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Inheritance of Virus Tolerance in Strawberry[1]

Bruce H. Barritt
Washington State University, Tree Fruit Research Center, Wenatchee, WA 98801.

Hugh A. Daubeny
Agriculture Canada, Research Station, 6660 N.W. Marine Drive, Vancouver, B.C., Canada V6T 1X2.

Additional index words. Fragaria x *ananassa*, fruit breeding, heritability, general combining ability, specific combining ability

***Abstract.* Seedlings of strawberry (*Fragaria* x *ananassa* Duch.) from 29 crosses were evaluated in a field trial over a 2½-year period for tolerance to a complex of viruses. The seedlings and plants of the parent clones were subjectively rated for tolerance on the basis of vigor, runnering, and appearance of virus symptoms. 'Totem' and 'Aiko' produced the highest percentage of tolerant-appearing seedlings, while 'Olympus', 'Belrubi', and 'Hood' produced the highest percentage of susceptible seedlings. At the end of the trial, when the symptoms were most severe, heritability for tolerance was 0.73. Specific combining ability variance was much smaller than general combining ability variance, indicating that a high proportion of genetic variance was additive. Therefore, rapid progress in breeding for tolerance can be expected from selecting parent clones on the basis of phenotypic performance.**

Many strains of a number of viruses commonly infect strawberries (9). Several of the viruses (mottle, mild yellow-edge, crinkle and vein banding) are transmitted by the aphids *Chaetosiphon fragaefolii* (Cockerell) and *C. thomasi* (Hille Ris Lambers) (9). The viruses often occur together as a complex in infected plants (14). Utilization of virus-tolerant cultivars is an important method of limiting yield losses caused by viruses in the Pacific Northwest (3, 7). Thus, selecting for tolerance is a major objective in breeding programs in the region (5, 16, 17). Although differences in tolerances have been reported from these and from other programs (4, 7, 17) there is no information on its inheritance. This study was undertaken to determine the nature of inheritance of tolerance in seedling populations obtained from parent cultivars and selections (both subsequently referred to as clones) representing varying levels of tolerance. Tolerance was evaluated as a single entity. It is recognized that the situation is probably more complex considering the number of viruses possible and the number of strains within each. The term "virus tolerance rating" was used to describe the overall appearance of the plant with respect to vigor and to characteristic virus-like symptoms which are probably, but

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not necessarily, caused by one or more of the aforementioned aphid-borne viruses.

Materials and Methods

Seedlings from 29 progenies (Table 1) were evaluated for virus tolerance. Five seedlings per progeny were planted in each of 6 replications in a randomized complete block design in June 1978, at the Northwestern Washington Research and Extension Unit, Mt. Vernon, Washington. Virus-free runner plants of the parent clones, except for 4 which were not available, were also planted with from 8 to 18 plants of each distributed among the 6 blocks. Each seedling plant and parent clone plant was allowed to produce a 0.9-m long matted row in rows 1 m apart. The plants were not sprayed to control the aphids, *C. fragaefolii* and *C. thomasi*.

Six *Fragaria vesca* 'Alpine' seedling plants also were planted in each block to estimate the extent of spread into the planting of viruses detectable by this indicator (8). The *F. vesca* 'Alpine' seedlings were taken to a greenhouse in Sept. 1978, sprayed to control strawberry aphids, and evaluated for virus symptoms.

The planting site was free of strawberry diseases and insects including red stele root rot, verticillium wilt, root weevils, and plant parasitic nematodes. Winter injury did not occur in strawberries during the experiment.

Each seedling and parent clone plant was given a virus tolerance rating in May 1979 and September 1980. In addition, each parent clone was also rated in October 1978, September 1979, and May 1980. The rating, on a 1 to 10 scale, was based on plant vigor, runnering, and the appearance of virus symptoms such as yellow leaf margins, reduced leaf blade size, and shortened petioles. A rating of 10 indicated freedom from virus symptoms and 1 indicated very severe symptoms. Ratings were made independently by 2 observers.

Heritability estimates for virus tolerance rating were determined for evaluations on May 1979 and September 1980 from the linear regression of mean offspring performance on average performance of their parents (2). Progeny evaluations were analyzed by the procedure described by Gilbert (10) for data from crosses not made in a systematic manner. The procedure estimates general combining ability (GCA) and specific combining ability (SCA) variances and determines their significance. The procedure also determines GCA parental values as a guide in breeding.

Results

Of the 34 *F. vesca* 'Alpine' virus indicator plants taken from the field 3 months after planting, 21 (62%) showed infection that indicated a virus complex. This suggested a rapid rate of spread of virus into the seedling planting during the first growing season.

For most clones, little change occurred in virus tolerance rating between October 1978 and May 1980, but by September 1980 each clone showed a reduction in rating (Fig. 1). For reasons of clarity, data for only 7 representative clones are presented. With 2 clones, 'Hood' and 'Olympus', the decline in rating was apparent as early as September 1979. 'Totem' showed the least decline. The May 1979 rating used in subsequent tables was primarily an evaluation of innate differences in vigor and not differences in virus tolerance, and therefore, these ratings served as a standard

Table 1. Virus tolerance ratings for 29 strawberry progenies determined in May 1979 and September 1980.

Parentage[y]	No. seedlings	Virus tolerance rating[z] May 1979	Virus tolerance rating[z] September 1980	Decline from May 1979 to September 1980 (%)
Totem x Ranier	28	(28) 5.8fg	(3) 5.3b	9
Northwest x Totem	25	(29) 4.4i	(11) 3.9cde	11
Aiko x Totem	30	(6) 7.2ab	(1) 6.3a	13
Aiko x Rainier	30	(17) 6.5bcdef	(2) 5.3b	19
Totem x Shuksan	30	(19) 6.2def	(6) 4.5bcd	27
Belrubi x Totem	28	(9) 7.1abc	(4) 4.8bc	32
Totem x Hood	30	(11) 6.9abcd	(7) 4.5bcd	35
Olympus x Totem	30	(8) 7.1abc	(5) 4.6bcd	35
Tyee x BC 73-9-79	29	(18) 6.4cdef	(9) 4.1cde	36
Rainier x Northwest	28	(28) 5.0hi	(25) 3.2e	36
SHRI 69DZ95 x Totem	27	(25) 5.8fg	(16) 3.6cde	38
BC 73-9-79 x Cambridge Favourite	29	(24) 5.9efg	(18) 3.5de	41
Rainier x Shuksan	29	(27) 5.4gh	(26) 3.1e	43
Olympus x BC 70-22-82	30	(10) 7.0abc	(10) 4.0cde	43
Olympus x Northwest	30	(23) 5.9efg	(23) 3.3e	44
OR-US 4459 x Totem	30	(13) 6.7bcde	(14) 3.7cde	45
Olympus x Shuksan	28	(22) 6.0efg	(24) 3.3e	45
SHRI 69DZ95 x BC 70-22-82	30	(1) 7.5a	(8) 4.1cde	45
Cambridge Favourite x Olympus	30	(21) 6.1efg	(21) 3.3e	46
Rainier x OR-US 4459	30	(16) 6.5bcdef	(17) 3.5de	46
Olympus x OR-US 4459	23	(20) 6.2defg	(22) 3.3e	47
BC 70-20R-15 x Olympus	16	(2) 7.4ab	(12) 3.9cde	47
BC 73-9-79 x SHRI 69DZ95	30	(5) 7.3ab	(13) 3.8cde	48
Northwest x Hood	30	(15) 6.6bcde	(19) 3.4e	49
Rainier x Hood	30	(3) 7.4bcde	(15) 3.7cde	50
SHRI 69DZ95 x Olympus	29	(14) 6.7bcde	(20) 3.3e	51
Olympus x BC 73-9-79	22	(12) 6.7abcde	(27) 3.1e	54
Belrubi x Olympus	28	(7) 7.2ab	(28) 3.1e	57
Olympus x Hood	28	(4) 7.3ab	(29) 3.0e	59

[z] Virus tolerance rating (visual symptoms in the field) on 1-10 scale, 10 being most tolerant. Mean separation within columns by Duncan's multiple range test, 5% level. Numbers in parentheses are ranks based on mean virus tolerance ratings.
[y] BC, SHRI and OR-US selections are from the British Columbia, Scottish Horticultural Research Institute and the Oregon State University-USDA breeding programs, respectively.

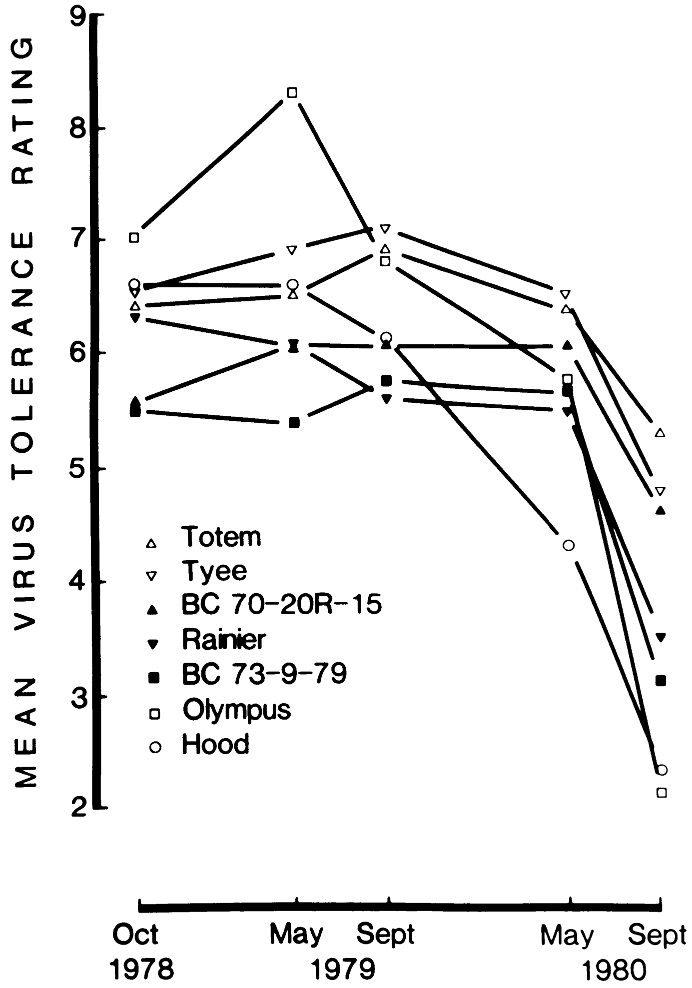

Fig. 1. Virus tolerance ratings (based on a 1 to 10 scale with 10 being the most tolerant) determined from October 1978 to September 1980 for seven representative strawberry clones.

for comparison with the severe decline symptoms observed in September 1980.

Virus tolerance ratings for 11 clones examined in May 1979 varied from 5.1 for 'Cambridge Favourite' to 8.3 for 'Olympus' (Table 2). From May 1979 to September 1980, relative differences among clones for tolerance rating changed greatly with 'Olympus' having the lowest rating, 2.2, and 'Totem' the highest, 5.3, in September 1980. The decline in tolerance rating from May 1979 to September 1980, as a percent of the May 1979 rating, is assumed to be a measure of the clone's ability to tolerate virus infection. The smaller the percent decline the greater the level of tolerance. 'Totem' showed the least decline, 19%, whereas 'Olympus' showed the most, 74%.

For the 29 progenies, significant differences in mean virus tolerance ratings were observed on each evaluation date (Table 1). The ranking of progenies changed greatly from May 1979 to September 1980. 'Totem' x 'Rainier' improved in ranking from 26 in May 1979 to 3 in September 1980. A lack of tolerance was indicated in 'Olympus' x 'Hood' which changed from a ranking of 4 in May 1979, to 29 in September 1980. The 4 progenies which showed the least decline in ratings were 'Totem' x 'Rainier' 'Northwest' x 'Totem', 'Aiko' x 'Totem', and 'Aiko' x 'Rainier', with decline percentages of 9, 11, 13, and 19, respectively. The progenies which showed the greatest decline were 'Belrubi' x 'Olympus' and 'Olympus' x 'Hood', with decline percentages of 57 and 59, respectively.

Genotypic parent values from the Gilbert analysis of progeny data showed that 'Aiko', 'Totem', and selection BC 70-22-82 (from the British Columbia breeding program) seedlings had the highest ratings for tolerance in September 1980 (Table 3), The least decline in ratings, from May 1979 to September 1980, occurred in progenies of 'Aiko' (12%), and 'Totem' (9%), whereas 'Hood' and selection OR-US 4459 (from Oregon State University-USDA breeding program) progenies had a decline of more than 60%. The analysis of variance of progeny data for tolerance ratings on the 2 evaluation dates showed that GCA variance was much higher than SCA variance (Table 4). Heritability estimates for ratings on September 1980 and May 1979 were .73 ± .17 SD and .84 ± .28, respectively.

Table 2. Virus tolerance ratings for 11 strawberry clones determined in May 1979 and September 1980.

Clone[y]	No. of plants	Virus tolerance rating[z] May 1979	Virus tolerance rating[z] September 1980	Decline from May 1979 to September 1980 (%)
Totem	18	6.5cd	5.3a	19
BC 70-22-82	12	5.8ef	4.5bc	23
BC 70-20R-15	12	6.1de	4.6b	24
Cambridge Favourite	8	5.1g	3.7de	29
Tyee	16	6.9b	4.8ab	31
Shuksan	11	5.8ef	3.9cd	32
Northwest	17	5.6fg	3.6de	35
BC 73-9-79	15	5.4fg	3.1e	42
Rainer	12	6.1de	3.5de	43
Hood	18	6.6bc	2.4f	64
Olympus	16	8.3a	2.2f	74

[z] Virus tolerance rating (visual symptoms in the field) on 1–10 scale, 10 being most tolerant. Mean separation within a column by Duncan's multiple range test, 5% level.
[y] BC selections from the British Columbia breeding program.

Table 3. Genotypic assessment of virus tolerance ratings for 13 strawberry parent clones determined in May 1979 and September 1980.

Parent[z]	No. seedlings[y]	General combining ability parent values for virus tolerance ratings May 1979	General combining ability parent values for virus tolerance ratings September 1980	Decline from May 1979 to September 1980 (%)
Totem	258(9)	3.04 ± .06	2.78 ± .09	9
Aiko	60(2)	3.88 ± .12	3.41 ± .17	12
Rainer	197(7)	2.86 ± .08	1.99 ± .11	30
Northwest	113(4)	2.16 ± .09	1.44 ± .12	33
Cambridge Favourite	59(2)	2.52 ± .13	1.64 ± .18	35
BC 70-22-82	60(2)	3.90 ± .12	2.50 ± .17	36
Shuksan	87(3)	2.77 ± .10	1.51 ± .14	46
BC 73-9-79	110(4)	3.59 ± .11	1.89 ± .16	47
Olympus	272(10)	3.35 ± .06	1.62 ± .08	52
SHRI 69DZ95	116(4)	3.33 ± .09	1.52 ± .13	54
Belrubi	56(2)	3.92 ± .12	1.75 ± .17	55
Hood	118(4)	4.18 ± .09	1.67 ± .12	60
OR-US 4459	83(3)	3.41 ± .10	1.33 ± .14	61

[z] BC, SHRI and OR-US selections are from the British Columbia, Scottish Horticultural Research Institute and the Oregon State University-USDA breeding programs, respectively.
[y] No. of families in brackets.

Table 4. Analyses of variance for virus tolerance ratings showing the significance of general (GCA) and specific (SCA) combining ability.

	May 1979			September 1980		
Source of variation	df	Mean square	F^z value	df	Mean square	F value
Additive parental effects (GCA)	14	49.98	34.06	14	64.12	23.23
Interactions (SCA)	14	12.63	8.61	14	8.14	2.95
Error (within families)	1625	1.47		1625	2.76	

^{z}All F values are significant, 1% level.

Discussion

Since 62% of the *F. vesca* 'Alpine' indicator plants showed virus infection within 3 months after the planting was made, it can be assumed that a similar proportion of the clonal and seedling plants also became infected during that period. Martin and Converse (14) found in Oregon that the percent of infected plants increased yearly, reaching 91% in the third year. It is probable that in the present study a similarly high percentage of the plants were infected at the end of the third summer (September 1980). They also noted a difference in the effect on fruit yield and plant weight of chronic and recent infections. With chronically infected plants, significant reductions in these traits occurred when compared to recently infected or healthy plants. The occurrence of severe virus-like symptoms (yellow leaf margins, small leaves, short petioles), and therefore lower virus tolerance ratings, in September 1980, but not earlier, confirms that severity of virus damage increases with time.

There was close agreement between phenotypic assessment from parent clones and genotypic assessments from progenies in virus tolerance ratings. This confirms the high heritability estimates and suggests that a parent whose progenies showed tolerance but was not in the planting, such as 'Aiko', will be tolerant. Likewise, OR-US 4459, whose progenies were very susceptible, will be susceptible.

Six of the clones, 'Totem', 'Northwest', 'Rainier' (WSU 1232), 'Shuksan', 'Olympus' (WSU 1142), and 'Hood' were examined 10 years earlier for tolerance at the Mt. Vernon site (7). In the earlier examination, as in the present one, 'Totem' showed greater tolerance than either 'Shuksan' or 'Northwest', and 'Olympus' and 'Hood' were susceptible compared to the others. 'Rainier' showed somewhat more tolerance in the earlier examination, but in the present one it still showed more tolerance than either 'Olympus' or 'Hood' and was comparable in its reaction to 'Northwest'. Comparisons between the 2 studies indicate that symptoms caused by the virus and/or strains of viruses (virus complex) have not changed to any great extent at the test site. In the earlier study (7), tolerance ratings also were made at a second site, Abbotsford, British Columbia, 120 km north of Mt. Vernon. The clones common to both sites showed relatively similar ratings. Moreover, recent observations at Abbotsford (Daubeny, unpublished) confirm the earlier evaluations and agree with the present ones at Mt. Vernon. It seems reasonable to assume, therefore, that the virus complex at Abbotsford, with respect to symptom expression at least, is similar to the one at Mt. Vernon and also has remained the same for at least 10 years.

It is likely that a similar situation exists in commercial fields of northwestern Washington and southwestern British Columbia, as commercial production is continuous between the 2 sites. Elsewhere in the Pacific Northwest there is general agreement that 'Totem' and 'Northwest' are tolerant to the complex and 'Hood' is susceptible (13). Since the expression of virus tolerance is similar throughout the Pacific Northwest, it can be expected that the mode of inheritance of tolerance for the various complexes found in the region will be similar. Thus appropriate parents for the region can be selected on the basis of phenotypic performance.

Most of the clones studied that had a high level of virus tolerance have 'Totem' or one of its parents, 'Northwest', as a parent and they originated from Pacific Northwest breeding programs. Three clones with tolerance do not have 'Totem' or 'Northwest' parentage. Of these, only BC 70-22-82 ('Cheam' x'Valentine') originated from a Pacific Northwest program; 'Cambridge Favourite' originated in England and 'Aiko' in California. Although these clones have some ancestry common to that of 'Northwest', each probably can be considered as a distinct source of tolerance. It seems obvious that additional sources of tolerance will exist in clones obtained from these and other programs. In addition, clones of the native beach strawberry, *F. chiloensis* L., should be given further consideration as sources of tolerance (15). By incorporating all possible sources of tolerance into the Pacific Northwest programs, the genetic vulnerability that exists with changes in the virus complex should be reduced.

The determination of relative differences in virus tolerance in the present study took more than 2 years from planting in the field in June 1978 until the final ratings for tolerance were made in September 1980. This contrasts with selection procedures for some of the other major strawberry diseases, such as red stele and verticillium wilt, for which a reaction is determined in the seedling stage prior to placement in the field (17). The present procedure is inefficient and selection technique must be developed at the seedling stage so that only virus-tolerant seedlings are placed in the field. With aphid-borne viruses this might be accomplished by using viruliferous aphids to inoculate young seedlings and subsequently determining their tolerance. Such a procedure would require more knowledge of the viruses which make up field complexes and more information on their transmission characteristics. It is imperative that the prevalent viruses and strains of each be included and that each virus be efficiently transmitted during the screening procedure.

Another approach aimed at avoiding aphid-transmitted viruses might be the breeding of strawberries resistant to the aphids (1). Such an approach is used to control viruses in other fruit crops. For example, immunity or high levels of resistance to the aphid vectors, *Amphorophora agathonica* Hottes and *A. idaei* (Börner) results in an absence of inflection by viruses of the raspberry mosaic complex (6, 11). In strawberry, resistance to *C. fragaefolii* and *C.thomasi* has been found in clones of *F. chiloensis* and this has been transferred to second backcross progenies (1, 18). It has not been determined if this level of resistance is sufficient to at least prevent spread of the noncirculative viruses, mottle and vein banding (12). It is reasonable to assume, however, that higher levels of aphid resistance do exist, since screening for aphid reactions in *F. chiloensis* has been done on a relatively limited scale. Thus, breeding for aphid resistance may be an alternative in the control of strawberry viruses. Moreover, combined resistance to the vector and tolerance to the virus complex would undoubtedly reduce the impact of viruses on production.

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Germination and Seedling Growth Characteristics of Three Tomato Species Affected by Water Deficits[1]

A. G. Taylor,[2] J. E. Motes, and M. B. Kirkham[3]
Department of Horticulture, Oklahoma State University, Stillwater, OK 74078

Additional index words: water stress, *Lycopersicon chilense*, *Lycopersicon esculentum*, *Solanum pennellii*

***Abstract.* Two species of tomato, *Lycopersicon chilense* Dun. and *Solanum pennellii* Corr., which have drought-resistant characteristics, were compared to the commercial tomato, *Lycopersicon esculentum* Mill. cv. Campbell 1327, to evaluate the effects of water deficits on germination and early seedling growth at 25, 30, and 35°C. Five levels or water stress (0, −2, −4, −6, and −8 bars) were maintained by solutions of polyethylene glycol (PEG) 6000. Germination of dry seed was inhibited more by water stress than by growth of the germinated seedlings of each species. Germinated seed of all species were able to continue growth at 35° plus water stress at all levels, while germination under the same conditions was totally suppressed. The water-sensitive phase of germination occurred just prior to radicle emergence. Emergence was not affected by sowing germinated seed in a drying soil; but sowing dry seed under the same conditions resulted in a decrease in emergence. Germination and seedling growth of *L. chilense* and *S. pennellii* were more sensitive to water stress than *L. esculentum* at 25°. At 30 and 35°, *L chilense*, *S. pennellii* and *L. esculentum* had similar rates of germination and similar amounts of early seedling growth.**

Germination and seedling-emergence problems are extensive in semi-arid and arid regions. In these areas, the rate of evaporation is high, soil crusting can occur, and soil salinity may result. High soil temperatures generally accompany dry soils. Although soil moisture may be adequate for growth of established plants, the surface layer of soil often may dry rapidly and prevent seed germination and seedling establishment. Sowing germinated seed is a possibility for assuring an adequate plant stand under such conditions.

A method for sowing germinated seed in a fluid gel has been reported (5). The seed are first germinated in controlled conditions and then suspended in a fluid gel which is extruded behind the furrow opener of a conventional planter. The major advantages of sowing germinated seed, compared to dry seed, are earlier and more uniform emergence (3). Another major advantage is the capacity of a germinated seed to continue growth at environmental conditions suboptimal for normal germination to occur. When lettuce (*Lactuca sativa* L.) cultivars, which have thermal dormancy and light requirements for germination, are first germinated in ideal conditions at optimal termperatures and in red light, the seed will continue growth at elevated soil temperatures (6).

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[2] Present address: Department of Seed and Vegetable Sciences, New York Agricultural Expt. Station, Geneva, NY 14456.

[3] Present address: Evapotranspiration Laboratory, Kansas State University, Manhattan, KS 66506.