The Fruit Revolution in the Genomic Era: Unveiling the Journey of Strawberry Genetic Improvement

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On March 19, 2024, research results from the Department of Plant Sciences at the University of California, Davis, were published in the journal Nature Communications. Mitchell J. Feldmann is the first author, and Steven J. Knapp is the corresponding author, with the paper titled "Genetic gains underpinning a little-known strawberry Green Revolution." This research was funded by the U.S. Department of Agriculture's National Institute of Food and Agriculture (NIFA) Specialty Crop Research Initiative (#2017-51181-26833; #2022-51181-38328). The study highlights the genetic basis for the significant increase in strawberry yields in the United States and globally since 1960, particularly through breeding achievements of the Green Revolution. The increase in strawberry yields is attributed to genetic improvements and advancements in cultivation techniques, including the introduction of "perpetual flowering" hybrid varieties that are not influenced by photoperiod, a breakthrough achieved in the 1970s that doubled strawberry production in California.

1 Experimental Data Analysis

The study assessed the contribution of breeding to strawberry yields by analyzing phenotypes of a century-old breeding population and its hybrids in coastal environments of California. Using genomic prediction methods, the study revealed that since the 1950s, transgressive segregation and increased phenotypic diversity have led to significant enhancements in additive genetic variation. The study also discovered that the introduction of "perpetual flowering" hybrid varieties in the 1970s was a key breeding breakthrough that facilitated the doubling of strawberry yields and rapid expansion of the California strawberry industry.

Figure 1 displays statistics on strawberry production in the US and Europe from 1961 to 2021. Data sourced from the United Nations Food and Agriculture Organization (https://www.fao.org/faostat/en/). The chart shows a growth trend over time for both the US, represented by solid blue circles, and Europe, represented by solid gray circles. Linear regression lines are shown in solid blue for the US and solid black for Europe, with a 95% confidence interval represented by a gray band. Additionally, it is evident that the US has experienced a steeper increase in production compared to Europe, as depicted in the first chart showing production per hectare. The second chart shows similar growth trends in cultivated area for both regions, though the increase is more pronounced in the US. The third chart, reflecting total production, reconfirms the significantly higher growth rate of the US compared to Europe.

Therefore, the data indicate that over the past 60 years, the US strawberry industry has experienced significant growth in production, cultivated area, and total output, likely linked to advancements in agricultural technology, breeding, and production efficiency. In contrast, Europe's growth, while stable, has been slower, possibly influenced by factors such as land use efficiency, agricultural policies, and market demand.
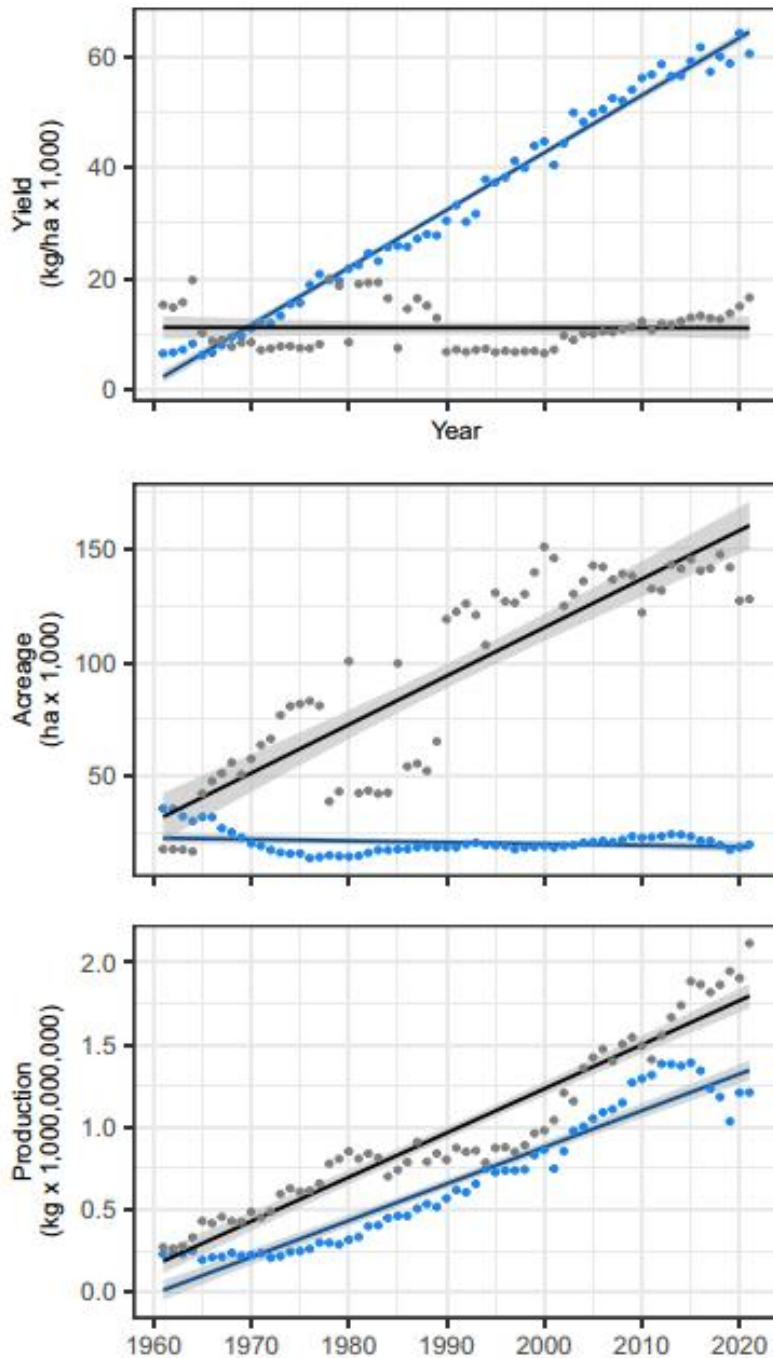
Figure 1 Strawberry production in the US and Europe (1961-2021)

Figure 2 shows the cumulative marketable fruit yields of modern short-day and day-neutral cultivars (hybrids) grown in coastal areas of California during the 2015—2016 and 2016—2017 growing seasons. The estimated marginal means (EMMs) depict the yield variations among different varieties at different locations. In Figure A, we observe the production of short-day varieties in the Oxnard region during 2016—2017, showing some variation in annual yields with a generally increasing trend. Notably, varieties such as Fronteras and Victor exhibited significant production increases. Figures B and C display the yields of day-neutral varieties in the Santa Maria and Prunedale regions. These varieties show a very significant trend of increasing annual production, with varieties like Royal Royce and Valiant demonstrating exceptional productivity. Figure D compares the yields of day-neutral varieties between the two years in these regions, showing that the production was relatively stable over the years, with the Royal Royce variety performing exceptionally well.

Overall, day-neutral varieties exhibit higher yields than short-day varieties, especially in specific areas like Santa Maria, and this trend remains consistent across different years. This likely relates to the genetic characteristics of the varieties and their adaptability to specific regional climate conditions. These findings are crucial for improving strawberry breeding and cultivation management strategies.
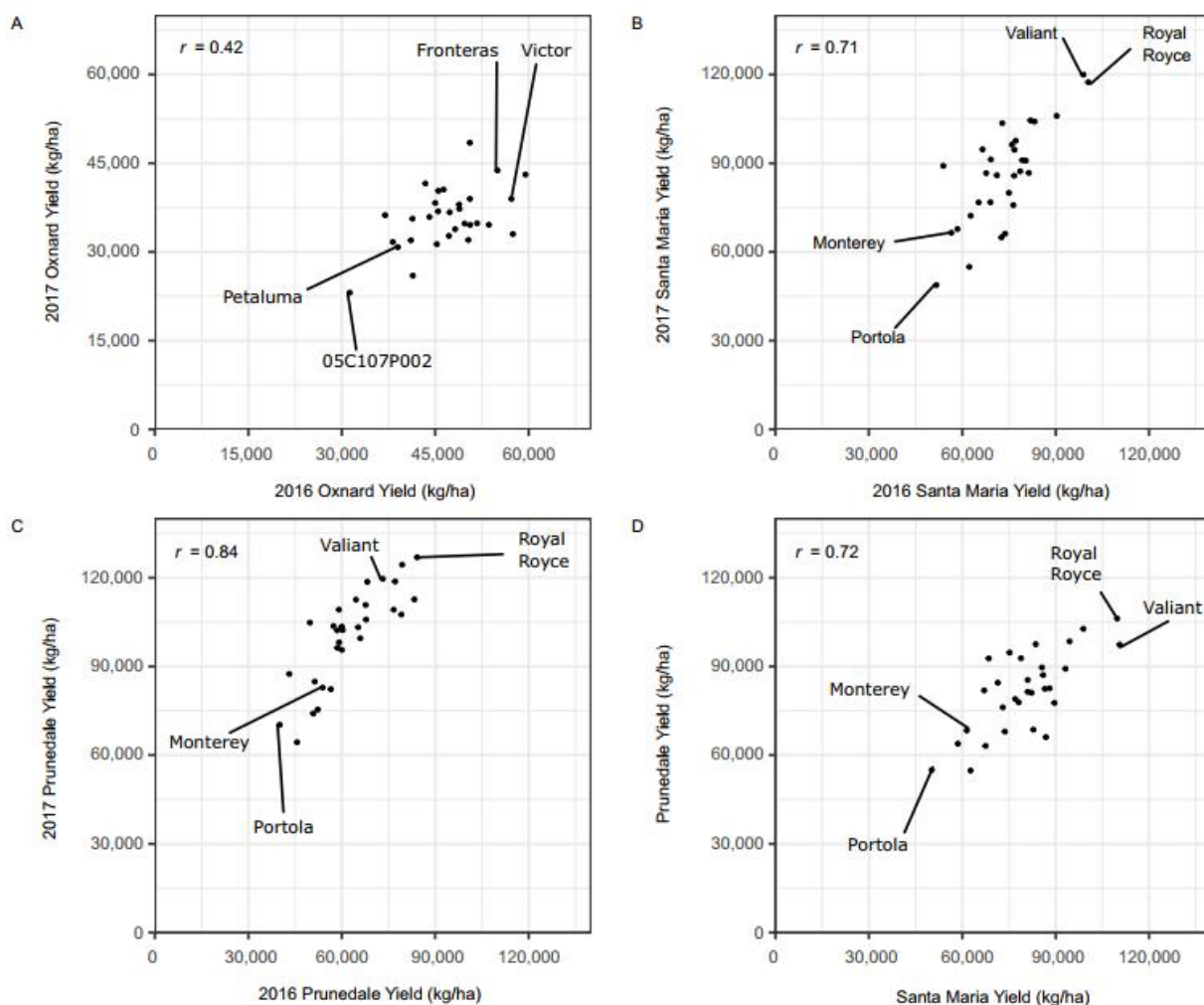

Figure 2 Cumulative marketable fruit yields of modern short-day and day-neutral cultivars (hybrids) grown in coastal California locations over the 2015-2016 and 2016-2017 growing seasons

Figure 3 displays the genetic diversity among early and modern strawberry hybrids. The first two principal components (PC1 and PC2) from principal component analysis (PCA) illustrate the genetic relationships among three groups of genotype individuals based on 28,513 single nucleotide polymorphisms (SNPs) in 1,406 hybrid varieties, ranging from the years 1775-2016. Blue dots represent 405 elite × elite hybrid varieties that have been phenotypically tested for fruit yield and quality; coral dots represent 131 elite × exotic and 8 exotic × exotic hybrid varieties, also phenotypically tested for yield and quality; grey dots represent a genetically diverse group of 434 cultivated varieties from California and non-California, and other hybrids developed between 1775-2015 that lack phenotypic testing.

Figure 3 shows significant differences in the PCA distribution of hybrid varieties with different genetic backgrounds, indicating rich genetic diversity. Elite × elite hybrids are concentrated on the right side of the PCA plot, suggesting closer genetic relationships and lower genetic diversity. In contrast, the coral and grey dots are more scattered throughout the plot, indicating more diverse genetic backgrounds. This genetic diversity is a valuable resource in breeding and crop improvement, providing potential genetic variations for future breeding efforts.
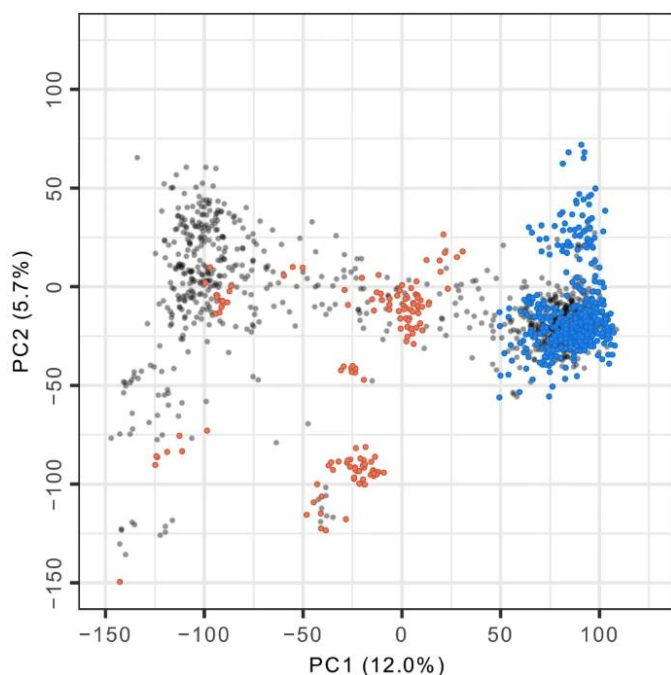
Figure 3 Genetic diversity among early and modern strawberry hybrids

Figure 4 reflects the phenotypic means after phenotyping 405 elite × elite hybrids (blue dots), 132 elite × exotic hybrids (red dots), and 8 exotic × exotic hybrids (black dots) in the Salinas area during the 2016-17 and 2017-18 growing seasons. Displayed traits include fruit yield (A), number (B), weight (C), firmness (D), total soluble solids (E; TSS), titratable acidity (F; TA), sugar-acid ratio (G), and anthocyanin concentration (H; ANC). The estimated marginal means (EMMs) for each trait are based on data collected from three replicates of fruit harvests conducted weekly for 11-13 weeks around the summer solstice each year. The displayed annual ranking correlations (r) are positive for all traits and statistically significant.

The figure shows that there are differences in trait performance between populations. Elite × elite hybrids perform better in yield, weight, and firmness, indicating these traits are likely focal points in the selection process. Elite × exotic and exotic × exotic hybrids show more diversity in quality traits such as total soluble solids, titratable acidity, and anthocyanin concentration.

Furthermore, data from different years show good correlation, indicating that these traits have stable genetic performance across growing seasons. This stability is crucial in breeding, as it indicates that the selected traits of varieties can remain consistent across different growing conditions.

Thus, the data from this figure can guide future strawberry breeding efforts, particularly in improving economic traits such as yield, fruit weight, and firmness, while also focusing on enhancing fruit quality traits to meet market demands for high-quality strawberries.

Figure 5 presents the genomic estimated breeding values (GEBVs) for agriculturally important traits in strawberries from 1775 to the present. These GEBVs are estimated using the single-step best linear unbiased prediction (ss-BLUP) method from pedigree (A) and genomic (G) relationship matrices. Blue dots represent 796 genotyped individuals, and grey dots represent 5,646 non-genotyped individuals, with known birth years. Dotted lines show the predicted GEBVs (population average) before and after the change point (CP) years, which vary among different traits from 1943—1962. The left column shows statistical data for traits such as fruit yield (A), number (D), weight (G), and firmness (J); the middle column displays total soluble solids (TSS) (B), sugar-acid ratio (TSS/TA) (E), titratable acidity (TA) (H), and anthocyanin concentration (ANC) (K); the right column shows Verticillium wilt (VW) resistance scores and area (AUDPS) (C, F) and Phytophthora crown rot (PhCR) resistance scores and area (AUDPS) (I, L). The resistance scores range from highly resistant (1) to highly susceptible (5).

Therefore, over time, there have been significant changes in the breeding values of traits such as yield, number, weight, and firmness in strawberry breeding. The predicted change point years represent a turning point in strawberry breeding, possibly related to the introduction of specific breeding techniques or changes in crop management practices. Additionally, changes in quality traits and disease resistance indicate the diversity of strawberry germplasm in these traits and the direction of strawberry breeding may have shifted over time with the accumulation and change of selective pressures. These data are valuable for understanding the historical process of strawberry breeding and for formulating future breeding strategies.
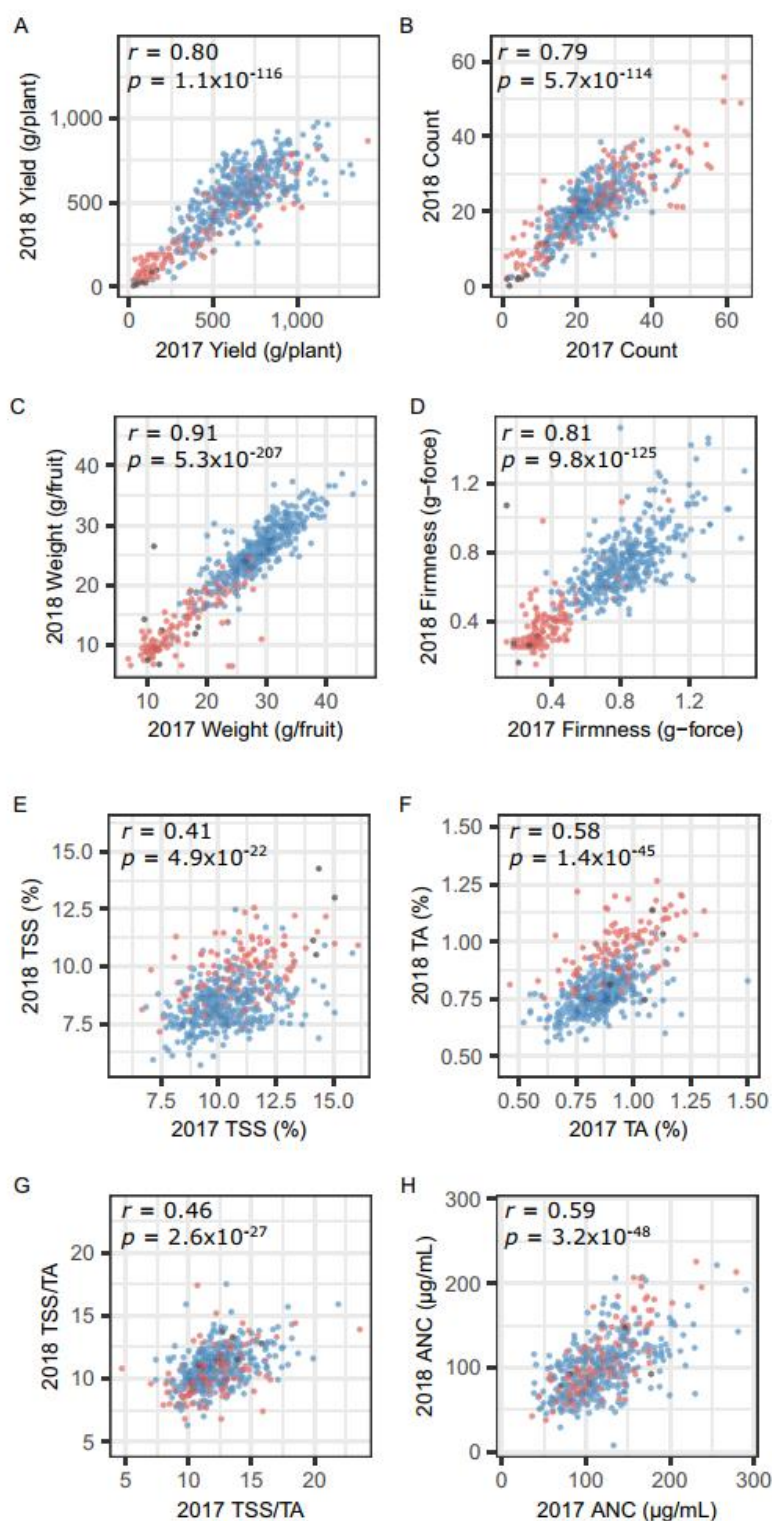

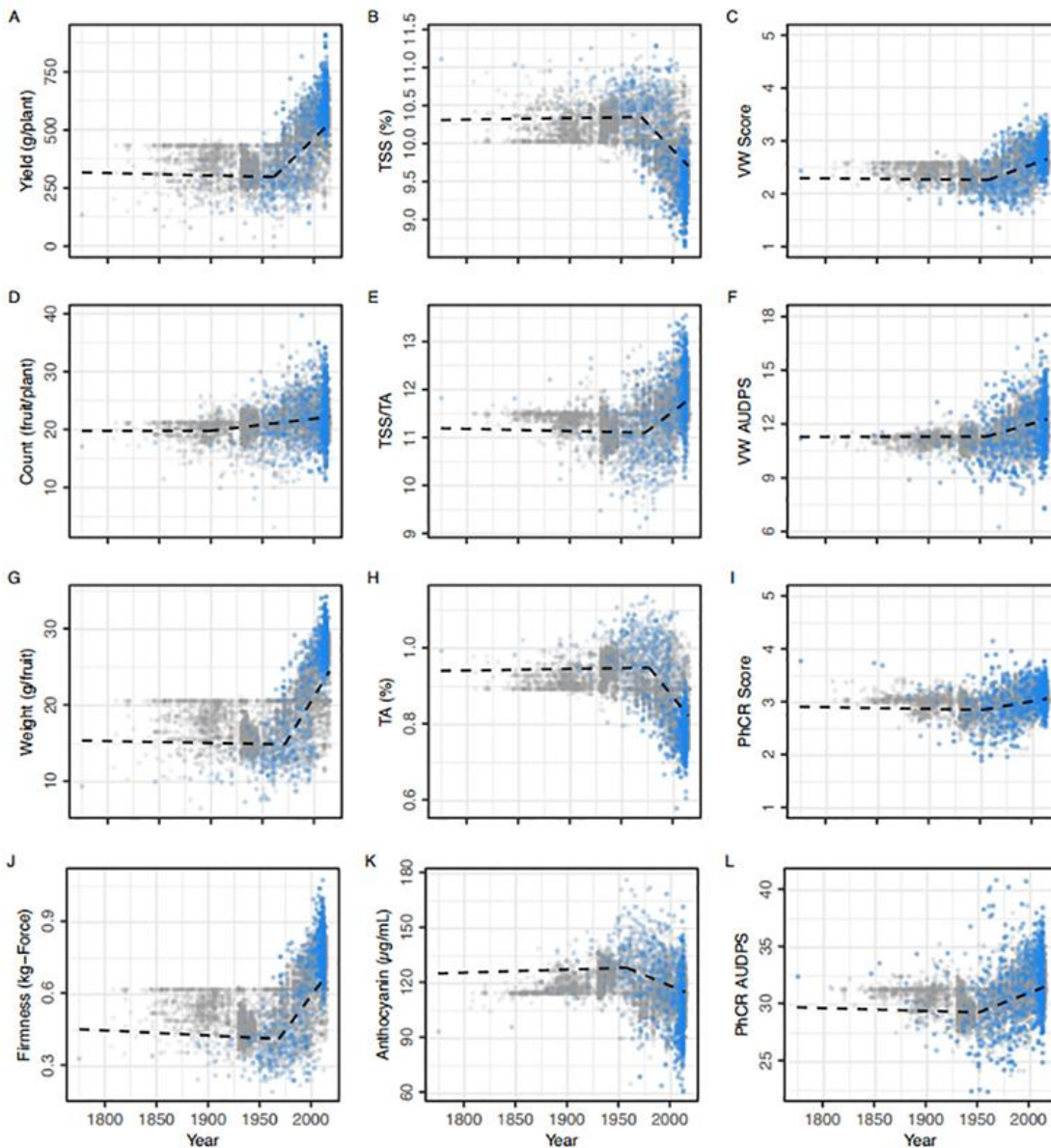Figure 4 Phenotypic means of training population hybrids

Figure 5 Genomic prediction of breeding values

Figure 6 displays the additive genetic correlations between strawberry fruit traits and disease resistance traits. These correlations are derived from the genomic estimated breeding values (GEBVs) of 796 genotyped individuals and 5646 non-genotyped individuals, whose individual birth years range from 1775 to 2015. Part A of the figure (lower triangle area) shows the estimated additive genetic correlations for all individuals from 1775 to 2015; Part B (upper triangle displays estimates before 1954, and the lower triangle shows estimates after 1954). The color gradient from red to blue represents the change in correlation from positive (+1) to negative (-1).

The figure illustrates strong genetic correlations between some traits. For instance, fruit yield correlates positively with the number, weight, and firmness, suggesting that these traits are often improved simultaneously in breeding programs. In contrast, correlations with total soluble solids (TSS), titratable acidity (TA), and other quality traits are weaker, indicating that productivity improvements and quality enhancements might need to be selected independently in breeding. Additionally, disease resistance traits, such as Phytophthora crown rot (PhCR) and Verticillium wilt (VW) resistance, show low or negative genetic correlations with productivity-related traits, suggesting that increasing yield and improving other agronomic traits could impact plant disease resistance.

Thus, the figure underscores the complex genetic links between different strawberry traits, which is crucial for future breeding strategies, especially when aiming to simultaneously enhance strawberry yield, quality, and disease resistance. This information aids breeders in choosing parents for hybridization, balancing traits to achieve optimal breeding goals.
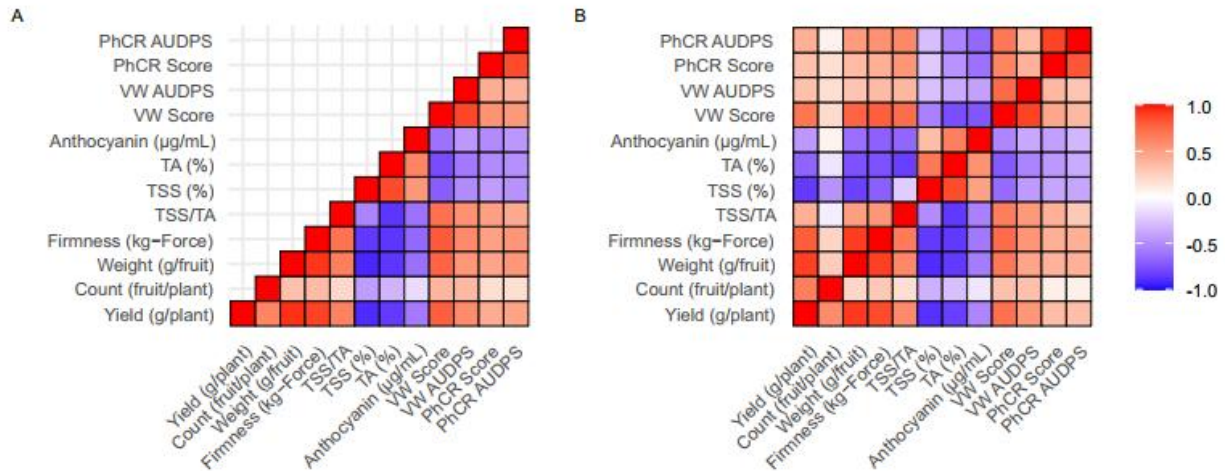

Figure 6 Additive genetic correlations

Figure 7 graphically summarizes the important milestones in strawberry domestication from 1715 to the present. The development of strawberries is depicted in watercolor, with each letter representing a specific stage of development. A: Post-1715, spontaneous hybrids between *F. chiloensis* subsp. *chiloensis* and *F. virginiana* subsp. *virginiana* emerged in Western European cultivation. B: Between 1715 and 1766, the earliest interspecific hybrid varieties appeared and were exchanged and cultivated in Western European botanical gardens such as the Versailles Gardens. C: Post-1766, Antoine Nicolas Duchesne discovered the interspecific hybrid origin of *F. × ananassa* and began producing early cultivated varieties through artificial hybridization and selection from interspecific offspring. D: In the early 1800s, iconic early cultivated varieties like Keen's Seedling and Downtown appeared in Western Europe, were widely disseminated and exchanged, and made their way to North America. E: At the turn of the 19th to the 20th century, iconic cultivated varieties such as Royal Sovereign and Nich Omher emerged in North America and Europe. F: Between 1899 and 1927, Alfred Etter introduced alleles from local F. chiloensis subsp. pacifica and *F. chiloensis* subsp. *lucida* into hybrids and started strawberry breeding along the California coast, donating his genetic resources to the University of California in 1928. G: Post-1924, early cultivated varieties such as Lassen, Fairfax, and Shasta emerged from populations in California and other parts of North America. H: Post-1953, short-day (photoperiod-sensitive) cultivars emerged from the California population during the Green Revolution. I: From 1953 to 1980, Royce S. Bringhurst began developing photoperiod-insensitive *F. × ananassa* cultivars by introducing alleles from native F. virginiana subsp. glauca in Utah. J: Post-1980, day-neutral (photoperiod-insensitive) cultivars emerged from the California population during the Green Revolution.

Therefore, the chart highlights key advances in strawberry domestication, including overcoming photoperiod sensitivity and the positive changes in genetic diversity and breeding of strawberry varieties, providing a crucial genetic foundation for strawberry breeding and agricultural production.

Figure 8 uses red and gray dots to represent the genomic predictions of population average values and additive genetic variance (VA) for agriculturally important traits in strawberry breeding history (1775—2015). Red dots represent the 87,893 simulated segregating populations produced by parental hybridization before the Green Revolution (1775—1953), while gray dots represent the 84,490 segregating populations produced after 1953.
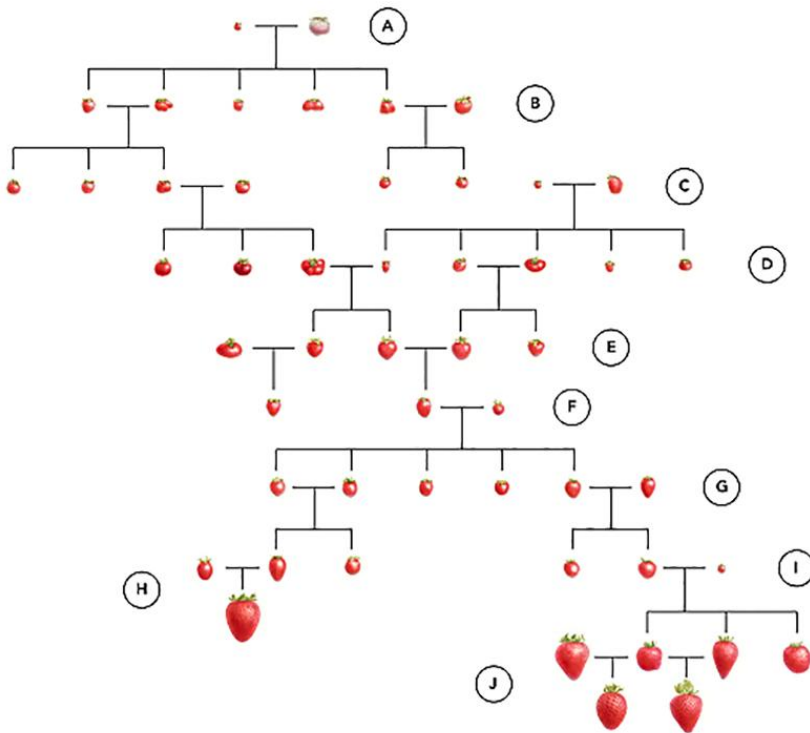
Figure 7 Graphical abstract of strawberry domestication milestones (1715-present)
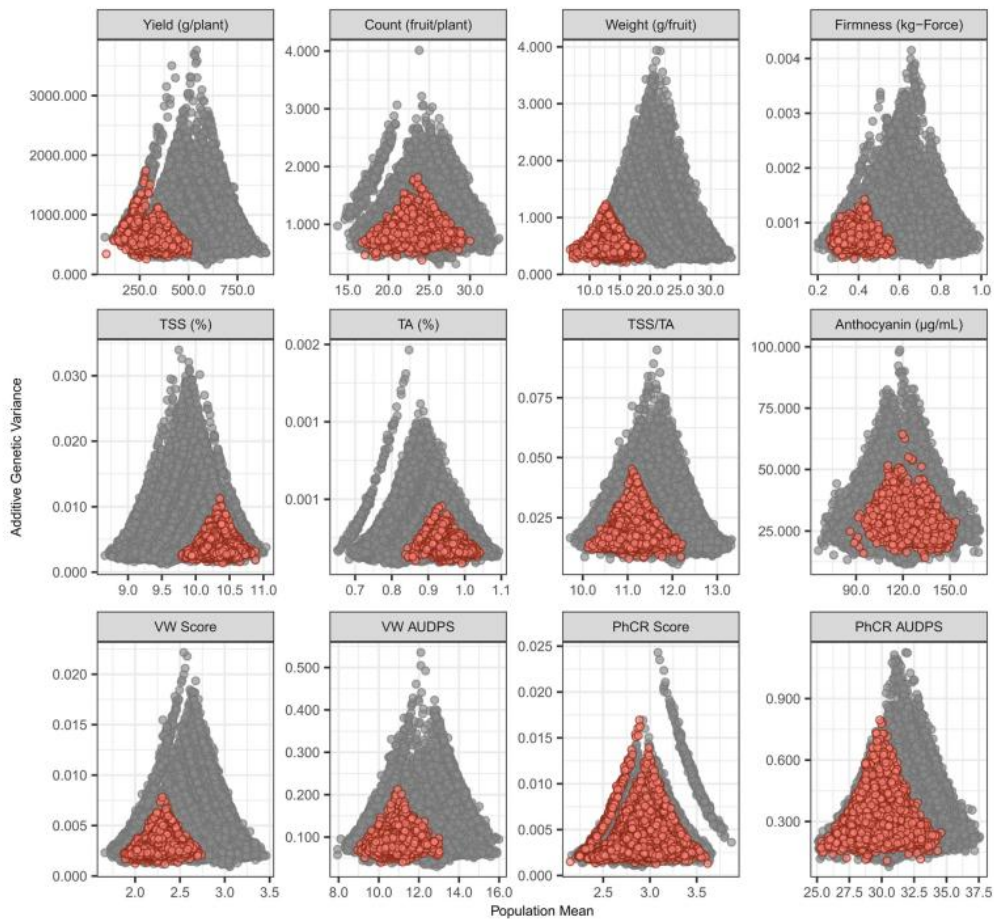

Figure 8 Genomic prediction of additive genetic variance

The figure shows significant changes in additive genetic variance before and after the Green Revolution for traits such as yield, fruit number, weight, firmness, total soluble solids (TSS), titratable acidity (TA), sugar-acid ratio (TSS/TA), anthocyanin concentration, and disease resistance traits like Verticillium wilt (VW) and Phytophthora crown rot (PhCR). The post-Green Revolution populations (gray dots) exhibit higher additive genetic variance, suggesting that breeding may have increased the genetic diversity of these traits.

Thus, the results indicate that post-Green Revolution, through selective and hybridization strategies, strawberry breeding may have successfully enhanced the genetic diversity of certain traits, which is crucial for adapting to environmental changes, improving quality, and increasing disease resistance. Additionally, the data in the chart imply that balancing various traits during the breeding process is necessary to ensure both increased yield and quality while maintaining or enhancing disease resistance. These insights are vital for understanding the historical progress of strawberry variety improvement and formulating future breeding strategies.

Table 1 shows the genetic gains achieved for 545 hybrid strawberry varieties phenotyped during the 2017-18 and 2018-19 growing seasons in the Salinas region of California. The table lists the gain values ($\Delta G = \text{EMM}_1 - \text{EMM}_2$) for marketable fruit yield and quality traits, derived through linear contrasts of the estimated marginal means (EMMs). These EMMs were obtained from a linear mixed model analysis based on phenotypic observation data from 10 to 13 harvests per year and three clonal replicates per hybrid variety each year.

The table also provides the REML estimates of broad-sense heritability (h^2), which indicate the genetic stability of traits based on clonal averages. Additionally, the ratio of genotype-by-year interaction variance to phenotypic variance is shown $(\sigma^2_{G \times Y} / \sigma^2_P)$, reflecting the impact of environmental conditions in different years on trait expression.

For each trait, the table lists two ΔG estimates: one using a low-performing elite × elite hybrid as a reference, and the other using a low-performing elite × wild hybrid as a reference. The percentage change in ΔG ($\Delta G(\%)$) is calculated based on the ratio of the gain value to EMM_2 multiplied by 100.

The table indicates that, compared to elite × elite hybrids, elite × wild hybrids typically show larger genetic gains in traits such as yield, number, weight, firmness, total soluble solids (TSS), titratable acidity (TA), sugar-acid ratio (TSS/TA), and anthocyanin concentration. This may suggest that introducing genetic material from wild species can significantly enhance the performance of specific traits.

The Pr(>t) values in the table indicate the statistical significance of non-zero genetic gains. A small value suggests sufficient evidence to reject the null hypothesis, confirming the presence of genetic gains. In most traits, this value is very small, indicating significant genetic gains. These data are crucial for evaluating and guiding future strawberry breeding efforts.

Table 2 presents changes in breeding values during the domestication process of strawberries from 1775 to 2015, from a genomic prediction perspective. The table provides the genomic estimated breeding values (GEBVs) for agriculturally important traits for 6,419 strawberry hybrid varieties estimated using the single-step pedigree-genomic BLUP method, along with the linear regression results of predicted values $(\hat{y})$ against birth year. The change point (CP years) in the table is determined through piecewise linear regression of GEBVs against birth years. The upper part of the table (see Figure 5) displays the changes in predicted GEBV values $(\Delta \hat{y})$, while the lower part (see supplementary Figure 2) shows the changes in GEBV residuals $(y - \hat{y})$ before and after the estimated CP years. For each trait, the table displays predicted values for three years (1775, estimated CP year, 2015) and the changes in predicted GEBV values between these years. The percentage changes are calculated based on the growth rate before and after the CP year.

The table shows significant changes in multiple traits around the CP years. For example, traits such as yield, number, weight, and firmness show significant increases after the CP years, suggesting that these traits may have been focal points in breeding targets. In contrast, growth in quality traits such as total soluble solids (TSS) and titratable acidity (TA) is relatively minor. Resistance scores and related AUDPS values for diseases like Verticillium wilt (VW) and Phytophthora crown rot (PhCR) show increases or decreases after the CP year, reflecting different breeding strategies and environmental challenges.

Table 1 Historical genetic gains

Trait[a]	$\hat{H}^2$ [b]	$\hat{\sigma}^2_{G\times Y}/\hat{\sigma}^2_P$ [c]	Benchmark[d]	EMM$_1$	EMM$_2$	ΔG	ΔG (%)[e]	Pr>t[f]
Yield (g/plant)	0.88	0.06	Elite × Elite	1091.3	36.7	1054.6	2873.6	0.003
			Elite × Wild		16.2	1075.1	6636.4	0.002
Count	0.92	0.04	Elite × Elite	40.4	2.6	37.8	1453.9	0.002
			Elite × Wild		1.0	39.4	3940.0	0.002
Weight (g/fruit)	0.93	0.02	Elite × Elite	41.7	12.7	29.0	228.3	0.004
			Elite × Wild		6.9	34.8	504.3	0.006
Firmness (kg-force)	0.75	0.04	Elite × Elite	1.39	0.41	0.98	239.0	0.006
			Elite × Wild		0.16	1.23	768.8	0.003
TSS (%)	0.59	0.13	Elite × Elite	15.2	5.5	9.7	176.4	0.110
			Elite × Wild		7.4	7.8	105.4	0.146
TA (%)	0.82	0.07	Elite × Elite	1.16	0.57	0.59	103.5	0.096
			Elite × Wild		0.64	0.52	81.3	0.094
TSS/TA	0.70	0.06	Elite × Elite	18.9	6.2	12.7	204.8	0.020
			Elite × Wild		7.7	11.2	145.5	0.011
Anthocyanin (ng/mL)	0.75	0.00	Elite × Elite	241.8	47.8	194.0	405.9	0.020
			Elite × Wild		45.4	196.4	432.6	0.019

Therefore, Table 2 provides a comprehensive view of how the breeding values of traits have fluctuated and transformed over time in the history of strawberry breeding, which is essential for understanding the progress of variety improvement and planning future breeding directions.

2 Research Results Analysis

This study, through phenotypic analysis and genomic prediction methods of the California hybrid population, confirmed the significance of breeding in the strawberry Green Revolution, especially the introduction of photoperiod insensitivity traits that contribute to increased yields. Additionally, the study demonstrated the expansion of additive genetic variation and phenotypic diversity achieved through genetic breeding.

Table 2 Genomic prediction of domestication-associated breeding value changes in strawberry

Statistic[a]	Trait[b]	CP Year[c]	Estimate			Change (%)[d]		Change/Year (%/Year)	
			1775	CP	2015	1775 to CP	CP to 2015	1775 to CP	CP to 2015
$\dot{y}$	Yield (g/plant)	1961	467.71	450.94	680.56	−3.59	50.92	−0.02	0.95
	Count	1893	21.52	21.31	23.80	−0.98	11.71	−0.01	0.10
	Weight (g/fruit)	1971	20.86	20.12	29.74	−3.56	47.79	−0.02	1.09
	Firmness (kg-force)	1969	0.58	0.54	0.81	−6.59	48.92	−0.03	1.06
	TSS (%)	1969	9.81	9.86	9.21	0.43	−6.55	0.00	−0.14
	TA (%)	1978	0.89	0.89	0.77	0.70	−14.14	0.00	−0.38
	TSS/TA	1976	11.31	11.22	11.91	−0.80	6.19	0.00	0.16
	Anthocyanin (ng/mL)	1959	117.84	120.45	107.13	2.22	−11.06	0.01	−0.20
	VW Resistance Score	1957	2.49	2.44	2.84	−2.15	16.29	−0.01	0.28
	VW Resistance AUDPS	1956	10.92	10.92	11.89	0.00	8.86	0.00	0.15
	PhCR Resistance Score	1953	3.00	2.94	3.15	−2.07	7.16	−0.01	0.12
	PhCR Resistance AUDPS	1952	30.39	29.92	32.14	−1.53	7.42	−0.01	0.12
$\sqrt{(y - \dot{y})^2}$	Yield (g/plant)	1940	50.84	49.81	98.92	−2.02	98.58	−0.01	1.32
	Count	1934	1.19	1.39	2.45	16.93	76.44	0.11	0.95
	Weight (g/fruit)	1940	2.10	1.78	3.70	−15.07	107.55	−0.09	1.43
	Firmness (kg-force)	1939	0.06	0.06	0.10	−4.05	73.00	−0.02	0.96
	TSS (%)	1937	0.16	0.13	0.33	−17.24	146.61	−0.11	1.87
	TA (%)	1930	0.03	0.03	0.06	1.39	122.15	0.01	1.44
	TSS/TA	1897	0.19	0.20	0.40	5.21	101.88	0.04	0.86
	Anthocyanin (ng/mL)	1927	5.88	5.79	9.93	−1.62	71.57	−0.01	0.82
	VW Resistance Score	1932	0.13	0.13	0.20	0.89	61.60	0.01	0.75
	VW Resistance AUDPS	1930	0.24	0.27	0.90	13.83	230.60	0.09	2.72
	PhCR Resistance Score	1984	0.13	0.15	0.11	16.24	−29.46	0.08	−0.94
	PhCR Resistance AUDPS	1924	0.97	1.04	1.31	7.30	26.11	0.05	0.29

3 Research Evaluation

The study delves into the genetic foundation of strawberry yield growth, revealing the lasting impact of Green Revolution breeding techniques on the strawberry industry. Its innovative methodologies and detailed analysis of genetic variation provide valuable insights for breeding research in other crops.

4 Conclusion

Genetic gains achieved through breeding are the primary reasons for the significant increase in strawberry production over the past half-century. The introduction of photoperiod-insensitive perpetual flowering hybrid varieties was a key breakthrough in the strawberry Green Revolution, significantly impacting the strawberry industry in California and globally.

5 Access the Full Text

Feldmann, M.J., Pincot, D.D.A., Cole, G.S. et al. Genetic gains underpinning a little-known strawberry Green Revolution. Nat Commun 15, 2468 (2024). https://doi.org/10.1038/s41467-024-46421-6.