

INFECTIOUS VARIEGATION IN THE APPLE¹

By F. C. BRADFORD, *Research Associate in Horticulture, Michigan Agricultural Experiment Station*, and LLOYD JOLEY, *Student, Michigan State College*²

INTRODUCTION

The variegation of apple leaves discussed in this paper appeared as an unexpected complication in an experiment on double working, raising new questions which had to be answered before the study as originally planned could proceed with any prospect of definite results. Since this secondary study has reached a point where separation of horticultural and pathological aspects seems possible, and since it deals with a matter which has received rather scant attention, its salient points are placed on record, together with such historical data as are available.

HISTORY OF THE DISEASE

Under various names, variegation of apple leaves has been mentioned several times in the literature. Stewart (12),³ in 1910, described sporadic cases found in New York State since 1896. In 1915 Clinton (5) described a manifestation in Connecticut which may have been identical. In the following year Morse (9) reported, as a leaf trouble "new to Maine" the occurrence of chlorotic areas in leaves of Baldwin, Northern Spy, and Harvey. The appearance of the leaves shown in his photographs is in every way similar to that of the diseased leaves discussed in this paper. Blodgett and others⁴ have reported as "apple mosaic" additional cases in New York, and have demonstrated that the disease is transmissible by budding and grafting. Blodgett states⁵ that specimen leaves from material used in the study here reported "certainly look identical" with the trouble he reported, that Whetzel has collected similar specimens in Michigan, and that others who have seen his specimens have recalled seeing similar cases in other States.

In northern Germany Braun (2) reports as "Buntblätterigkeit" or "Panaschierung" the occurrence in 1928 of "white spots in otherwise sound green leaves" in scattered trees of the apple varieties Fettapfel and Rosenapfel.

Though a rather extensive search of the classic papers on infectious variegation yields no mention of this disease in the apple, it is not to be inferred that it is particularly new. Inasmuch as the early European reports have been overlooked or discredited, and inasmuch as they should constitute a rather important chapter in the history of infectious variegation, a detailed statement is presented here.

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³ Reference is made by number (*italic*) to Literature Cited, p. 908.

⁴ ORTON, C. R., and WOOD, J. I. DISEASES OF FRUIT AND NUT CROPS IN THE UNITED STATES IN 1923. U. S. Dept. Agr., Bur. Plant Indus. Plant Disease Rpt. Sup. 33 : 82. 1924.

⁵ BLODGETT, F. M. Correspondence. Aug. 15, 1932.

In 1867 Bossin (1), without giving citation, stated that Vibert had described a variety of apple with variegated leaves. This, according to Bossin's recollection, occurred about 1827. Bossin made no mention of the variegation being infectious, though the nature of his topic gave him occasion to note a fact of this nature.

In 1830 Sageret (11) stated that he had read in the Philosophical Transactions an account (presumably Cane's (3) published in 1720, describing an observation made in 1692) of transmission of variegation from scion to stock in jasmine. In 1825 Noisette (10), whose nursery was near Paris, had reported observing, on several occasions, transmission of variegation from scion to stock in several kinds of woody plants, which he did not specify. Apparently Sageret had not seen Noisette's statement, for he mentioned the account of the jasmine without, as he said later (reported by Duchartre (6)), giving it full credence, because he knew of no parallel case. Vibert, upon seeing Sageret's statement concerning the jasmine, reported to him that he had seen transmission of variegation in the apple. Some years later Vibert (13) gave an account of this occurrence, as follows:

Some time ago, and during several years, I have seen, at the establishment of a brother of Noisette, the nurseryman, at La-Queue-En-Brie, apple trees which, having been shield-budded with varieties with variegated leaves, and their grafts failing from any cause whatever, none the less produced branches with variegated leaves. Astonished at this strange anomaly, I repeated at home the same operation, on Paradise, using as scion the pommier à feuilles d'Aucuba. In the following spring I completely destroyed all my scions, and all the stocks produced shoots with leaves more or less variegated, even those whose grafts had perished after being inserted.

Vibert recorded at the same time a similar subsequent experience with the rose on dog-rose stock.

In 1839, according to Leroy (7, v. 3, p. 301-302), the nurseryman Noisette gave the initial description of the "pommier à feuilles d'Aucuba," so called because of its variegated leaves, and Leroy secured specimen trees from the vicinity of Paris at that time. Noisette's mention in 1825 of transmission, his initial description of a variegated variety, and his brother's experience seem to warrant the belief that the apple was one of the plants on which he based his 1825 report. If it was not, Vibert had demonstrated transmission in the apple by 1835, when Sageret reported Vibert's statement, as mentioned by Duchartre (6).

Sageret, having been somewhat sceptical of the jasmine case, encountered similar scepticism of his own report concerning the apple. Morren (8) stated some years later:

Pyrame de Candolle, Poiteau, and others of the time attached true importance to it, but without being convinced of its authenticity. Sageret's observation was never cited except with hesitation. The new facts [i.e., those available in 1870] established the truth of the phenomenon in an incontestable manner.

Apparently Sageret's report came too early. Had it been made in 1870 its historical importance in antedating nearly all of the better known cases would undoubtedly have gained wider recognition.

Other reports indicating infectious variegation in the apple are rare and vague. A specimen submitted by Simirenko, as reported by Carrière and André (4) in 1889 suggests a manifestation of infectious variegation, but is not evidence. Consideration should, however, be given the fact that trees raised in well-conducted nurseries have little opportunity of manifesting variegation in the seedling roots where the

potentiality for manifestation is greater. Leroy cultivated the pommer à feuilles d'Aucuba in his nursery at Angers, and stated in 1873 that it was more notable for its variegation than valuable for its fruits and that nurseries were no longer interested in it, but he made no mention of infectiousness of the variegation. Leroy's training and interests seem to warrant the inference that had he noted the occurrence he would have recorded it. If the variegation in Leroy's trees was not infectious, Noisette's trees of the same variety manifested the not impossible but highly improbable coincidence of infectious variegation with a noninfectious variegation. The probability is, therefore, very strong that Leroy cultivated infection-carrying trees without noting the infectious nature of the variegation. Others may have done the same thing.

METHODS

In the spring of 1928 the Department of Horticulture of the Michigan Agricultural Experiment Station began an experiment designed to determine whether the practice, rather common among nurserymen, of working certain weak-growing varieties of pear and apple on vigorous intermediate varieties has any effect beyond making a good nursery tree. For stocks, 2-year-old apple seedlings, raised at East Lansing in 1926 and lined out for one year, were used. These were grafted close to the ground (but high enough to preclude scion rooting) with scions of the Red Canada (Steele Red⁶) apple and of other varieties designed to serve as intermediates to Steele. The Steele scions were secured from an orchard at Ovid, Mich., where they were grown as top grafts on Tolman Sweet. The further history of this strain is not known beyond the fact that the scions were secured by the late T. A. Farrand from an orchard which he described as the best Steele orchard in Michigan. No other Steele grafts or buds were used in the nursery until 1931.

During the growing season of either 1928 or 1929, small spots, some yellow and some cream white, of irregular outline (fig. 1), were noted on some leaves of the Steele grafts, but no significance was attached to them, and the work of building double-worked trees went ahead in 1929 and 1930, according to the original plan. When the leaves opened in 1930, a seedling which had been unsuccessfully grafted with Steele in 1928 showed yellow spotting in a very pronounced degree. Further examination revealed several other seedlings similarly affected; in all cases, however, they were seedlings which had been grafted to Steele, unsuccessfully. Variegation was found on a considerable number of living Steele scions, and in a few—not all—cases where seedling sprouts had not been completely eliminated variegation was found on their leaves. On a few trees which had been root-grafted in 1927 and top-grafted to Steele, with scions of the same origin, variegation was found in Steele leaves, in leaves of the Nixonite intermediate, but not in leaves of Virginia Crab used as an intermediate. Careful scrutiny of every tree in the nursery revealed no variegation in any tree except some of those which had been grafted, successfully or unsuccessfully, to Steele.

The manifestly infectious nature of this variegation raised two questions: (1) Whether the disease is endemic in the Steele variety and (2) whether other varieties are resistant or immune.

⁶ In Michigan two distinct strains of Red Canada have been recognized, and one has been designated Steele, the name used in this paper. The material used was supposedly of the Steele strain.

The belief that the disease might be endemic was strengthened by vague reports that this variegation is more or less characteristic of Steele in the nursery. Though an inspection of all trees of this variety in two large nurseries in June, 1930, revealed no trace of variegation, the question was not regarded as definitely settled inasmuch as variegation had been found on seedling sprouts of trees whose Steele leaves showed no trace of it, and this seedling index was unavailable in most of the nursery trees. In addition, the usual slow growth of Steele trees and the common lack of vigor in variegated plants seemed to lend some support to this view. Accordingly, in the spring of

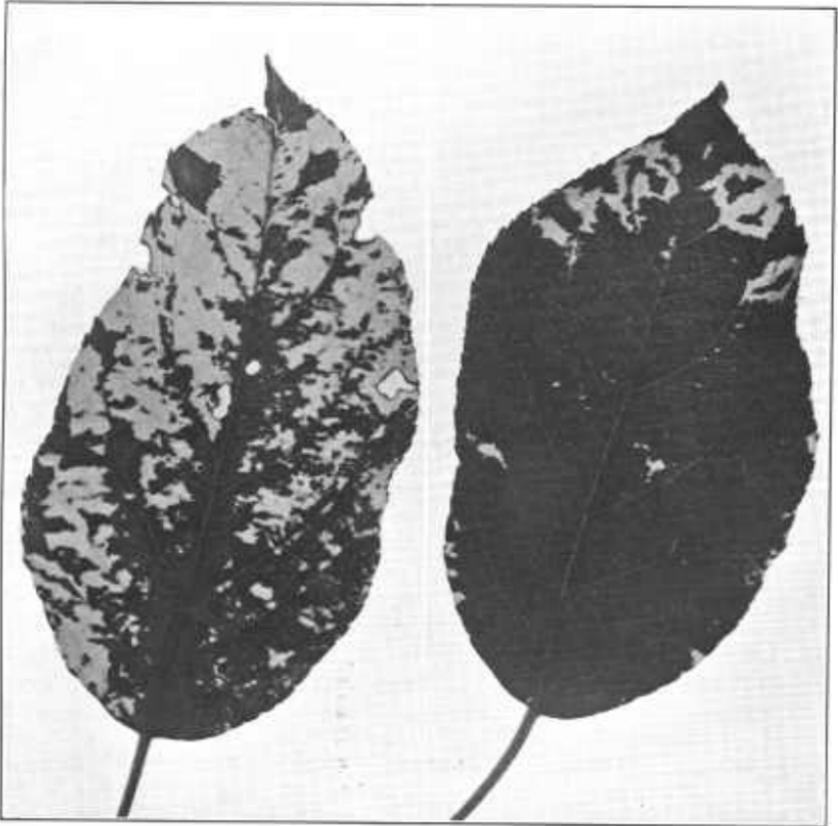


FIGURE 1.—Apple leaves showing infectious variegations

1931, scions from two other orchards, as well as those tracing to the original diseased strain, were used. Grafts of several other varieties were set on seedlings, high enough to permit retention of seedling leaves as indicators of transmission. These were budded in the ensuing August, record being kept of the source of buds in each case. With the unfolding of the leaves in 1932, the effects of these various manipulations could be appraised.

In 1930 variegation was recorded by the senior author; in 1931 and 1932 by the junior author. Since differentiation between very small spots due to variegation and others due to insects is a rather nice matter, the junior author made his diagnosis in ignorance of the

history of the trees, which were marked only by jumbled numbers. This removal of personal bias makes some of the findings particularly striking. Variegation was arbitrarily recorded as "trace", "moderate", and "heavy." Though no rigid standard was maintained, classification was made on the basis of conspicuousness, which, analyzed, signifies the development of large variegated areas rather than number of leaves affected.

RESULTS OF EXPERIMENTS

Three-year records (1930-1932) are available for 109 trees of Steele worked directly on seedlings. Of the 40 which showed variegation in the first year, 33 have shown it in the other two. Of the 69 which showed no variegation in 1930, 47 showed it in 1931; of the remainder, 11 showed it in 1932. Only 11 have shown no variegation in any of the three years. It is possible that some of these are free from variegation, since four buds from one of them set in Fameuse grafts in 1931 failed to produce variegation, a sequence not equaled in any budding from trees obviously infected. The increase in percentage of trees affected from 1930 to 1931 is not interpreted as evidence of the spread of the disease from tree to tree, for trees not grafted to Steele, although intermingled freely with those that were grafted to Steele, in no case developed the disease.

In these first trees propagated before variegation was recognized, efforts were made to prevent development of sprouts from the seedling stocks. Consequently data on transmission to the stocks must be drawn from observations on generally very reduced sprouts on 40, 35, and 26 trees in the respective years. The small number of growing points on these sprouts obviously reduced the chances of observation. In those cases in which observation was possible, however, variegation was found in 15 per cent in 1930, 34 per cent in 1931, and 19 per cent in 1932.

More reliable figures on transmission to seedlings are available from 93 grafts of the same strain set higher on seedlings in May, 1931. In June, 1932, 63 per cent of these scions and 46 per cent of their stocks showed variegation. No explanation is offered for the smaller percentage of variegation on the older trees in 1932 beyond the possible effect of transplanting on a portion of them. Those that were dug in the fall of 1931 and reset in the spring of 1932 showed much less variegation in the following summer.

Steele scions from another orchard were set in the spring of 1931. Of these, 109 were set on seedlings and 60 top-worked into various varieties, and in the following August 58 buds from these scions were set. In all, then, 257 opportunities were afforded this lot to show variegation; actually, 1 case was found. Accounting for this single case is not attempted; a mixture of scions is possible, since on one or two occasions the operator carried two lots at the same time. Nine scions from a third orchard failed to develop any visible variegation or to transmit it to young seedlings, and 112 of them top-worked into a mature tree failed to develop any symptom of variegation. Apparently, then, infectious variegation is not universal in this variety. On the other hand, buds taken from a mature Steele tree in the college orchard in 1931 developed variegation in stocks on which they were worked, and in shoots developing them, though examination of this tree in 1930, 1931, and 1932 revealed no variegation.

The best comparable data available on varietal susceptibility is that afforded by the grafts and buds set in 1931, as recorded in June, 1932. These are presented in Table 1. These percentages would probably be greater if the experiment were continued another year, but it appears at present that Tolman Sweet and Northern Spy are much less inclined to show variegation than the other varieties. Not only is the percentage of visibly affected trees smaller, but the amount of variegation as measured by percentage of leaves and area per leaf involved is distinctly lower.

TABLE 1.—*Appearance in 1932 of infections variegation in apple trees of several varieties top-worked with infected Steele scions in 1931*

Intermediate variety	Trees observed	Variegation shown in—		
		Steele scion	Intermediate	Seedling stock
	<i>Number</i>	<i>Per cent</i>	<i>Per cent</i>	<i>Per cent</i>
None (worked direct).....	93	63	-----	46
Tolman Sweet.....	44	57	9	9
Wolf River.....	19	95	47	44
Northwestern Greening.....	14	100	79	21
Fameuse.....	69	64	42	22
Delicious.....	17	77	53	(a)
Yellow Bellflower.....	10	50	40	(b)
Oldenburg (Duchess).....	9	100	38	38
Northern Spy.....	16	56	0	13
Virginia Crab.....	26	71	46	(c)

^a Root-grafted.

^b No observations possible.

The danger of attaching significance to one year's results is illustrated by the Virginia Crab. Eight nursery trees of this variety were top-worked in 1928 with Steele scions which subsequently proved to be variegated; others were top-worked with similar scions in 1930 and 1931. Variegation appeared in the Steele scions rather consistently in 1930 and 1931, but none was found in Virginia Crab, and until the leaves unfolded in 1932 this variety was regarded as immune. In these earlier propagations comprising 35 trees the sole case of variegation in Virginia Crab occurred in 1932. The figures presented in Table 1 represent a later propagation and present a totally different condition.

The lower percentage of seedling stocks showing variegation, as contrasted with the grafts set on them, has been attributed to the smaller number of leaves available for observation, rather than to resistance. This view is taken because of their more pronounced manifestation of variegation when it does occur. Without exception, the proportion of cases of pronounced variegation to all cases found was higher in seedling stocks than in the scions (Table 2). The small number of observations vitiates the results with Oldenburg, Northwestern Greening, and Northern Spy, but the consistency of the direction of the differences compensates in some measure for the paucity of material. Apart from this consideration, any attempt to differentiate between conditions which might be distinguished as susceptibility, manifestation of infection, tolerance, or resistance would be unwarranted on the basis of the evidence here available. Since varieties appear to differ, at least in their manifestation, seedlings probably do likewise. Consequently triple-worked trees, or

clonal rootstocks, would be necessary for further progress in this direction.

TABLE 2.—Percentages of variegation cases classified as pronounced.

Name of intermediate	Steele	Interme- diate	Root
Direct.....	25	-----	36
Fameuse.....	18	18	58
Tolman Sweet.....	25	0	50
Wolf River.....	22	11	88
Oldenburg.....	22	0	33
Northwestern Greening.....	6	8	33
Northern Spy.....	0	(^a)	50
Combined.....	20	13	46

^a No variegation recorded.

Transmission from stock to scion has occurred. Scions uninfected when set in 1931 into a mature tree, which in 1930 had shown a slight evidence of variegation, were rather heavily infected in 1932, though traces on the stock were still very inconspicuous. Variegated scions set in mature trees produce variegation which spreads throughout the tree, even to the tips of ungrafted limbs.

No indication of rapid spread of this disease from tree to tree has been observed. With the one exception already noted, no case has been found in the nursery which could not be traced to a graft, successful or unsuccessful, with infected scions. Infected and uninfected trees have been intermingled thoroughly, and no effort at insect control has been made. Spread through meeting and natural grafting of roots seems entirely possible, since sprouts originating on roots below ground have shown variegation, but no such case has been observed.

No opinion can be advanced here as to the effect of this disease. Two mature variegated trees are dying back at the tips of the branches; two others are distinctly subnormal, but since these trees have other troubles their weak condition can not be definitely attributed to variegation. In the nursery, variegated trees have shown no noticeable diminution of vigor.

Other cases showing identical symptoms have been observed. Two mature trees, one of the variety Marks and the other unidentified, in the college orchard have given clear, if inconspicuous, indication of the disease; a tree of Star has become infected by infected grafts, and a clon of root sprouts taken in 1926 from a tree since removed from the college orchard is thoroughly infected. Single cases occur in other parts of Michigan, involving mature Baldwin, Wolf River, and Fameuse trees; in one case variegated leaves were sent in as specimens of spray burn. Transmission from variegated Baldwin scions through a mature Wolf River tree to other Baldwin scions has occurred at the Graham Horticultural Experiment Station, Grand Rapids, Mich.

Attention is called to the apparent suitability of the apple as material for fundamental investigation of infectious variegation. The large number of clonal varieties with clear and well-recognized differences in vigor and responsiveness to environmental conditions, together with the general ease of handling the apple in the field and

in the laboratory, provide an unusually good foundation for pathological studies.

SUMMARY

Attention is called to the fact that one of the first cases of infectious variegation recorded was in the apple.

Varieties of apple differ, if not in susceptibility, at least in manifestation of infectious variegation.

None of the varieties tested is regarded as wholly immune.

Seedling stocks showed higher proportions of pronounced manifestations of this disease than did the varieties worked on them.

Buds taken from a tree showing no variegation produced it in seedling stocks.

Isolated apparent cases of variegation on several varieties are mentioned.

The effect of the disease on the tree has not yet been determined.

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