

Strawberry Genetics.

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There have been several comprehensive English language historical reviews of strawberry genetics and improvement, notably those of Darrow (1937, 1966) and Scott and Lawrence (1975). Gaining an understanding of strawberry genetics is complicated by varying species ploidy levels, hybrid origin of several of the polyploid species, and a combination of discontinuous (discrete or Mendelian) and continuous (quantitative or multifactorial) inheritance patterns for various traits within the same plant.

Genetic exchange within and among species in the genus *Fragaria* is further limited by sexual dimorphism in some of the species, and by partial or complete cross-incompatibility in both heteroploid and in some homoploid hybridizations. Fortunately, exchange among the octoploid species, including the garden or cultivated strawberry and its ancestral American parent species, is relatively unrestricted.

An attempt will be made in this review to outline major trends in strawberry genetics research since the Scott and Lawrence paper, or roughly the period from 1970 to 1989. Cytogenetic, evolutionary, and ecological facets of the strawberry genetics picture will be treated lightly, or not at all, because these topics will be treated by others in this series.

BREEDING SYSTEM CHARACTERIZATIONS

This active area of inquiry consists of continuing studies that determine the amount of genetic diversity present in a population, largely for selecting parents for the next generation of improvement. Populations of strawberry clones are grown under certain environmental conditions or are subjected to artificial or natural screening to discern the phenotypic response(s) of each clone. Many times it may be necessary to partition a character (or set of characters) into their components before selection. These components may then be

analyzed for heritability. In the process of the heritability analysis, clones are identified that possess good or poor combining ability. Further, the presence of significant amounts of additive and non-additive genetic variance suggests which breeding strategies may be particularly successful.

Genetic diversity

Narrow genetic bases for cultivars of our principal food crops has become a matter of increasing concern and has stimulated considerable recent germplasm exploration, collection, and evaluation. Sjulín and Dale (1987) analyzed a population of 234 North American strawberry cultivars introduced between 1960 and 1985 for genetic diversity. They demonstrated that the strawberry is in a better position than many crops, in that 53 "founding clones" contributed genetic materials to the 134 cultivars. These founding clones (originated in the 19th and 20th centuries) had mean genetic contributions of <0.1% to 11%. The extensive use of the 'Howard 17' clone as a parent led to the contribution of seven founding clones (all in the 'Howard 17' parentage) to at least 130 of the 134 cultivars. The cultivars were clustered by genetic parent contribution into 11 groups that were strongly related to area of geographic origin. Inbreeding coefficients were calculated for the 134 cultivars, and they varied from 0.0 to 0.875. Three suggested strategies for maintaining and increasing genetic diversity in genetic improvement programs were: a) increasing the number of parents per generation, combined with a controlled system of mating; b) introduction of partially or completely unrelated *F. × ananassa* germplasm into the breeding population; and c) introducing unimproved germplasm from wild *Fragaria* species. Such measures have been adopted by many genetic improvement programs and are important in a species where one cycle of self-pollination will reduce vigor, yield, and fruit size.

Table 1. Examples of parent source character identification in strawberries during the period 1970–1989.

Trait	Literature source	Possible parent clones
Aphid resistance (virus vectors)	Crock et al., 1982	'Benton', 'Del Norte', and 29 clones in North American <i>F. chiloensis</i>
Starch gel electrophoresis isozyme patterns of PGI, LAP, and PGM	Bringhurst et al., 1981	Separation of 14 of 22 cultivars into unique classes
Two-spotted spider mite tolerance	Shuster et al., 1980	'Florida Belle', 'Sequoia'
Root-knot nematode tolerance	Edwards et al., 1985; Szczygiel and Danek, 1984	'Apollo', 'Earliglow', 'Prelude', 'Glima', 'Senga Sengana'
Berry mold resistance	Popova et al., 1985	'Badgerglo', 'Troubadour', 'Atlas', 'Arnika', 'Redgauntlet', 'Holiday', 'Oreshuk', 'Kulon', <i>Zh 16-223</i>
	Maas and Smith, 1978	'Earliglow'
Resistance to strawberry root weevil and black vine weevil	Shanks et al., 1984	A number of native North American <i>F. chiloensis</i> clones, especially CL-5 and GCL-8
Adaptation to mechanization and fruit quality	Sistrunk and Moore, 1980	'Cardinal' and A-5344
Jam production	Skrede, 1980	'Jonsok', 'Totem', 'Bounty', 'Senga Sengana'
Freezing quality	Daniels et al., 1982	'Darrow', 'Earliglow', 'Vesper'
Resistance to red stele root rot	Maas et al., 1989	Eastern U.S. cultivars resistant to several Western U.S. red stele races; 'Darrow', 'Delite', 'Earliglow', 'Guardian', 'Lateglo', 'Midway', 'Scott', 'Sparkle', 'Surecrop', 'Tribute', 'Tristar'
Verticillium wilt resistance	Maas et al., 1989	High resistance: MD-683, 'Del Norte', 'Aberdeen'; moderate resistance: 'Midway', 'Pocahontas', 'Surecrop', 'Guardian', 'Tristar', 'Tribute', 'Micmac', 'Delite', 'Earliglow', 'Lester', 'Lateglo'
Virus tolerance	Daubeny et al., 1972	'Totem', 'Northwest', 'Cheam', BC26, BC5, WSU1054, 1165, 1169, 1217, 1232, 1238; 'British Sovereign', 'Cambridge Favourite'

Cytogenetics

A considerable body of quantitative genetic data for the cultivated strawberry octoploid species is based on the assumption of regular diploid bivalent pairing during meiosis. Early chromosome association studies by Ichijima (1926), Longley (1926), and Powers (1944) suggested that this assumption was correct. Later observations by Staudt (1951, 1952) with the hexaploid species *F. moschata* and the tetraploid species *F. orientalis* showed multivalent associations present at diakinesis, but their terminalization into bivalents by Metaphase I. Mok and Evans (1971), in an attempt to determine the probability of polysomic inheritance in strawberry cultivars, studied diakinesis of nine eastern North American cultivars. They found multivalent pairing in each of the nine cultivars in each of 2 years, varying from quadrivalents and hexavalents to occasional octovalents. Bivalent pairing varied in closeness of association and some secondary pairing was observed. The authors concluded that tetratomic inheritance is likely to be important in the cultivated strawberry. However, they noted that the rest of the meiotic cycle appeared normal.

Byrne and Jelenkovic (1976), studying chromosome pairing of nine cultivars and 32 S₂ seedlings of *F. ×ananassa*, reported all chromosome pairing as bivalents, indicating cytological diploidization. Five cells with apparent multivalents were interpreted as pseudomultivalents because of their end-to-end or side-to-side associations rather than the typical ring and chain multivalent associations. A completely sterile seedling was found to have complete bivalent pairing at pachytene, but desynapsis to an almost completely unpaired condition by diplotene. Pentaploid hybrids between *F. ×ananassa* and the unrelated diploid species *F. nubicola* averaged 11.6 bivalents per PMC and frequent multivalent associations, indicating a residual homology between ancestral genomes of the octoploid strawberry. The usual lack of pairing among homologous chromosomes in the cultivated strawberry was attributed by the authors 'to a genetic control leading to preferential pairing of homologous chromosomes within genomes. (Also, selection by breeders for highly fertile types probably automatically results in a correlated selection for regular bivalent pairing and disjunction.)

A later chromosome pairing study of four strawberry (8x) seedling progenies cultivated in Iowa and their parent clones (Ibrahim et al., 1981) agreed with the findings and interpretations of Byrne and Jelenkovic (1976) of complete bivalent pairing with some sec-

ondary association of bivalents as pseudo-multivalents.

Berezenko (1976, 1981) made comparative studies of meiosis in a group of sterile garden strawberry (8x)-hautboy strawberry (6x) hybrids and their parent clones. Meiosis was essentially normal in the parent clones. The heptaploid (7x, 2n = 49) sterile hybrids exhibited the following abnormalities: presence of univalents, trivalents, tetravalents, and pentavalents at diakinesis; cytomixis during Prophase I; chromosome alignment off the spindles and premature chromosome movement to the poles in Metaphase I and Anaphase I; laggards at Anaphase I; and chromosome ejection into the cytoplasm at Telophase I. These abnormalities were repeated during the second meiotic division, leading to abnormal spore numbers and sterile pollen grains. In the 1981 paper, the proportion of large (diploid) and small pollen grains are characterized for size and shape for each hybrid.

Parent source identification

It is always critical to have parent sources for particular characteristics identified so that future genetic recombination and selection is possible. Considerable progress was made in this period in identifying parents for diverse strawberry traits (Table 1).

Correlated phenotypic traits

Character component studies, which identify and assess the genotypic and environmental influences on the expression of correlated phenotypic traits, are becoming more frequent. Knowledge about correlated traits is most important to the strawberry geneticist, because selection can be directed to improving individual aspects of a complex character such as fruit yield or appearance more readily than the entire characteristic. For example, the resistance of *F. chiloensis* clone CL-5 to feeding by adult black vine weevils was traced to the dense covering of simple hairs on abaxial leaf surfaces of this clone (Doss et al., 1987).

The strength of expression of the day-neutral (everbearing) character was related to plant structure (Nicoll and Galletta, 1987). Strong, or continuous-blooming, day-neutrals are basically small plants with below-average numbers of leaves and meristems and an average number of crowns with high meristem development as flower trusses. Intermediate, or periodic-blooming, day-neutrals are small to medium leafy plants with many crowns and axillary meristems.