

DOMESTICATION HISTORY OF STRAWBERRY: SELECTION AND BOTTLENECKS SHAPING THE OCTOPLOID HYBRID COMPLEX

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Background

Domesticated strawberry (Fragaria x ananassa) is an octoploid hybrid (2n=8x=56) of Chilean beach strawberry (F. chiloensis [L.] Miller) and North American common strawberry (F. virginiana Miller) originating in the mid-18th century. Subsequent breeding established elite genetic architectures of F. x ananassa. Hybrids developed at the University of California represent a unique modern group, accounting for 60% of worldwide consumption. To explore key events underlying the emergence of globally important strawberry populations, we studied the impacts of selection, population bottlenecks, and migration on restructuring of genetic diversity within the F. x ananassa hybrid complex using a panel of 1,300 elite and wild octoploid Fragaria genotypes. The panel was genotyped with 16,492 subgenome-specific single nucleotide polymorphisms anchored to an improved diploid reference assembly. We show that significant restructuring of the hybrid complex followed domestication, including historic selection favoring the North American wild progenitor genome, and a 20^{th} century bottleneck separating UC genotypes from octoploids bred elsewhere in North America and Europe. Greater divergence was uncovered between modern UC and non-UC F. x ananassa (Fst=0.207) than non-UC cultivars and their wild progenitors (F_{ST}=0.182). This bottleneck exploited post-domestication subspecific introgressions that redirected selection toward the South American genome and photoperiodinsensitive flowering from a high-elevation ecotype of F. virginiana subsp. glauca, causing a transition from complex polygenic day-neutrality to QTL regions on a single chromosome arm, independent of the TERMINAL FLOWERING1 source discovered in diploid ancestor Fragaria vesca. We report that strawberry breeding targeted genes controlling hormone-mediated fruit expansion, and expression pathways within developing achenes.

Genetic Relationships of Octoploid Fragaria

Phylogenetic lineages of octoploid strawberry germplasm. Clear separation of University of California *F. x ananassa* from non-UC *F. x ananassa* revealed west coast strawberry to be genetically distinct from their progenitors.



Figure 1. Phylogenetic tree of strawberry octoploids – F. chiloensis (orange), non-UC F. x ananossa (green), F. virginiana (blue), and University of California F. x ananossa (turquoise). Red clades indicate polytomy. Exterior heatmaps indicate release year (layer 1) and maturity phenotype (layer 2; green = day neutral, white = short day).

Selection of Distinct Hybrid Ancestral Genomes

F. x ananassa breeding at the University of California redirected selection from the F. virginiana ancestor toward South American F. chiloensis.



Figure 2. Wild hybrid progenitor frequencies of alleles selected in non-UC F. x ananassa (green), historic (pre-1970) UC F. x ananassa (blue), and modern (post-2000 UC F. x ananassa (gold).

Genetic Restructuring Effects of Day-Neutral Strawberry Breeding

STRUCTURE analysis revealed strawberry genetics were restructuring over time along lines of maturity phenotype as a result of selection of photoperiod-insensitive flowering at UC, with distinct groups having increasing day neutrality since 1980s.



Figure 3. Temporal structuring of strawberry genetics as related to selection for day-neutral flowering trait. (A) Population structure of octoploid strawberry diversity panel. (B) Descriptions and rates of UC strawberry genetics, day-neutral flowering within each population group. (C) Plot of release year and maturity phenotype for cultivated population groups.

Distinct Genetic Mechanisms of Day-Neutral Flowering

Parallel GWAS and analysis of selective sweeps in short-day versus day-neutral octoploids uncovered a transition from polygenic additive mechanisms in historic germplasm to simpler genetic control by QTLs on a single chromosome arm in modern day-neutral genotypes.



Figure 4. Selective sweeps and GWAS results for day-neutral flowering trait (A) Genome-wide view of allele fixation (F₅₇) comparing short-day strawberry to pre-1990 and post-2000 day-neutral types. (B) Manhattan plot of pre-1990 day-neutral flowering GWAS. (C) Manhattan plot of post-2000 day-neutral flowering GWAS.

UC Strawberry Bottleneck

Marker nucleotide diversity and allele fixation (F_{ST}) of wild and cultivated groups indicated bottlenecking of UC diversity over time, accompanied by increased selective pressure impacting a large percentage of SNP loci.



Figure 5. Metrics revealing increased selective pressure within the UC strawberry breeding program, including marker nucleotide diversity (rn) estimates of wild and cultivated strawberry groups (left panel) and distribution of allele fixation (F_{ST}) strength between wild species and cultivated strawberry groups (right panel).

This work is supported by the Specialty Crops Research Initiative (#207:51181-26833) from the USDA National Institute of Food and Agriculture. Any oplinions, findings, conclusions, or recommendations expressed in this publication are those of the author(s) and do not necessarily reflect the view of the LIS Department of Agriculture.