

## Components of Genetic Variance for Plant Survival and Vigor of Apple Trees\*

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**Summary.** The additive and non-additive variance components were estimated from progenies derived from two samples of parents (representing a northern continental type climate) for five factors relating to plant survival and two composites of the factors. It was found that additive variance made up 90 and 100%, 91 and 100%, 91 and 100%, 100 and 100%, 82 and 59%, 91 and 100%, and 90 and 100% of the total genetic variance for leafing-out date, leafing-out percent, tip injury, stem damage, root damage, a shoot composite, and a shoot-root composite for the two samples respectively. A third sample had 100% additive variance for plant height while, in contrast, a sample of rootstocks, differing from each other in their ability to dwarf grafted scions, had approximately 50–70% additive variance for plant height. It was shown that breeding progress for both winter survival and plant height could be achieved by exploiting the additive variance, the total genetic variance, or (where progenies were the selection unit rather than individuals) by progeny selection. By exploiting the additive variance, it should be possible to improve plant survival and change plant height in each of several successive generations. It is predicted that (with the exception of selection for vigor in a population having a range of dwarfing abilities) potential parents could be efficiently screened phenotypically and so obviate the need for genotypic evaluation. A total of 9180 progeny trees were involved in the analyses considered in this paper.

### Introduction

The total genetic variance may be divided into two components: a portion reflecting the average effects of genes called the additive variance, and the non-additive genetic variance resulting from allelic and non-allelic interactions of genes. A good plant breeder should take cognizance of the relative importance of these components. It is logical to expect the maximum genetic progress, either short or long term in a breeding procedure based on a knowledge of the genetic components. Thus, in apple trees, if it is found that most of the genotypic variance is additive, then a simple breeding procedure of crossing the best phenotypes with the best over several generations should make good use of the available genetic variance. In contrast, if it is found that the non-additive variance is much more important than the additive variance, then procedures that use all the genetic variance should be considered. In the event that genotype  $\times$  environment interaction is found to be of major importance, testing at several locations would be necessary.

It was shown (Comstock *et al.*, 1958; Morrow *et al.*, 1958; Watkins and Spangelo, 1968) that the strawberry conformed with the suggestion of Wright (1956) that in a species where there is a combination of mostly vegetative reproduction with occasional sexual

crossbreeding, non-additive variance may be expected to be of major importance. It would be interesting to know if apple trees which man propagates vegetatively but which in nature are propagated by sexual crossbreeding have a genetical architecture reflecting the artificial or the natural propagating procedure.

The present paper presents estimates of additive and non-additive variance for five apple tree survival characters and for two composites derived from the main characters. Independent estimates were obtained from two samples of trees. Similar estimates of variance components for tree vigor were obtained using a further two sets of apple tree progenies. The results were used to estimate the breeding progress to be expected in one generation using two selection methods for individuals and one selection method for whole progenies.

### Materials and Methods

*Plant survival 5  $\times$  5 diallel:* Five clones taken from the population of cultivars used in breeding apple rootstocks at Ottawa were used as parents. The five parents were as follows: Antonovka, a variety proven hardy in Canada during the last 70 years and extensively used in Canada as a source of open-pollinated seed for the production of hardy rootstocks; Columbia (*Malus baccata*  $\times$  Broad Green), selected at Ottawa in the late 1890's; Heyer 12, a very hardy seedling selected at Neville, Saskatchewan, where winter temperatures commonly reach  $-40^{\circ}\text{C}$ ; *Malus robusta* 5, selected at Ottawa in the late 1920's from among *Malus robusta* open-pollinated seedlings; and Osman (Siberian crab  $\times$  Osimoe), selected at Ottawa in the late 1890's. These were crossed according to diallel mating design called Method 4 by Griffing (1956) to give a total of ten progenies.

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In addition to the ten progenies, vegetatively propagated plots of the standard rootstock cultivar *M. robusta* 5 were also included in each block to provide a standard for estimating genetic progress. Records were taken on an individual plant basis.

The *M. robusta* 5 was derived from stoolbeds which have been indexed for virus and found to be free. Since there is no evidence of pollen transfer of virus diseases in apples, it is assumed that all progenies were also free from virus diseases when planted. Since no grafting of scions was practiced on any of the trees and since the trees were not near virus-infected trees to which they could be accidentally root grafted, it was assumed that they remained free of viruses throughout the experiment.

The seed of the progenies were sown in flats in January and allowed to stratify in the dark for nine weeks at 1° to 2 °C. They were then transferred to cold frames to germinate and then transplanted in the field in the summer when the seedlings were approximately 30 cm high. The following spring, when the seedlings had grown to a size which on the average was comparable to plants from the stoolbed, the *M. robusta* 5 was planted.

The field planting consisted of a randomized complete block design with 29 replicates. Each progeny and cultivar was represented in each replicate by a plot of 18 plants. In the winter following the planting of the control cultivars, the blocks were subjected to artificial cold stresses similar to those occurring in severe winters. The following stresses were included: December — air temperature to -46 °C, soil at a depth of 102 mm to -15 °C; January and February — air temperature to -52 °C, soil at a depth of 102 mm to -29 °C; March — air temperature to -44 °C, soil at a depth of 102 mm to -19 °C. The stresses were applied for varying periods up to 47 hours depending on the stress to be achieved. Based on previous experiments, the stresses at particular times were designed to give as low temperatures as possible without causing severe damage to the control cultivar *M. robusta* 5. A portable low temperature chamber which was large enough to do an entire block at one time was used to apply the stresses (Scott and Spangelo, 1964).

In the spring and summer following the cold stress, the following characteristics were recorded: leafing-out date, leafing-out percent (five weeks after the earliest leafing-out date), plant height, tip injury (expressed as the length of stem measured from the top which was dead), stem diameter (305 mm above ground level), stem damage (305 mm above ground level expressed as a diameter), root diameter (76 mm below ground level) and root damage (76 mm below ground level expressed as a diameter). From these basic characteristics the following derived characters were calculated:

- C(1) = Leafing-out date expressed as the day of the year.
- C(10) = The arcsin transformation of the leafing-out percent.
- C(11) = The arcsin transformation of percentage tip injury.
- C(12) = The arcsin transformation of percentage stem damage.
- C(13) = The arcsin transformation of percentage root damage.
- C(17) = Shoot composite  
= 480 - C(1) + C(10) - C(11) - C(12)
- C(16) = Shoot-root composite  
= 570 - C(1) + C(10) - C(11) - C(12) - C(13).

For C(17) and C(16) severely injured plants would have low values while plants showing little injury would have high values. The values 480 and 570 were chosen to ensure that no plant could receive negative values.

The data were analyzed using Method 4 Model 2 of GRIFFING (1956) to obtain estimates for general combining ability components ( $\sigma_g^2$ ) and specific combining ability

components ( $\sigma_{SA}^2$ ). These were used to obtain estimates of additive ( $\sigma_A^2$ ) and non-additive genetic variance ( $\sigma_{NA}^2$ ).

The interpretation of the results of the analyses is based on the assumption of bivalent chromosome pairing at meiosis. There is no evidence that the diploid apple cultivars used as parents behave abnormally. Values for the genetic variance within progenies ( $\sigma_{pw}^2$ ) were calculated as twice the general combining ability component plus three times the specific combining ability component. The total genetic variance ( $\sigma_{gt}^2$ ) was obtained by adding to  $\sigma_{pw}^2$  the genetic variance between progenies ( $2\sigma_{pw}^2 + \sigma_{pw}^2$ ).

The estimates of additive and non-additive variance were obtained by assuming that epistatic variance was insignificant, that additive variance was equal to four times the general combining ability component, and that the non-additive variance was equal to four times the specific combining ability component. If epistatic variance was assumed to be unimportant, then the non-additive variance would be equal to the dominance variance.

Percentage genetic progress (Watkins and Spangelo, 1968) for each character was calculated as follows, using the values for additive and non-additive variance discussed above, for each of the three breeding methods which were compared:

$$\left[ \pm \frac{100 (\text{Mean of progeny population} \pm \text{Expected response} \pm \text{Mean of control cultivar})}{\text{Mean of control cultivar}} \right]$$

The expected response, which followed the Falconer (1960) definition, was either positive or negative depending on the desired direction of response for a particular character. All genetic progress estimates which indicated better plant survival than the control cultivar were given positive values.

Three breeding procedures were compared for their relative levels of genetic progress for 50% selection. The three methods were as follows: exploitation of the additive variance in each of several successive generations; exploitation of all the genetic variance by one generation of selection; and selection of the best entire progenies. The first two procedures would be pertinent where selected individuals would be used as vegetatively propagated rootstocks or scion varieties while the third procedure would be relevant when considering seed-propagated rootstocks.

**Plant survival 6 × 6 diallel:** Six clones selected at Ottawa for their outstanding rootstock characteristics were used as parents. The six parents were as follows: Ottawa 1 (Robin × Malling VII), Ottawa 4 (Quaker Beauty open pollinated), Ottawa 5 (*Malus baccata* open pollinated), Ottawa 7 (*M. baccata* open pollinated), Ottawa 8 (*M. baccata* var. *gracilis* × Malling VII) and Ottawa 13 (*M. baccata* var. *siberica* open pollinated). These were crossed using the same diallel mating design as for the 5 × 5 diallel to give a total of fifteen progenies.

Ottawa Hybrids 1 and 3 were included in both the 5 × 5 and 6 × 6 diallels as a means of comparing the two experiments. The two hybrids are very hardy seed-propagated experimental rootstocks.

The procedure for germinating the seed and planting the seedlings and the method of applying the artificial stresses were similar to those used for the 5 × 5 diallel. The field planting consisted of a randomized complete block design with 24 replicates. Each progeny and hybrid was represented in each replicate by a plot of five plants.

Records on an individual plant basis were taken in the same way as for the 5 × 5 diallel, and the resulting data were subjected to the same analyses. However, since the Ottawa Hybrids 1 and 3 were hardier than the hardiest plants in the fifteen progenies, no positive estimates of genetic progress were obtained. Therefore, the breeding progress potential was expressed as expected response rather than genetic progress.

Table 1. Means together with general and specific combining ability variance components for apple winter survival characters following Griffing's Method 4 Model 2 procedure. The figures are for a  $5 \times 5$  diallel with 252 d. f. for error and for a  $6 \times 6$  diallel with 322 d. f. for error

Character <sup>1</sup>	Mean <sup>1</sup>		General combining ability		Specific combining ability	
	5 × 5	6 × 6	5 × 5	6 × 6	5 × 5	6 × 6
Leafing-out date	125	143	40.0**	25.5**	1.1**	0 N.S.
Leafing-out percent	43	10	22.7**	2.1**	2.1*	0.2 N.S.
Tip injury	22	65	40.1**	22.7**	4.1*	4.9 N.S.
Stem damage	37	74	29.2**	3.1*	2.1 N.S.	0.4 N.S.
Root damage	9	59	18.7*	13.3*	4.1*	9.2*
Shoot composite	345	206	463.2**	144.0**	47.0*	13.9 N.S.
Shoot-root composite	426	238	659.5**	232.9**	73.1**	55.4 N.S.

\*\* and \* = significant at the .01 and .05 levels of probability respectively.

N.S. = non-significant at the .05 level of probability.

<sup>1</sup> Character and units described in Materials and Methods.

*Plant vigor 'scion' selections:* Eight scion selections from the population of those used at Ottawa in breeding for resistance to scab (*Venturia inaequalis* (Cke.)) were used as parents. The eight parents used were as follows: Delicious (a chance seedling), T-397 (Delicious × Linda), T-3916 (Delicious × Sandow), T-3919 (Delicious × McIntosh), O-521 (Melba × R6T68), O-522 (Melba × R6T68), O-523 (Melba × R16T52), and O-543 (McIntosh × Dg20-9). These were divided into two groups consisting of the non-scab resistant selections (Delicious, T-397, T-3916, and T-3919) and the scab resistant selections (O-521, O-522, O-523, and O-543) respectively. All possible crosses except reciprocals were made between the two groups to give a total of sixteen progenies.

The procedure for germinating the seed and planting the seedlings in the field was the same as for the  $5 \times 5$  diallel. The field planting consisted of a randomized complete block design with 12 replicates. Each of the sixteen progenies was represented in each replicate by a plot of five plants.

After one growing season, the plant heights were recorded. The data were analyzed following the procedure called Experiment II by Comstock and Robinson (1952) and the results interpreted in a manner similar to that for the  $6 \times 6$  diallel.

*Plant vigor 'rootstock' selections:* The rootstock selections Ottawa 1, Ottawa 4, Ottawa 5, Ottawa 8, and Ottawa 13 were crossed using the same diallel mating design as used for the  $5 \times 5$  and  $6 \times 6$  diallels. The field planting consisted of 24 replicates with five plants per progeny in each replicate. Height data were collected as for the scion selection progenies and analyzed following the same procedure as for the  $6 \times 6$  diallel.

## Results

Table 1 shows the significance of the general and specific combining ability components for apple tree winter survival characters (and composites) for the  $5 \times 5$  and  $6 \times 6$  diallels. For the  $5 \times 5$  diallel, only the specific combining ability for stem damage was non-significant at the .05 level of probability. In contrast despite the higher number of degrees of freedom for the specific combining ability for the  $6 \times 6$  diallel (9 d.f.) than for the  $5 \times 5$  diallel (5 d.f.) all characters in the larger diallel were non-significant for this component with the exception of root damage. While failure to show a significant specific combining ability component does not prove that such a component has

a zero value, it is consistent with a hypothesis that it is of very small magnitude. Furthermore, the significant specific combining ability components with 5 degrees of freedom and the non-significant values for the same character with 9 degrees of freedom indicate that the true values of the components for the  $6 \times 6$  diallel are probably smaller than those for the  $5 \times 5$  diallel.

Table 2 shows the significance of the general and specific combining ability components for apple tree vigor (height) for scion and rootstock selections. The significant specific combining ability component for 'rootstocks' with 5 degrees of freedom and the non-significant value for it for 'scions' with 9 degrees of freedom indicates that the true value of the component for the 'scions' is probably smaller than that for the 'rootstocks'.

Table 2. Means together with general and specific combining ability variance components for apple tree vigor (height) obtained from progenies of scion selections (165 d. f. for error) and from progenies of rootstock selections (207 d. f. for error)

Types of parent	Mean height cm	General combining ability	Specific combining ability
Scion selections	91	3.0**	0.9 N.S.
Rootstock selections	101	16.0*	6.5**

The relatively uniform low percentages of non-additive variance are a striking feature of Table 3 with all except root damage having values of 10% or less. Even when, following the assumptions used in the Watkins and Spangelo (1968) paper, the non-additive variances were re-estimated for the  $5 \times 5$  diallel, assuming that all the non-additive variance was due to epistasis, the maximum estimate obtained (excluding the character root damage) was only 22%. Even for root damage a reasonable estimate of the upper limit for the non-additive variance would not be more than 50% of the total genetic variance, since

Table 3. Estimates of the additive and non-additive variances expressed as percentages of the total genetic variance for apple progeny winter survival characters. The main figures are for a  $5 \times 5$  diallel and the bracketed ones for a  $6 \times 6$  diallel

Character	Additive variance	Non-additive variance
Leafing-out date	90 (100)	10 (0)
Leafing-out percent	91 (100)	9 (0)
Tip injury	91 (100)	9 (0)
Stem damage	100 (100)	0 (0)
Root damage	82 (59)	18 (41)
Shoot composite	91 (100)	9 (0)
Shoot-root composite	90 (100)	10 (0)

The genetic variance was assumed to be all additive when the specific combining ability was non-significant.

Table 4. Estimates of additive and non-additive variances for vigor (height) in apple trees expressed as percentages of the total genetic variance

Types of parents	Additive variance	Non-additive variance
Scion selections	100	0
Rootstock selections	71	29

the average of the values in Table 3 is only 30%. Hence, there is no evidence to show that either epistasis or dominance is a major component of the genetic variance for any of the winter survival characters, with the possible exception of root damage.

The progenies from the scion selections gave no evidence that non-additive variance was a significant component of apple tree vigor. In contrast, the progenies from the rootstock selections, which were known to include individuals differing widely in their ability to dwarf grafted scions, had a specific combining ability effect which was significant at the .01 level of probability (Table 2). This corresponded to an appreciable estimate of non-additive variance (Table 4). If it is assumed that the general and specific combining ability components for the rootstock were well estimated, then, following the procedure of the previous paragraph, the maximum non-additive variance (all epistatic variance) would be approximately 50%. Hence, the results obtained for winter survival as measured on roots (for both the  $5 \times 5$  and  $6 \times 6$  diallels) and for plant vigor as measured on the rootstock progenies suggest that non-additive variance (which may or may not include epistatic variance) may be an important component of genetic variance for certain apple tree characters.

Table 5 shows the relative importance of genetic progress for plant survival for the three breeding

procedures outlined in the Materials and Methods under *Plant survival 5x5 diallel*. Genetic progress is positive whenever selected plants have a better average survival than the control cultivar (in this case the commercially important *M. robusta* 5). The particularly high values for genetic progress were mainly caused because for all plant survival characters the average values for the progenies were equal to or better than those for the control *M. robusta* 5. Hence, in contrast to the results obtained with strawberries (Watkins and Spangelo, 1968), genetic progress was always equal to or better than genetic advance.

The main figures in Table 5 were estimated assuming that all the non-additive variance was due to dominance, while the bracketed figures were estimated assuming that it was all due to epistasis. The choice of assumptions made very little difference to the genetic progress to be expected for a given character and method. The only exception was for Method 2 for root damage where the large amount of non-additive variance resulted in significant differences for the two assumptions. Furthermore, for both assumptions, there was little to choose between the merits of the three breeding methods. Again, the only exception occurred with root damage where Methods 2 and 3 were distinctly better than Method 1.

Method 2 is not included in Table 6 because, with non-additive variance estimated at zero for the  $6 \times 6$  diallel for all characters except root damage, there would be no difference between Methods 1 and 2. None of the progenies in the  $6 \times 6$  diallel had plant survivals which were better than the controls (Ottawa Hybrids 1 and 3). Therefore, selection from the population represented by the six parents would need to be justified on the basis of characters which were lacking in the Ottawa Hybrids. For this purpose 50% selection of either individuals (Method 1) or of progenies (Method 3) would ensure that the level of plant survival was maintained while still leaving a large enough population for effective selection for other

Table 5. Genetic progress towards better plant survival following 50% selection for one generation among progenies of a  $5 \times 5$  diallel — showing comparative figures for three breeding methods expressed as percentage improvement relative to the hardy control cultivar *Malus robusta* 5

Character	Method 1 Selection based on additive variance only	Method 2 Selection based on all the genetic variance	Method 3 Progeny selection
Leafing-out date	3.0 ( 2.9)	3.3 ( 3.7)	3.0
Leafing-out percent	34.7 (34.4)	35.8 (37.2)	38.2
Tip injury	46.0 (45.7)	47.4 (49.2)	54.1
Stem damage	23.7 (23.7)	23.7 (23.7)	29.5
Root damage	29.9 (28.3)	37.2 (46.2)	54.8
Shoot composite	15.2 (15.1)	15.8 (16.6)	16.9
Shoot-root composite	13.0 (12.9)	13.7 (14.4)	14.6

The main figures were calculated assuming that there was no epistatic variance in the non-additive variance while the bracketed figures correspond to the assumption that it consisted entirely of epistatic variance.

Table 6. *Percentage expected response in one generation towards better plant survival from a 6 × 6 diallel — showing comparative figures for three intensities of selection and two breeding procedures*

Character	Method 1* Selection intensity			Method 3* Selection intensity	
	50%	10%	1%	50%	10%
Leafing-out date	2	5	7	4	8
Leafing-out percent	7	16	24	15	32
Tip injury	5	10	15	8	18
Stem damage	1	2	3	2	5
Root damage	3	7	10	7	16
Shoot composite	4	8	13	6	14
Shoot-root composite	4	9	16	7	16

\* Methods 1 and 3 as for Table 5.

characters. However, if it was considered to be desirable to significantly improve plant survival, it would be necessary to increase the selection intensity for individuals to somewhere between 10 and 1%. For progenies a selection intensity of 10% would give an expected response approximately equivalent to that for 1% selection of individuals. (Table 6 does not show the 1% selection intensity for progenies since this would involve selection of less than a full progeny.)

The vigor of the 'scion' progenies, like the plant survival characters of the 6 × 6 diallel, showed no significant non-additive variance and hence there were no differences between Methods 1 and 2 (Table 7). Furthermore, the potential for making progress by selecting for vigor differences and, subsequently, for other characters was poor because a selection intensity high enough to make significant progress for vigor would leave too restricted a population for effective selection of other characters. In contrast, a significant change in the mean value for the 'rootstock' vigor could be achieved by Methods 1, 2, or 3 at the 50% selection intensity, thus leaving scope for selection for other desirable characters.

If any appreciable portion of the non-additive variance in the 'rootstock' progenies was due to

epistatic variance, then, Method 2 would be expected to be significantly better than Method 1 (Table 7). Although this rootstock experiment was not designed to prove that the non-additive variance did include epistatic variance, it did not exclude the possibility that it was important. Following the hypothesis of Wright (1956) one would expect to find epistasis where selection processes had constructed a population consisting of a wide diversity of types which were propagated asexually. The rootstocks used as parents (with their range of dwarfing abilities) might be considered to be such a population.

### Discussion

The experimental results should be considered in the context of their limitations. First, they are limited because of the nature of the experimental material which does not make it easy to conduct large experiments involving many parents such as would be desirable in order to have as many degrees of freedom for general and specific combining ability as have been deemed necessary in other crops. There can be no question that it would have been desirable to have had higher degrees of freedom for both these components for the individual characters in any one of the experiments. The question then arises whether to wait until someone can do the 'ideal' experiment or whether to do a series of experiments on a number of characters and, from the many parts, construct a picture comparable to that obtainable from the 'ideal' experiment. The authors believe that a single character in a single analysis in this paper has only moderate value when considered alone — because of the above-mentioned limitation. However, several such characters when viewed in relation to each other and in relation to other similar experiments do make it possible to build a coherent picture — a picture which can be added to or subtracted from in the light of additional work. It is in this context that the present paper has been presented.

Secondly, they are limited since the estimates were only obtained at one location and hence, particularly for the plant survival characteristics, would only be applicable to similar environments. In this respect it would have to be classified as a northern continental climate. For the winter survival characters the added artificial stresses intensified the severity of the cold stress to a degree comparable to those of very bad natural winters. Northern areas subject to coastal influences, resulting in mild midwinter periods, should be excluded from the areas to which the results for the winter survival characters particularly apply.

Table 7. *Percentage expected response in one generation towards more or less height for three selection intensities, three breeding procedures, and two apple tree populations*

Apple population	Selection intensity	Method 1 Selection based on additive variance only	Method 2 Selection based on all the genetic variance	Method 3 Progeny selection
'Scions'	50%	± 3	± 3	± 5
	5%	± 9	± 9	—
	1%	± 11	± 11	—
'Rootstocks'	50%	± 10 (± 9)	± 14 (± 19)	± 12.
	5%	± 26 (± 24)	± 37 (± 50)	—
	1%	± 34 (± 31)	± 48 (± 64)	—

The non-bracketed figures for 'rootstocks' were calculated assuming that there was no epistasis in the non-additive variance while the bracketed figures were calculated assuming that it consisted entirely of epistatic variance.

Thirdly, they are limited with respect to the population of plants to which the results apply. Samples of four, five, and eight parents must be very representative if the results are to accurately reflect the characteristics of particular populations. In answer to this it should be noted that all five parents used in the  $5 \times 5$  winter survival diallel are widely adapted to Canadian winter conditions, including those on the Canadian Prairies, having been tested widely under natural stresses for between thirty and seventy years. All five have at least one parent derived from north-eastern Europe or Siberia. Although they differ in their response to winter conditions, all five have survived while many thousands of similar seedlings have died. This survival over an extended period shows that they are not representative of all apple seedlings to be found in a continental climate but are, in fact, a sample taken from the population of apple trees capable of extended survival under harsh continental climatic conditions. Hence, it is to this restricted population that the results of the winter survival  $5 \times 5$  diallel more particularly refer. The parents involved in the  $6 \times 6$  diallel are representative of a slightly more restricted population having all been selected at Ottawa under less variable environmental conditions. The vigor results, for the crosses involving scion selections, are probably representative of what might be expected in scab resistance breeding programs in other parts of the world. Similarly, the vigor results, for the crosses involving rootstock selections, are probably representative of what might be expected in any other rootstock breeding program where size control was a factor. The interpretation of the results should therefore be considered in the context of the appropriate base populations.

The two populations sampled for plant survival may have survived the pressure of natural selection due to the presence of a similar gene complex for plant survival. Hence, there may be less non-additive variance expressed in their progenies than if the parent sample had also included cultivars lacking the ability for extended survival in a harsh northern continental climate. Thus, for example, if some of the relatively tender East Malling rootstocks (Hunter, 1964; Hunter, 1967) or the relatively tender dessert cultivars such as Cox's Orange Pippin, Delicious, Gravenstein, Jonathan, or Northern Spy (Macoun, 1929; Davis *et al.*, 1954; Filewicz and Modlibowska, 1955) had been included with the five hardy types, more non-additive variance may have been detected in the resulting progenies.

The uniformity of the percentages of additive and non-additive variances (Table 3) and of the genetic progress values for leafing-out percent and tip injury (Table 5) were consistent with a hypothesis that both characters were dependent on a common group of genes. The following relatively high correlation be-

tween these two characters was consistent with such a hypothesis:

$$\text{Leafing-out percent vs tip injury} = .842$$

(The scale for characters was inverted where necessary to ensure that high values represented good plant survival — hence a good correlation would be expected to have a high positive value.)

In contrast, correlations involving leafing-out percent and tip injury with stem damage were lower with the following values:

$$\text{Leafing-out percent vs stem damage} = .710$$

$$\text{Tip injury vs stem damage} = .762$$

The correlations of these three characters with leafing-out date and root damage were even poorer having the following values:

$$\text{Leafing-out date vs leafing-out percent} = .602$$

$$\text{Leafing-out date vs tip injury} = .646$$

$$\text{Leafing-out date vs stem damage} = .546$$

$$\text{Leafing-out date vs root damage} = .562$$

$$\text{Leafing-out percent vs root damage} = .620$$

$$\text{Tip injury vs root damage} = .578$$

$$\text{Stem damage vs root damage} = .503$$

These lower values suggest that either plant survival was conditioned by different genes for roots and leafing-out date than for leafing-out percent, tip injury and stem damage; and/or the expression of the characters was confounded with the expression of characters which were not associated with plant survival. Thus, the low correlations for leafing-out date were such as would be expected if this character involved genes controlling date of leafing-out in addition to those genes for plant survival which showed their expression through leafing-out date. The responses from roots may be further confused due to the insulating effect of the soil causing a lower rate of change of temperature and less severe temperature stresses relative to the rest of the plant.

Although correlations between the five basic characters and the two composites are not such as it is normally wise to use, since they involve correlations where one character is a part of the other character, they do have merit on a relative scale. Thus the correlations between leafing-out percent, tip injury and shoot damage on the one side and the two composites on the other side were all high with values close to .9. The leafing-out date and root damage vs composite correlations were distinctly lower with values close to .7. These relative correlation values combine to lend further support to the conclusions drawn in the previous paragraph. In addition the three shoot composite correlations with leafing-out percent, tip injury and shoot damage were only

depressed in absolute magnitude by less than .03 by inclusion of root damage into the composite (shoot-root composite). Consequently, it can be predicted that the inclusion of the root damage values should not cause undue disturbance to a composite rating. Since composite correlations involving root damage were lower in absolute value than those involving leafing-out date and yet caused no serious disturbance of the composite correlations, it can be concluded that the presence of leafing-out date in a composite should not cause undue disturbance to a composite rating. Furthermore, since both leafing-out date and root damage are involved in plant survival, it can be argued that they may be expected to make a useful contribution to an overall estimate of plant survival such as may be obtained by using a shoot-root composite rating. Composites have the further advantage that on an individual plant basis they are less subject to large error than simple characters since serious errors in individual characters are subjected to the mitigating influence of satisfactory estimates for the remaining characters.

This paper has been concerned with the genetic constitution of the population of apple trees well adapted to man's needs in a northern continental type of climate. It is therefore logical to consider the implications of such a genetic architecture on the effectiveness of various breeding procedures aimed at improving plant survival. It is apparent from a comparison of Methods 1 and 2 in Table 5 that little or no advantage is to be gained by trying to exploit all the genetic variance rather than just the additive variance. Hence, exploiting the additive variance over several generations (Method 1) by mating the best phenotypes with the best, taking necessary care to avoid undue inbreeding, would probably be an effective breeding procedure. But, recognizing the limitations imposed by a long generation time on such a procedure, it would probably be even better to spend considerable time screening potential parents for desirable phenotypes and intercross only those which between them combine those characters desired (Method 2). Even when it is necessary to continue a breeding program over several generations (Method 1), it would still be desirable to phenotypically screen potential parents in each generation before using them as the parents of the next generation.

Inspection of the genetic progress estimates for Method 3 (Tables 5 and 6) indicates that when progeny selection is the objective (as would be the case when breeding for a seed propagated hybrid rootstock) genetic progress may be expected to be at least as good as for selection of clonally propagated types (Method 1 or 2).

An examination of the data from related experiments indicated that it is desirable to correct leafing-out date by making an adjustment using the normal

leafing-out date of each individual under low stress conditions. Thus, a group of well-adapted parents have progenies with characteristic leafing-out dates which are not necessarily very closely associated with their plant survival. In contrast, an inspection of other experiments where adapted and non-adapted material was included indicated that the leafing-out date had a fair predictive value. These points are substantiated by the following correlations between leafing-out date and the other basic characters for individuals in progenies involving adapted parents and for two experiments involving cultivars with a greater range of hardiness:

	Progenies	Cultivars
Leafing-out percent	= .602	.866 .932
Tip injury	= .646	.849 .941
Stem damage	= .546	.835 .820
Root damage	= .562	.849 .941

The first experiment involving cultivars included the moderately hardy Bancroft, the hardy McIntosh, the very hardy Antonovka and the exceptionally hardy *Malus robusta* 5. The second cultivar experiment had an even greater range of hardiness including both very hardy rootstocks and tender scion selections from Delicious crosses.

Genetic progress would be expected to decrease fairly rapidly in successive generations as it becomes increasingly difficult to detect damage at a given stress level. However, if the stress level were increased in each generation, it should be possible to continue to make genetic progress until all of the genetic variability has been exhausted. An ideal stress level for any particular generation would be one which caused very severe damage in the poorest individuals or progenies and little or no damage in the best. Alternatively, genetic progress in a given generation could be increased by increasing the selection intensity. In practice this would usually be unrealistic since it would leave too small a sample of plants for subjection to selection for other desirable horticultural characteristics. The relatively good level of genetic progress possible (in the  $5 \times 5$  diallel), even with 50% selection, in a single generation would be a more than adequate level of achievement in many plant breeding programs. Hence, the need to proceed to subsequent generations or to more intensive selection may not arise.

In general, it is necessary to have very large seedling populations when dealing with polygenic characters in apples. Although this is true, the numbers required will be very much smaller when the genetic variance for a character is mostly additive. Furthermore, while it is more convenient to work with single major genes controlling desirable characters, it should

be possible to include polygenic hardiness and other major gene characters such as pest resistance simultaneously since many varieties and selections combine good plant survival with such desirable characters. For example, the Ottawa dessert selection O-521, which has derived hardiness from such ancestors as Melba, is resistant to scab (*Venturia inaequalis* (Cke.) Wint.) and mildew (*Podosphaera leucotricha* (Ell. & Ev.) Salm.) and, in addition, is of acceptable fruit quality and type. Similarly, *Malus robusta* 5, which is the hardest apple rootstock in commerce in Canada, combines this with a useful level of tolerance to the common viruses of Eastern Canada, resistance to collar rot (*Phytophthora cactorum* (Leb. & Cohn) Schroet), resistance to woolly aphids (*Eriosoma lanigerum* (Hausm.)), easy propagation by stooling or softwood cuttings, a strong well anchored root system and a tree suitable for nursery grafting or orchard topworking.

The very small proportion of the total genetic variance which was non-additive variance (Table 3) was an important genetic attribute of the plant survival characters for the population of apple rootstocks sampled. These low estimates are in marked contrast to the high estimates of non-additive variance obtained for total, marketable, early and late yields for strawberries — namely, 65.8%, 69.3%, 50.8%, and 42.6% respectively (WATKINS and SPANGELO, 1968). The relatively high estimates of epistasis for strawberries had been expected since they substantiated the theory of WRIGHT (1956) regarding the importance of epistasis in a species which is mostly vegetatively propagated. It is interesting to note that in strawberries, where man's artificial vegetative propagation procedures have continued an important natural propagation procedure, epistasis is relatively high. In contrast, the apple, which in nature is almost entirely seed propagated and only under man's practices has been vegetatively propagated, shows little evidence, from the winter survival and vigor characters studied, of epistatic variance. The only possible exceptions were for root damage and vigor. It might be speculated that apple fruit quality characters which have been the subject of many cycles of vegetative propagation interspersed with occasional sexual reproduction steps, combined with selection for a diversity of types, would be more likely to have epistatic variance than plant survival characters which have been less subject to selection for a diversity of types.

Today, there is considerable interest in producing trees of specified vigor and shape. The results of the two analyses on vigor indicate that in certain material, particularly that derived from parents having varying abilities to control the size of grafted scions, there is sufficient genetic variability for height to permit it to be included as an effective part of a general breeding program.

### Zusammenfassung

Für Symptome, die Frostschäden bei zwei Stichproben eines nördlich-kontinentalen Klimatyps des Apfels anzeigen, wurden die additiven und nicht additiven Varianzkomponenten von fünf einfachen und zwei zusammengesetzten Faktoren geschätzt. Die Werte der additiven Varianz betrugen für beide Stichproben 90 und 100%, 91 und 100%, 91 und 100%, 100 und 100%, 82 und 59%, 91 und 100% sowie 90 und 100% der Gesamtvarianz für Zeitpunkt der Knospenentfaltung, Prozentsatz der Knospenentfaltung, Schäden an Triebspitzen, Stammschäden, Wurzelschäden sowie für das komplexe Schadbild Sproßschäden und Wurzelschäden insgesamt. In einer dritten Stichprobe betrug die additive Varianz für das Merkmal Pflanzenhöhe 100%, im Gegensatz zu einer Stichprobe von Unterlagen, die Zwergwüchsigkeit bei aufgepfropften Reiserh hervorruft, bei der die additive Varianz 51–70% betrug. Es konnte gezeigt werden, daß Fortschritte in der Züchtung auf Frostwiderstandsfähigkeit und Wuchsstärke durch Ausnutzung der additiven Varianz, der Gesamtvarianz oder, wo Nachkommenschaften und nicht Individuen selektiert worden sind, durch Nachkommenschaftsselektion erreicht werden können. Durch Ausnutzung der additiven Varianz sollte es möglich sein, Frostwiderstandsfähigkeit und Wuchsstärke in den folgenden Generationen zu verbessern. Mit Ausnahme auf Starkwüchsigkeit in einer Population mit der Tendenz zur Zwergwüchsigkeit können Elternpflanzen wirksam auf Grund ihres Phänotyps selektiert werden, so daß eine genotypische Analyse entbehrlich ist. Insgesamt wurden für die in der vorliegenden Veröffentlichung mitgeteilten Schätzungen 9180 Sämlinge bonitiert.

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