



# SunUp and Sunset genomes revealed impact of particle bombardment mediated transformation and domestication history in papaya

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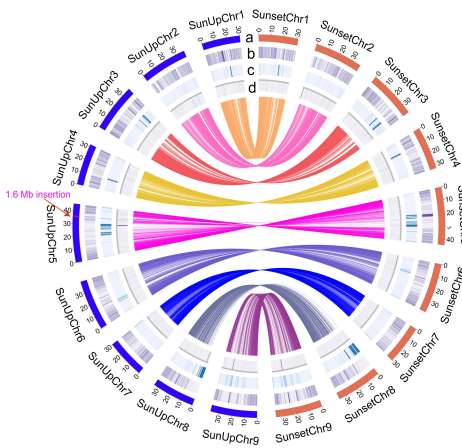
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## Abstract

Transgenic papaya is widely publicized for controlling papaya ringspot virus. However, the impact of particle bombardment on the genome remains unknown. The transgenic SunUp and its progenitor Sunset genomes were assembled into 351.5 and 350.3 Mb in nine chromosomes, respectively. We identified a 1.64 Mb insertion containing three transgenic insertions in SunUp chromosome 5, consisting of 52 nuclear-plastid, 21 nuclear-mitochondrial and 1 nuclear genomic fragments. A 591.9 kb fragment in chromosome 5 was translocated into the 1.64 Mb insertion. Resequencing 86 genomes revealed three distinct groups, validating their geographic origin and breeding history. We identified 147 selective sweeps and defined the essential role of zeta-carotene desaturase in carotenoid accumulation during domestication. Our findings elucidated the impact of particle bombardment and improved our understanding of sex chromosomes and domestication to expedite papaya improvement.

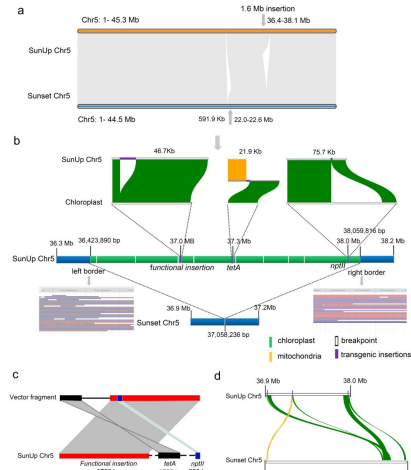
## Results

### 1. Distribution of genomic features along the SunUp and Sunset genome



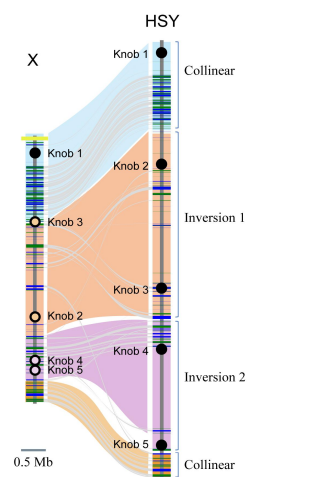
**a**, 9 chromosomes of SunUp (SunUpChr1-Chr9, left semicircle) and Sunset (SunsetChr1-Chr9, right semicircle). **b** gene density, **c** transposable element abundance, **d** gene structure variation and the center showed the synteny relationships between SunUp and Sunset chromosomes, which were displayed with connecting lines.

### 2. Integration site of transgenic insertions in SunUp genome



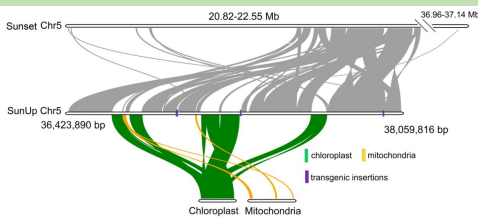
**a**, Syntenic comparisons between SunUp and Sunset. A 1.6 Mb insertion was identified on SunUp. **b**, Graphical alignment of SunUp 1.6 Mb insertion to Sunset. **c**, Vector fragment. **d**, SunUp Chr5. 36.9 Mb. 36.0 Mb. 29.8 Mb. 22.5 Mb. Transgenic insertions.

### 3. Comparison of the gapless HSY and its counterpart X

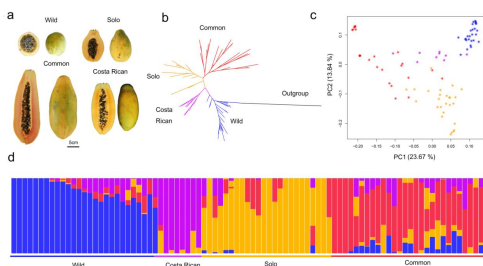


Genes in sense direction and antisense direction are indicated by blue and green horizontal lines.

### 4. Sequence origin of the 1.64 Mb insertion

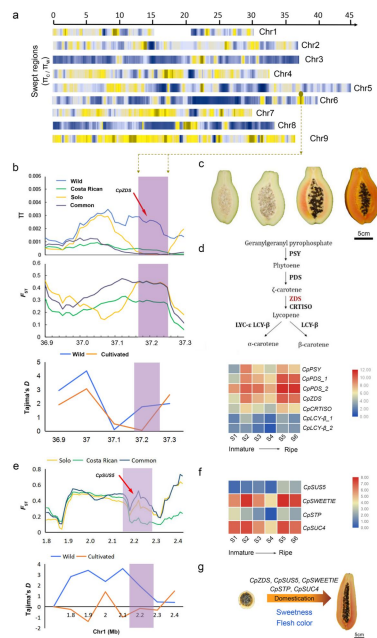


### 5. Population structure of cultivated and wild papaya



**a**, Representative fruit from three groups (Solo, Costa Rican and "Common papaya") and wild fruit collected from Costa Rican. **b**, Maximum likelihood phylogenetic tree. **c**, Principal component analysis (PCA) plots for the first two components. **d**, Model-based analysis using ADMIXTURE showing the four distinct subgroups.

### 6. Signatures of artificial selection and evidence of domestication in cultivated papaya



**a**, Density and distribution of the domestication sweeps across the nine papaya chromosomes. **b**, Reduced nucleotide diversity and high population differentiation around the sweep region. **c**, Series of ripening "Solo" papaya fruit show increasing lycopene accumulation and red coloration. **d**, Top, simplified carotenoid biosynthesis pathway with ZDS highlighted in red. **e**, Signals of artificial selection in the gene CpSUSS. **f**, Expression of artificially selected genes in six stages of ripening papaya fruit. **g**, Proposed model of papaya domestication process.

## Conclusion

- The genome of the SunUp transgenic papaya cultivar includes a complex 1.64-Mb insertion that contains 3 transgenic fragments integrated with 61 nuclear genome fragments from the progenitor Sunset cultivar and 13 organelle genome fragments.
- Between the SunUp and Sunset genomes, 607 genes were differentially expressed and 306 had a variable promoter or coding sequence.
- A gapless 9.8 Mb hermaphrodite-specific region of the Yh chromosome (HSY) and its 6.0 Mb X counterpart resulted in additional genes.
- Population genomic analyses yielded 147 selective sweeps during papaya domestication, which include essential flesh color and sugar content genes.



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