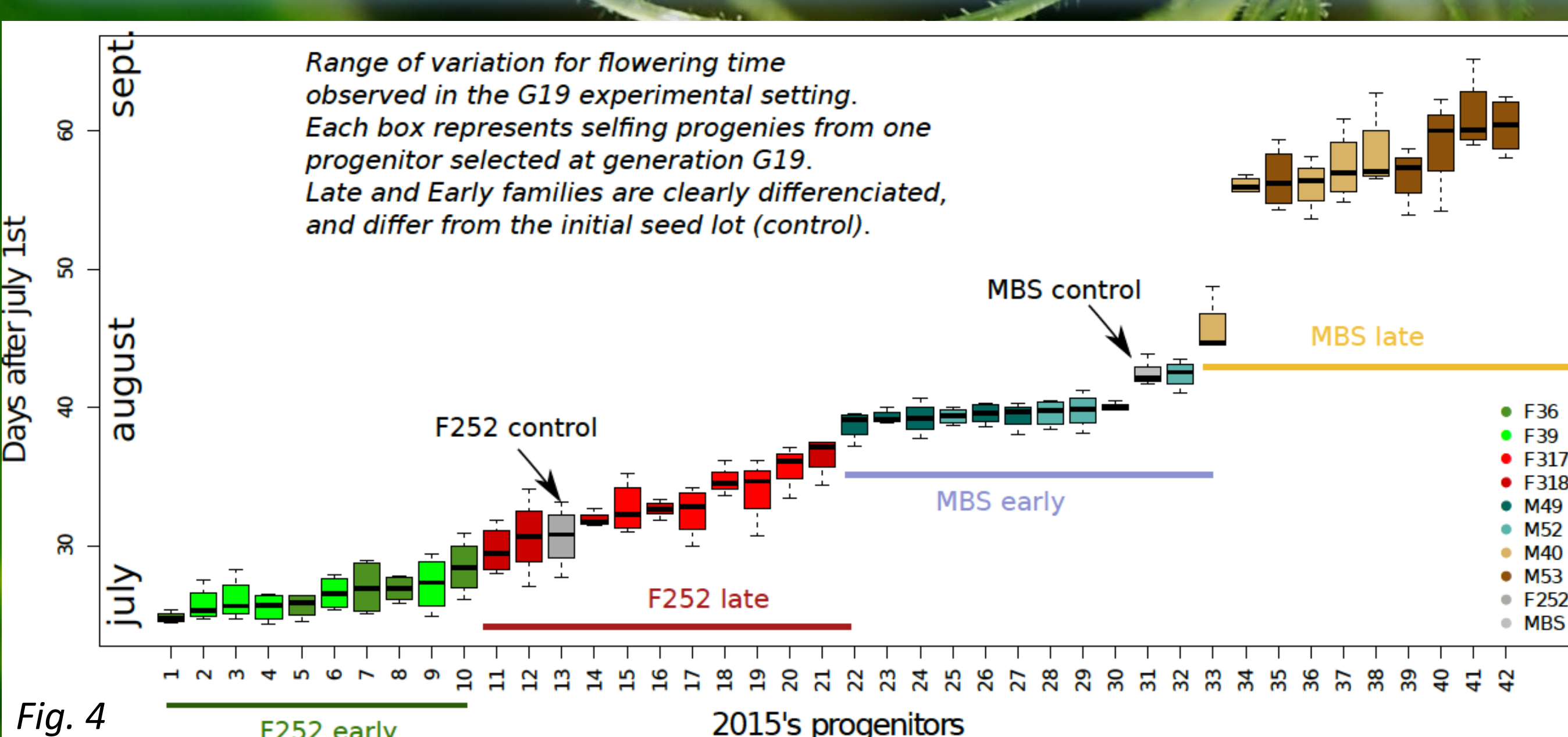
In 2012 and 2013: 20 to 31 meristems were collected from offsprings of 5 selected genotypes at G13 and pooled by Meristem status (Fig. 1: V, T, R) and Genotypes (FE, FL, FVL, ME, ML). Total RNAs were extracted to build and sequence 25 libraries (single reads Illumina 51 bp).



RNASeq snapshots of SAMs reveals a distinction between Lines (F and M), among Meristem status, and points to a set of genes whose expression increases or decreases significantly at FT. Some of these genes have been targeted by selection for Early and Late genotypes (GxE interactions, Fig. 3C). We established a list of 107 genes known to/potentially involved in FT. A subset of 67 are included in our DE genes, among which 56 are correlated to the first 3 PCs (Fig. 3). This represents a significant enrichment (P-value=2.10⁻⁴). We point to genes included in the FT network such as *ZMM4*, *ZFL1*, *DFL1* [7,8] as well as new genes.

Developmental sequences

Flowering time was recorded in 2015 which corresponds to 19 generations of selection (G19, Fig. 4). Nine genotypes at G13 including the 5 that were used for the RNASeq (see above) were phenotypically evaluated in 2014 (triangles) and 2015 (circles) through their life-cycle (Fig. 5). Developmental traits including the height and number of leaves at maturity, the time interval between male (emergence) and female (silking) flowering and the rate of visible leaves emergence (phyllochone) were recorded. Mean values and 95% confidence intervals for these traits are presented (Fig. 5). In addition in 2016, we dissected for a single Early and Late MBS genotype, 10 plants per genotype at regular time intervals, and measured meristem elongation through time (Fig. 6).



Developmental sequences among genotypes (Fig. 5) reveal that: (1) Late genotypes in MBS and Very Late genotypes in F252 produce more leaves than corresponding Early genotypes; (2) Plant height is similar across genotypes but differ sharply between years; (3) In both lines, the time interval between male and female flowering is increased in Late genotypes. Interestingly while the time of FT differ between Early and Late genotypes (Fig. 6), phyllochone, and meristem elongation are not affected by selection.

By applying divergent selection on inbred lines, we have created a unique material to relate genotypes to phenotypes, and dissect a complex genetic pathway. We have shown that response to selection can take different routes, and timing of transition rather than developmental rates were targeted. We now aimed at integrating various sources of data (RNASeq, developmental assays, metabolomic and proteomic data, measures of soluble sugars) to model maize FT network.

Acknowledgements:

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Maeva Mollion

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