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 nonadditive 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. Sjulin 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 *F. chiloensis*
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', *Zh 16-223*
	Maas and Smith, 1978	'Earliglow'
Resistance to strawberry root weevil and black vine weevil	Shanks et al., 1984	A number of native North American *F. chiloensis* 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', 'Lateglow', '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', 'Lateglow'
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 mutlivalent 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 S_1 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 secondary 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.

Table 2. Quantitative inheritance of strawberry traits in the period 1970–1989. (Outstanding parents and crosses are identified by the authors in combining analysis studies.)

Trait(s) and references	Breeding materials	Findings[z]
Seed germination and seedling vigor (Melville et al., 1980b)	Intercrossed, selfed, outcrossed population of two S_1, two S_2 and two non-inbred selections	Most intercrossed and outcrossed inbreds had similar germination, germination rate, and shoot and root weights as the non-inbred control cross. Selfs had lower vigor than most intercrosses. The S_3 progeny had lower germination total and rate than the control.
Red stele resistance (Melville et al., 1980a)	Same as Melville et al. (1980b); six-parent diallel	Level of inbreeding and type of inbred cross was not related to transmission of red stele resistance. Self-pollinations transmitted less resistance than cross-pollinations. There was significant SCA for weighted progeny mean score and for percent resistant.
Aphid resistance (Barritt and Shanks, 1980)	Five clones and two BC1 seedling progenies from *F. chiloensis* 'Del Norte'	Segregation occured in BC1 generation. Resistant clones were selected from both crosses, but they did not have quite as high a level of resistance as the source clone.
Cornicle (Infl?) no., Flowering time per plot (beginning), yield (total wt.) (Ulyukin et al., 1976)	Six cultivars diallel, 28 progenies, three blocks with two replications per plock, 80 seedlings per plot	Cornicle no. and flowering time were GCA significant; yield was GCA and SCA significant. No reciprocal effects seen in these characters.
Twospotted mite resistance (Barritt and Shanks, 1981)	Fifteen crosses involving three cultivars and five selections two locations in field and greenhouse	GCA and SCA significant at both locations for mean no. of mites/leaflet. GCA > SCA. Heritabilities (parent/offspring regressions) were high. Additive genetic variance important in mite resistance.
Powdery mildew resistance (Simpson, 1987)	Four everbearing and three short-day cultivars in a half diallel w/o selfs (Expt. 1) Expts. 2–5 EB and DN clones crossed to eight short-day clones	Expt. 1 GCA and SCA significant in both years. GCA SCA. Expt. 2. findings same as Expt. 1—additive and non-additive gene effects important.
Leaf spot resistance (Shaw et al., 1988)	Two years—66 crosses from 18 parents with 15 reciprocals; 2nd year—30 crosses from 14 parents	0–5 scalar scores, significant GCA and SCA, heritabilities improve with seasonal progression. Genetic gain is improved by multistage rather than mass selection.
Fruit quality factors taste, consistency, anthocyanin content, vitamin C content, R-active catechin content (Zubov and Stankevich, 1982)	Five parent diallel, 20 progenies, four replications of 100 seedlings in a lattice design	Significant differences among seedlings for all characters except taste. GCA and SCA significant for other four characters GCA > SCA except for vitamin C.
Primary : secondary fruit size relationship (Pelofske and Lawrence, 1984)	Seventeen cultivars and selections, six crosses—50 seedlings per cross	Frequency distributions of P:S ratios within progeny and comparison with parent and midparent values indicates quantitative inheritance.
Fruit detachment traits (Brown et al., 1975)	Seven clones and six crosses	Capping force, capping percent, and pedicel breaking force evaluated. *F. virginiana* is an excellent capping source. Progeny means for pedicel breaking were near the low parent mean.
Easy calyx removal (Barritt, 1976)	Twenty-seven clones and 79 seedling families	GCA and SCA significant GCA 4× SCA. Heritability estimate 0.84 GCA correlated with parent phenotype (r = 0.828).
Machine harvesting (Lawence and Martin, 1980)	Thirty-seven cultivars and selections parent evaluation for transmission	Evaluated traits: Capping ease—'Olympus' and ORUS 4637 most effective parents; concentrated ripening, fruiting habit—'Totem', 'Benton', ORUS 4637, and ORUS 4003 transmitted good fruit support.
Harvest mechanization (Moore and Sistrunk, 1980)	Review of progress and characters	Important characters: Concentrated ripening, productivity, easy fruit detachment, firmness, color, processing quality. 'Cardinal' released, prepotent selections for the other traits identified.
Virus tolerance (Barritt and Daubeny, 1982)	Twenty-nine progenies + parent clones RCB, six replications, five seedlings per replication	'Totem' and Aiko' produced the highest proportion of tolerant seedlings. GCA and SCA signficant. GCA > SCA. Heritability when disease was worst was 0.73.
Virus tolerance (Sjulin et al., 1986)	Four-parent diallel + parents, excluding selfs, all test plants inoculated by virus-bearing aphids	Inoculated plants had reduced vigor, petiole length, leaf width, leaf dry wt., and more leaves than controls. GCA significant for all characters.
Fruit yield and related characters (Aalders and Craig, 1974)	Diallel of seven inbred clones	Total yield: Nonadditive significant factor. Berry wt: Nonadditive and additive significant. Runner no.: Both are significant. Plant area: Nonadditive significant.
Root-knot nematode resistance (Szczygiel and Danek, 1984)	Seven cultivar crosses.	'Glima' was prepotent for transmitting galling index lowering and increasing the number of seedlings without galls. Seedling and mature reactions were well-correlated.
Soluble solids, titratable acidity, and fruit firmness (Shaw et al., 1987)	Twenty-eight crosses among 16 parents from California breeding population	Narrow-sense heritabilities; 0.07, 0.48, and 0.38 for solids, acid, and firmness, respectively. Broad-sense hertiabilities: 0.35, 0.78, and 0.38 for the same traits suggest dominance variation for solids and acids, but not for firmness.
Sugars and organic acids (Shaw, 1988)	Twenty-five selections in two sets	Gentoypic variation and correlation estimated for soluble solids, titratable acidity, and their major constituents. Genotypic variation was significant for sucrose, glucose, and fructose, but not for total sugars or solids. Genotypic variation for acids is large.

(continued)

(Table 2 continued)

Trait(s) and references	Breeding materials	Findings[z]
Early flowering in day-neutrals (Barritt et al., 1982)	Fifty-four crosses between day-neutral and short-day clones	Percent flowering by September and earliness of flowering evaluated. Crosses producing the highest proportion of day-neutrals also produced the highest proportion of early flowering. GCA was more important than SCA in early flowering.
Autumn fruiting (Jennings, 1989)	Three nisqually progenies subjected to principal component analysis.	Two vectors were identified—one describing the negative association between reproductive and vegetative vigor, and another that describes vegetative vigor independent of reproductive vigor. This makes possible the identification of vegetatively vigorous autumn-fruiting types, and supports the idea of two distinct types of response to photoperiod–temperature factors that are conditioned by major genes.

[z]GCA = general combining ability (additive genetic variance); SCA = specific combining ability (nonadditive genetic variance).

Meristem development is medium, basically as flower trusses and branch crowns. Weak day-neutrals (sporadic bloomers) are large plants with few leaves, crowns, or meristems. However, a high proportion of the axillary buds develop into runners.

Many studies correlated vegetative and reproductive trait performance during this period (Nicoll and Galletta, 1987; Strik and Proctor, 1988; Lal and Seth, 1980; Lacey, 1973; Swartz et al., 1982; Hancock et al., 1982; Popenoe and Swartz, 1985; Swartz et al.,, 1985; Durner and Poling, 1986). (There are more references to yield component studies in the literature cited in these papers.)

Basically, a strawberry cultivar needs to be planted at the proper time and spacing, with sufficient nutrients and moisture available, to develop enough plant body and flower bud. initiation sites to permit maximum flower bud initiation and development, fruit set, and fruit maturation. There are distinct genotype-cultural system interactions.

For winter and early spring production in the intensive double or quadruple hill, raised bed, clear polyethylene-mulched California growing system, selection has been directed to clones that produce many flowers continually at low temperatures, while growing very slowly as temperatures increase. Selection has also emphasized ability to mature and size attractive fruit under a variety of climatic stresses (R.S. Bringhurst, personal communication).

In the rest of the United States and Canada, and in Europe and Asia, where a variety of cultural systems are used, the vegetative-reproductive interactions for each cultivar are more complex. There are significant positive correlations, usually between yield and fruit number, inflorescence number, leaf number, and crown number. There are often negative correlations between yield and plant size or volume, root size, leaf area, petiole length, and runner number (Nicoll and Galletta, 1987).

Yield is the product of its primary components-fruit number and fruit size. Fruit number and fruit size are negatively related, and fruit number is more important to yield. The influence of plant size and leaf number on yield varies with time of year (Lacey, 1973).

La1 and Seth (1981) partitioned their correlation values into phenotypic, genotypic, and environmental contributions. Fruit yield was negatively correlated with runner number and positively correlated with days to runner formation, inflorescence number, fruit number, fruit length and diameter, and number of achenes. Fruit number (genotypic) was positively correlated with leaf number, inflorescence height, inflorescence number, and total soluble solids, and negatively correlated with flower size and fruit diameter. Fruit length was genotypically negatively correlated with leaf number, runner number, inflorescence height, soluble solids concentration, and fruit number, and positively correlated with days to runner formation, days to maturity, fruit diameter, and number of achenes. Fruit diameter was negatively correlated with leaf number, runner number, inflorescence height, and total soluble solids content, and positively related to days to runner formation, days to flowering, days to maturity, fruit length, and achene number. Achene number was negatively related to runner number, and positively related to days to runner formation and ascorbic acid, in addition to fruit length, diameter, and yield.

Strik and Proctor (1988) studied genotypes with diverse yield potentials in matted rows and as single plants. Within genotypes, yield per plant mainly depended on fruit number in either cultural system. Potential yield differences within genotypes are apparently established before or during flower bud differentiation. Vegetative variables were highly correlated with yield when the genotypes were grown as matted rows. When grown singly with less interplant competition, reproductive variables were correlated with yield among genotypes. In some genotypes, runnering and fruiting may have competed for assimilates. Genotypic yield variability suggested that genotypes with similar yield can have different routes to yield.

Swartz et al. (1982) studied plant crown competition effects of several cultivars in matted rows with the same bed configuration in one year and variable configurations in the second year. In the same bed configuration trial, yield differences among genotypes on an area basis were equalized on a per-crown basis because cultivar differences among various yield components tended to balance. Narrow beds were more productive than wide beds. There were no yield differences in raised vs. flat beds. At high plant densities, intercrown competition reduced the number of inflorescences per crown, percentage fruit set, and fruit weight. Flower density was a better predictor of fruit set than crown density. Fruit weight correlated negatively with increased crown, flower, and fruit densities, contributing to reduced fruit yields per crown. Yield per square foot (0.09 m^2) was maximized at crown densities of six or 12 crowns per square foot in the 2 years, when yield per crown was regregressed onto crowns per square foot.

Hancock et al. (1982) demonstrated genotypic variation in yield response to plant spacing and runner removal. Popenoe and Swartz (1985) cataloged yield component shifts in two genotypes across two growing seasons for five cultural systems. Durner and Poling (1986) showed genotypic variation in crown productivity of fruit at various spacings. Swartz et al. (1985) characterized 14 cultivars and breeding selections for yield component differences in leaf productivity, fruit set, fruit weight, yield per inflorescence, per plant crown, per plant, and per acre. Again, high yields were produced by various genotypes in diverse manners. Regressions of various of the yield components produced several predictive equations for evaluating genotype performance in wide or narrow matted row culture.

BREEDING SYSTEM MANIPULATIONS

Recently, experiments have been performed to manipulate or change the strawberry system by intergeneric or species hybridizations or by in vitro culture of strawberry plant parts. In some cases, the objective was to introduce exotic germplasm into the strawberry; in

Table 3. Genetic variation studies with strawberries, 1970–1989.

Author(s)	Methods	Characters and major findings
Watkins and Spangelo (1971)	Additive and nonadditive variance limiting values, calculation of discriminant function selection index for seven characters, two-step selection—progeny and individual	Mildew resistance, flower stalk no., fruit appearance, fruit no., marketable yield, leaf scorch, and processing desirability—as much as 40% of the total genetic variance was nonadditive for an average of the seven characters and the index.
Spangelo et al. (1971)	Heritability and genetic variance for 20 characters in 64 progenies involving 31 North American and one German clone. North Carolina design II crossing scheme. Random and mixed models	Yield-total, mkt., late, late mkt., three high picks (HPK), Berry no., berry wt*., fruit/stalk*, yield/stalk, flower stalk#, petiole no., petiole diam., vigor, first pick No. of three HPK, firmness, easy capping, ext. appear., inter. appear., pH*, soluble solids*. _____ = more than 50% of genetic variance non-additive. * = high heritability, or over 37%.
Gooding et al. (1975)	Two locations, 8 × 8 partial diallel to identify parents that transmit yield stability and its components, and to identify genotypes prone to barrenness. GCA, SCA, years, sites, G/E interactions	Plant size, crown no., infl./crown, fruit/infl., fruit size, estimated yield. Site had a major effect on inflorescences per crown (I/C). Low I/C was partially compensated by greater Fr/I. Site had a minor effect on fruit size. Site and GCA effects were more important than their interactions; hence, total yield and high Fr/I were less influential in yield stability than selection for High I/C.
Hortynski (1979)	Simple phenotypic, genotypic, environmental correlations, path coefficients, multiple correlations, and coefficients of determination estimated between vegetative and reproductive characters for 15 full-sib F_1 families over three growing seasons.	Seedling yield was best determined (R = 0.96) by a combination of the components fruit no., flowers/inflor., and fruit wt. Seedling size and vigor and leaf area during harvest or the preceeding fall were also influential (R = 0.61 and 0.53, respectively). Environmental influences were high in correlations between yield and vegetative characters.
Lal and Seth (1979)	Thirty cultivars from North America, Europe, and India. Twenty samples per cultivar. Variance partitioning, heritability, and genetic advance calculated for 15 characters	High GA + H = additive gene effects for leaf, inflorescence, fruit and achene numbers and fruit yield. Nonadditive effects for runner no., days to runner formation, flowering, or ripening, inflor. height, flower or fruit size, soluble solids or vitamin C.
Wenzel (1980)	Four character analyses of five RCB experiments, each containing at least 18 genotypes and five replications. Phenotypic and genotypic correlations, selection indices, and expected genetic responses	Yield (Y), berry size (S), freezing ability (FA), and total soluble solids concn. (SS). Correlations:-Positive : Y-S;, S-FA; Negative: SS and Y, S, and FA. Selection indices did not aid in yield advances expected responses, but aided in selection of desirable genotypes for all characters.
Hortynski (1980)	Fifteen full-sib random progenies (450 seedlings) RCB, three replications, Griffings random model genetic variance, broad-sense heritability, genetic variance analysis—hierarchial, random model, upper limits of heritability—repeatability coefficient, 3 years	Seven plant size, vigor, and leaf area components; eight fruit yield components. Most traits had large nonadditive gene effects, but both additive and nonadditive effects effects are important. Some maternal effects occur.
Lal and Seth (1981)	10 × 10 Complete diallel, GCA and SCA recorded, Griffings method I, model I. Ninety F_1 and F_2 progenies, four character analysis	GCA and SCA effects significant for inflor. no., flower no., fruit no., and days to maturity in both generations. GCA : SCA ratios varied from 5 to 17 in the F_1 and 1.5 to more than 10 in the F_2. Cytoplasmic effects were significant in all generations and characters.
Lal and Seth (1982)	Same methods as 1981, five different characters: fruit length, diameter, weight, yield, and total soluble solids concn.	GCA, SCA, and reciprocal effects significant for all characters and generations. GCA > SCA.
Hortynski (1989)	Genotype–environment interaction analyses using three segregating F_1 populations, two estimation methods: traditional—phenotypic variation from ANOVA; trg—based on interclass genetic correlation combining genetic variance components with environmental factors	trg Components were considered the superior method of estimation. Fruit yield is more dependent on genotype × year than on genotype × block interactions. The reverse is true for fruit size.

others, it was to secure strawberries with various chromosome levels or to regenerate strawberry plantlets from plant parts. One recent large experiment on inbred line development was also reported.

Inbred line development

Niemirowicz-Szczytt (1989) tried to develop S_2 and S_3 lines of 17 octoploid strawberry cultivars by self-pollination. It was possible to secure S_2 and S_3 generations from only 10 of the 17 original cultivars. In agreement with previous reports, reduced seed germination and plant viability, fertility, and yield were found. The number of S_1 genotypes (and hence genetic variability) was reduced in the S_2 and S_3 generations. However, considerable yield variation occurred among individuals of the S_2 generation, and among S_3 generation individuals for pollen stainability and size. Inbreeding depression was previously reported by the same author among induced polyhaploid individuals at the tetraploid (2n = 28) level.

Diverse (wide) hybridizations

Wide crosses within *Fragaria* and among *Fragaria* and closely related species (chiefly *Potentilla)* have been made for basically two reasons. One was to introduce exotic genes into the garden strawberry, and the other was to produce polyhaploid individuals that could be doubled to yield isogenic lines.

Sukhareva (1970) reviewed the literature of apomictic development in the strawberry from remote hybridization and induced polyploidy. Tetraploid individuals arising from intercrosses of colchiploid octoploid *F. orientalis* individuals with 8 × *F.* × *ananassa,* 6 × *F. moschata,* or 2× *F. collina* gave the best evidence of haploid pseudogamy (development of unfertilized haploid egg cells).

Evans (1974) reviewed the poor results reported by numerous workers from intercrosses of diploid × hexaploid and diploid × octoploid strawberry species. He then compared his own experiments crossing diploid (2 ×) and amphidiploid (4 ×) species or species hybrids by *F. moschata* (6 ×) representative clones. The 2 × by

6 × crosses produced little or no seed and no viable seedlings. The 4 × by 6 × crosses produced small amounts of seed, half or more of which germinated and produced all pentaploid individuals. Four diploid species crossed by octoploid species or synthetic octoploids (colchiploid individuals from species hybrid crosses) produced little or no seed that did not germinate or produce inviable or matroclinous seedlings. In comparative crosses of diploid (2 ×) and amphidiploid (4 ×) species hybrids by octoploid (8 ×) species or species hybrids, only the amphidploids × synthetic octoploids produced a few viable seedlings that were true hybrids and hexaploid (6×). Evans believed that chromosomal or genic imbalance in the endosperm or between zygote and endosperm was the most likely cause of failure to produce viable strawberry plants from 2 × by 6 × and 2 × by 8 × crosses.

Evans (1977) summarized several methods of producing "synthetic" octoploid plants incorporating genetic material from *Fragaria* species of lower levels of ploidy. He produced six synthetic octoploids from various combinations (hybridizations and chromosome doubling) involving one hexaploid, two tetraploid, and four diploid species. Three of the synthetic octoploids were malefertile and were successfully crossed onto octoploid strawberry cultivars. Evans (1982) described the origin and intercrossing of two "multispecific" octoploids (breeding clones) derived from crossing synthetic octoploids with cultivated strawberries. The intercross of two multispecific breeding clones produced 22 seedlings. All but one of these fruited and were tolerant to common leaf diseases. Evans selected 11 clones as potential cultivars and three as parents. Two of the clones were subsequently introduced as germplasm lines.

Asker (1971) summarized the literature on intergeneric hybridization of *Fragaria* and *Potentilla*, and added several interesting observations. Some degree of success is attained only when polyploid *Fragaria* species are the female parents. Diploid *F. vesca* crossed by 10 *Potentilla* species gave sublethal hybrids and matroclinous seedlings when crossed with *P. palustris* and *P. anserina.* Hexaploid *F. moschata* by diploid *P. fruticosa* crosses averaged 10 seeds per pollination, of which 5% to 10% germinated. Fifty percent of the germinated seedlings survived to maturity and were hybrids. When octaploid *Fragaria* clones were used as females, hybrids were found only in crosses with diploid *P. fruticosa* as the male parent. Maternal ("false hybrid") strawberry seedlings resulted from crosses of octoploid *Fragaria* clones with pollen from *P. erecta, angelica, davurica, anserina,* and 4 × *fruticosa.*

Anther culture and haploid production

Rosati et al. (1975) were not successful in producing polyhaploids from another culture of nine strawberry clones in four culture media. However, anthers of four of the clones produced normal octoploid plantlets from the undifferentiated callus, principally on the Gresshoff and Doy "1" tomato anther medium. Fifteen tetrahaploid (2n = 28) plants were secured by Niemirowicz-Szczytt and Zakrzewska (1980) from the 'Redgauntlet' octoploid strawberry by culturing anthers on a Linsmaier and Skoog medium in which the cytokinin benzylaminopurine had been substituted for kinetin. The polyhaploids did not survive to maturity.

Uematsu (1980) reported a frequency of morphological variants of 7×10^{-3} in plants of the cultivar Hohkohwase that had been produced from anther culture. These plants were rogued, and a subsample of the normal plants grown to maturity showed no fruit or plant deviations from type. Further anther culture experiments by Niemirowicz-Szczytt et al. (1983) produced 166 plants, of which 99 survived. Chromosome counts of 85 of the survivors showed that 34 were diploids (2n = 2× = 14), 33 were tetraploids (2n = 4 × = 28), one was hexaploid (2n = 6× = 42), and 17 were mixoploids. By the summer of the second year, almost all of these plants had fruited. The proportion of each ploidy level with germinable seed, the mean seed number per fruit, the percent seed germination, and pollen size classes were calculated.

Few polyhaploids had been obtained through pollination of cultivated strawberries with pollen of *Potentilla anserina* (4×) (Barrientos and Bringhurst, 1973) and with *P. anserina* and *P. fruticosa* pollen (Hughes and Janick, 1974). However, Jelenkovic et al. (1983) failed to secure any haploids from many octoploid and hexaploid *Fragaria* species flowers pollinated by diploid and tetraploid *Potentilla* species pollen. A total of 134.5 fruits bearing an estimated 46,100 seeds resulted from these pollinations. *P. anserina* pollen produced octoploid matroclinous seedlings (considered to be contaminants). *P. fruticosu* pollen produced matroclinous octoploids and intergeneric hybrids, including a sterile nonaploid (2n = 9× = 63). Sayegh and Hennerty (1989) were not successful in producing strawberry haploids from anther culture, but they did secure several haploids from pollinations of several European strawberry cultivars by *Potentilla fruticosa* pollen, followed by aseptic embryo rescue techniques at 21 to 28 days following pollination.

Ploidy manipulations

Shoot apex treatment of rooted seedlings yielded much better survival and polyploid production than germinated seedling treatments (Sebastiampillai and Jones, 1976). A 2% colchicine solution applied by "dropper" to the shoot apices for 24 to 48 hr was the preferred method. A differential response to colchicine was observed within and among various diploid species and diploid and tetraploid hybrids. Niemirowicz-Szczytt et al. (1984) produced polyploids from in vitro meristem culture of *F. vesca* 'Baron Solemacher', derived from in vitro seed germination. Colchicine at 0.01% and 0.05% filtered onto the culture medium increased polyploid production. Pollen grain diameters, number of inflorescences per plant, number of seeds per fruit, and 100-seed germination rate variation were compared for diploids and tetraploids.

Fukui and Niizeki (1982) established callus cultures from shoot tips, petioles, and anthers of the octoploid cultivar Hokowase on a Linsmaier and Skoog medium to which 0 to 85 mg of para-fluorophenylalanine (PFP)/liter had been added. Higher levels of PFP yielded a higher level of 7 × (septaploid) and mixoploid plants at lower than the original 8 × level. Further shoot tip culture of 7 × individuals with 30 mg of PFP/liter reduced chromosome levels of resulting plants to 6 × , or to a mixture of 5× -4× .

In vitro regeneration and selection

Germinating seeds were proliferated on a Boxus medium to secure identical individuals from the same seed (Izak and Izhar, 1983). This procedure permitted a shortening of the breeding cycle by allowing initial selection and repeat testing to be carried on at several locations simultaneously. There appeared to be no variation among plants originated from a single seed.

Regeneration of strawberry plantlets from leaf mesophyll protoplasts was reported by Nyman and Wallin (1988). This technology is a necessary prerequisite for future somatic hybridization, gene transfer, or induction of somaclonal variation.

Malone and Dix (1986) reported an attempt at screening strawberry callus cultures and shoot tip cultures with the herbicides simazine and chlorsulphuron. Callus cultures of the strawberry clone CL-3 were not inhibited by concentrations of up to 80 mg of simazine/liter. Strawberry shoots were sensitive to all levels (5 to 40 $mg \cdot liter^{-1}$) of simazine. Single strawberry shoots could tolerate rates of 2 mg of simazine/liter. Strawberry shoots were treated with a 10 µM solution of nitrosomethyl urea (NMU) for 90 min, followed by repeated washings with sterile distilled water. This mutagenic treatment resulted in 25 of 64 shoots tolerating subsequent exposure to 10, but not 20, mg of simazine/liter. Chlorsulphuron was toxic to callus cultures of CL-205 strawberry. A very low concentration ($0.003\ mg \cdot liter^{-1}$) allowed some growth of preestablished callus, but inhibited callus formation on leaf explants of strawberry. These results suggest that callus or cell suspension cultures would be suitable for resistance testing.

INHERITANCE PATTERNS

Our understanding of strawberry inheritance patterns has been expanded by many studies over the past 20 years, as demonstrated by examples of studies on Mendelian and quantitative inheritance.

Mendelian inheritance

In the diploid wood strawberry *(Fragaria vesca* L.), non-runnering (r/r), the everbearing habit (j/j), and the arborea (long internode, runner-forming, non-crown-forming) type (arb/arb) had previously been shown to be homozygous recessive mutants. Guttridge (1973) studied segregation in a cross between a long-stemmed type *(F. vesca* L. *arborea* Staudt) and an alpine (non-runnering) everbearing clone *(F. vesca semperflorens* Duch., 'Baron Solemacher'). Only three of the expected four classes of everbearing segregants occurred. The non-runnering, arboreal, everbearing type (rr, arb arb, jj) was missing, suggesting that the arboreal gene in the double recessive is epistatic to the gene for runner formation. This was confirmed from backcross studies because double homozygous arboreal runnering (arb/arb, +/+) and double homozygous arboreal non-runnering (arb/arb, r/r) segregants both had similar runners and runnering habits.

Arulsekar and Bringhurst (1981) proposed a single locus, three-allele model for the phosphoglucoisomerase (PGI; EC 5.3.1.4) allozymes observed in California populations of diploid *Fragaria vesca.* They designated the alleles Pgi-2^b, Pgi-2^c, and Pgi-2^d, and offered evidence of three additional alleles at this locus in other European and Asiatic diploid *Fragaria* species.

Arulsekar et al. (1981) proposed a tentative four-locus genetic model for octoploid strawberries at the PGI-2 locus, in which the four "loci" represent the gene site on the four homologous genomes of the cultivated strawberry *(Fragaria ×ananassa* Duch.). Two of the four loci with four alleles were found in *F. ananassa* cultivars. The other two loci were inferred from banding patterns in the octoploid *F. chiloensis* and in pentaploid *F. chiloensis* × *F. vesca* hybrids. These isozyme analyses give additional support to the highly diploidized nature of *F.* × *ananassa.*

Oydvin (1980) determined that appressed stem pedicel pubescence (ss) is a monogenetic recessive to spreading hairs *(S)* in octoploid cultivated strawberries. The cultivars Abundance, Dybdahl, and Soltwedel have appressed stem hairs. Cultivars with spreading pubescence were found to be either heterozygous (Ss) ('Pocahontas', 'Tamella', and 'Zefyr') or homozygous dominant (SS) ('Belrubi', 'Glima', 'Redland Crimson', and 'Senga Sengana') for the trait.

Van de Weg et al. (1989) determined inheritance of resistance to an undetermined race of *Phytophthora fragariae* (red stele root rot) in a field near Zundert, Netherlands. Parents of 24 tested seedling progenies segregated into the classes: completely resistant (six American cultivars and selections from the Beltsville, Md. program), a high level of partial resistance (United Kingdom, 'Cambridge Favourite'), and a low level of partial resistance (eight Dutch cultivars and selections). The proportions of symptomless seedlings from completely resistant by partially resistant (susceptible) parent crosses was usually about 50%, suggesting that the American parents had one major resistance gene effective against the race(s) present in the test field. Van de Weg (1989a, 1989b) reinterpreted his own data and that of others concerning red stele root rot on the basis of a gene-for-gene system. In his proposed model, there are at least five host resistance and five fungal virulence genes. Proposed virulence genes were assigned to many of the known red stele fungus races, and proposed resistance genes were assigned to the differential cultivars used by plant pathologists to discriminate among the fungal races. Seventeen of 18 resistant by susceptible crosses fit the expected model (50% symptomless seedlings expected). A review of host-pathogen interaction studies for fungus races A-1 to A-6 from the literature showed that 26 of 40 reports agreed with the proposed, five gene-for-gene model.

Quantitative inheritance

There has been a proliferation of quantitative strawberry inheritance information during the review period (Table 2). The studies have ranged from statistical analyses of progeny mean differences of scores to sophisticated heritability determinations, including variance partitioning into types of genetic vs. phenotypic or environmental contributions. Several elegant multivariate analyses are also included. It should be stressed that the results of individual quantitative studies cannot be generalized, but depend on the composition of the test strawberry population, interactions with the environments in which they are grown, and the analytical methods used.

Genetic variability was determined for diverse characters by various authors. Methods and findings are summarized in Table 3.

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