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. 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.
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.

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, 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 1. Examples of parent source character identification in strawberries during the period 1970-1989.

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<tr>
<th>Trait</th>
<th>Literature source</th>
<th>Possible parent clones</th>
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<tr>
<td>Starch gel electrophoresis isozyme patterns of GPl, LAF, and PGM</td>
<td>Brinkhurst et al., 1981</td>
<td>Separation of 14 of 22 cultivars into unique classes</td>
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<td>Two-spotted spider mite tolerance</td>
<td>Shuster et al., 1980</td>
<td><em>Florida Belle</em>, ‘Sequoia*</td>
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<td>Resistance to strawberry root weevil and black vine weevil</td>
<td>Maas and Smith, 1978</td>
<td>A number of native North American <em>F. chiloensis</em> clones, especially CL-5 and GCL-8</td>
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<tr>
<td>Adaptation to mechanization and fruit quality</td>
<td>Shanks et al., 1984</td>
<td>‘Cardinal’ and A-5344</td>
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<td>Freezing quality</td>
<td>Daniels et al., 1982</td>
<td>‘Darrow’, ‘Earliglow’, ‘Vesper’</td>
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| Trait(s) and references                                                                 | Breeding materials                                                                 | Findings*
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<tr>
<td>Seed germination and seedling vigor (Melville et al., 1980b)</td>
<td>Intercrossed, selfed, outcrossed population of two S&lt;sub&gt;1&lt;/sub&gt;, two S&lt;sub&gt;2&lt;/sub&gt; and two non-inbred selections</td>
<td>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&lt;sub&gt;2&lt;/sub&gt; progeny had lower germination total and rate than the control. Level of inbreeding and type of inbred cross was not related to transmission of red stelle resistance. Self-pollinations transmitted less resistance than cross-pollinations. There was significant SCA for weighted progeny mean score and for percent resistant in segregation occurred 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.</td>
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<td>Red stelle resistance (Melville et al., 1980a)</td>
<td>Same as Melville et al. (1980b); six-parent dialel</td>
<td>Cornicle no. and flowering time were GCA significant; yield was GCA and SCA significant. No reciprocal effects seen in these characters.</td>
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<td>Aphid resistance (Barratt and Shanks, 1980)</td>
<td>Five clones and two BC1 seedling progenies from F. chitoensis ‘Del Norte’</td>
<td>GCA and SCA significant at both locations for mean no. of mites/leaflet. GCA &gt; SCA. Heritabilities (parent/offspring regressions) were high. Additive genetic variance important in mile resistance.</td>
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<td>Cornicle (Infl?) no., Flowering time per plot (beginning), yield (total wt.) (Ulyukin et al., 1976)</td>
<td>Six cultivars dialiel, 28 progenies, three blocks with two replications per ploek, 80 seedlings per plot</td>
<td>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. 0–5 scalar scores, significant GCA and SCA, heritabilities improve with seasonal progression. Genetic gain is improved by multistage rather than mass selection. Significant differences among seedlings for all characters except taste. GCA and SCA significant for other four characters GCA &gt; SCA except for vitamin C.</td>
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<td>Twospotted mite resistance (Barratt and Shanks, 1981)</td>
<td>Fifteen crosses involving three cultivars and five selections two locations in field and greenhouse</td>
<td>Frequency distributions of P:S ratios within progeny and comparison with parent and midparent values indicates quantitative inheritance. Capping force, capping percent, and pedicle breaking force evaluated. F. virginiana is an excellent capping source. Progeny means for pedicel breaking were near the low parent mean. GCA and SCA significant GCA 4× SCA. Heritability estimate 0.84 GCA correlated with parent phenotype (r = 0.828). 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. Important characters: Concentrated ripening, productivity, easy fruit detachment, firmness, color, processing quality. ‘Cardinal’ released, prepotent selections for the other traits identified. ‘Totem’ and ‘Aliso’ produced the highest proportion of tolerant seedlings. GCA and SCA significant. GCA &gt; SCA. Heritability when disease was worst was 0.72. Inoculated plants had reduced vigor, petiole length, leaf width, leaf dry wt., and more leaves than controls. GCA significant for all characters. Total yield: Nonadditive significant factor. Berry wt: Nonadditive and additive significant. Runner no.: Both are significant. Plant size: Nonadditive significant. ‘Glima’ was prepotent for transmitting gallaging index lowering and increasing the number of seedlings without galls. Seeding and mature reactions were well-correlated. Narrow-sense heritabilities: 0.07, 0.48, and 0.38 for solids, acid, and firmness, respectively. Broad-sense heritabilities: 0.35, 0.78, and 0.38 for the same traits suggest dominance variation for solids and acids, but not for firmness. Genotypic 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.</td>
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<td>Powdery mildew resistance (Simpson, 1987)</td>
<td>Four everbearing and three short-day cultivars in a half dialiel w/o selves (Expt. 1) Expts. 2–5 EB and DN clones crossed to eight short-day clones</td>
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<td>Leaf spot resistance (Shaw et al., 1988)</td>
<td>Two years—66 crosses from 18 parents with 15 reciprocals; 2nd year—30 crosses from 14 parents</td>
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<td>Fruit quality factors taste, consistency, anthocyanin content, vitamin C content, R-active catechin content (Zubov and Stankevich, 1982)</td>
<td>Five parent dialiel, 20 progenies, four replications of 100 seedlings in a lattice design</td>
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<td>Primary : secondary fruit size relationship (Poloński and Lawrence, 1984)</td>
<td>Seventeen cultivars and selections, six crosses—50 seedlings per cross</td>
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<td>Fruit detachment traits (Brown et al., 1975)</td>
<td>Seven clones and six crosses</td>
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<td>Easy calyx removal (Barratt, 1976)</td>
<td>Twenty-seven clones and 79 seedling families</td>
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<td>Machine harvesting (Lawrence and Martin, 1980)</td>
<td>Thirty-seven cultivars and selections parent evaluation for transmission</td>
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<td>Harvest mechanization (Moore and Sistrunk, 1980)</td>
<td>Review of progress and characters</td>
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<td>Virus tolerance (Barratt and Daubeney, 1982)</td>
<td>Twenty-nine progenies + parent clones RCB, six replications, five seedlings per replication</td>
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<td>Virus tolerance (Sjulin et al., 1986)</td>
<td>Four-parent dialiel + parents, excluding selfs, all test plants inoculated by virus-bearing aphids</td>
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<tr>
<td>Fruit yield and related characters (Aalders and Craig, 1974)</td>
<td>Diallel of seven inbred clones</td>
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<td>Root-knot nematode resistance (Szczegiel and Danek, 1984)</td>
<td>Seven cultivar crosses.</td>
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<td>Soluble solids, titratable acidity, and fruit firmness (Shaw et al., 1987)</td>
<td>Twenty-eight crosses among 16 parents from California breeding population</td>
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<tr>
<td>Sugars and organic acids (Shaw, 1988)</td>
<td>Twenty-five selections in two sets</td>
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*continued*
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).

Lal 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 genetically 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.

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

BREEDING SYSTEM MANIPULATIONS

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<td>Early flowering in day-neutrals (Barritt et al., 1982)</td>
<td>Fifty-four crosses between day-neutral and short-day clones</td>
<td>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. 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 autumnumfruiting types, and supports the idea of two distinct types of response to photoperiod-temperature factors that are conditioned by major genes.</td>
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<td>Autumn fruiting (Jennings, 1989)</td>
<td>Three equally progenies subjected to principal component analysis.</td>
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aGCA = general combining ability (additive genetic variance); SCA = specific combining ability (nonadditive genetic variance).
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*₂ 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.

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6 x crosses produced little or no seed and no viable seedlings. The 4 x by 6 x 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 (colchidiploid 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 x ) and amphi-diploid (4 x ) species hybrids by octoploid (8 x ) species or species hybrids, only the amphidiploids x synthetic octoploids produced a few viable seedlings that were true hybrids and hexaploid (6 x ). Evans believed that chromosomal or genic imbalance in the endosperm or between zygotene and endosperm was the most likely cause of failure to produce viable strawberry plants from 2 x by 6 x and 2 x by 8 x 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 male-fertile 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 poly-ploid Fragaria species are the female parents. Diploid F. vesca crossed by 10 Potentilla species gave subthalid hybrids and matroclinous seedlings when crossed with P. palustris and P. anserina. Hexaploid F. moschata by diploid P. fruticosa crossed averaged 10 seeds per pollination, of which 5% to 10% germinated. Fifty percent of the germinated seedlings survived to maturity and were hybrid. When octoploid 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, davarica, anserina, and 4 x 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 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. 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 chlorosulphon. 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/liter) 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. Chlorosulphon was toxic to callus cultures of CL-205 strawberry. A very low concentration (0.003 mg/liter) 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 (rr), the everbearing habit (jj), and the arborea (long internode, runner-forming, non-crown-forming) type (ar/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, ar, bb, 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 running (arb/arb, rr) and double homozygous arboreal non-runnering (arb/arb, rr) segregants both had similar runners and running habits.

Arulsekar and Bringhurst (1981) proposed a single locus, three-allele model for the phosphoglucosomerase (PGI; EC 5.3.1.4) allozymes observed in California populations of diploid Fragaria vesca. They designated the alleles Pgi-2*, Pgi-2*, and Pgi-2*, 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 xananassa 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 aspaped stem pedicle pubescence (ss) is a monogenetic recessive to spreading hairs (S) in octoploid cultivated strawberries. The cultivars Abundance, Dybdahl, and Soltwedel have aspaped stem hairs. Cultivars with spreading pubescence were found to be either heterozygous (Ss) (“Pocahontas”, “Tamella”, and “Zélyr”) or homozygous dominant (SS) (“Belrubu”, “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 parent had one major resistance gene effective against the races present in the test field. Van de Weg (1989a, 1989b) reinterpreted his own 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.

Literature Cited


Guttridge, C.G. 1973. Stem elongation and runnering in the mutant straw-


Hughes, H.G., and J. Janick. 1974. Production of tetraploids in the cul-


Jennings, D.L. 1989. The use of multivariate analyses for study of autumn-


Mok, D.W.S. and W.D. Evans. 1971. Chromosome associations at diacli-

Mok, D.W.S. and W.D. Evans. 1971. Chromosome associations at diacli-

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