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International Organization of Citrus Virologists Conference Proceedings (1957-2010)

Title
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Permalink
https://escholarship.org/uc/item/7k52c75w

Journal
International Organization of Citrus Virologists Conference Proceedings (1957-2010), 2(2)

ISSN
2313-5123

Authors
Schneider, Henry
Cameron, J. W.
Soost, R. K.
et al.

Publication Date
1961

DOI
10.5070/C57k52c75w

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HENRY SCHNEIDER, J. W. CAMERON, R. K. SOOST,
and E. C. CALAVAN

Classifying Certain Diseases as Inherited

Research workers tend to group apparently-inherited disorders with virus diseases, under such categories as virus-like, nontransmissible, and noninfectious. Apparently-inherited disorders often have many of the characteristics of virus diseases, but their inclusion with virus diseases does little to stimulate further study of them. Plant pathology textbooks classify toxicities and nutritional disorders, some of which are virus-like, as distinct diseases, but apparently-inherited disorders usually are not mentioned.

In several tree crops, apparently-inherited disorders are of major importance. For example, much of the decline of maturing lemon trees that has plagued the lemon industry in California from its beginning is due to lemon sieve-tube necrosis and to sour orange rootstock necrosis. Dr. George Nyland (personal communication) states that in California sweet cherry crinkle leaf (5) and sweet cherry deep suture (9) equal or surpass the cherry virus diseases in causing crop reduction in older Bing and Tartarian cherry trees.

The purpose of this paper is to present criteria for judging whether a disorder is inherited; to describe the characteristics and behavior of some of the inherited and probably-inherited disorders in citrus and other plants; and to discuss control measures for them.

Criteria Indicating Inheritance

Direct evidence.—Mendelian segregation of a character is strong evidence that the character is inherited. Characters controlled by single genes show simple inheritance patterns. Examples are bush-type growth versus vine-type in beans, and sugary versus starchy endosperm in corn. Simple inheritance patterns do not however distinguish between the direct inheritance of a disorder and inheritance of susceptibility to some unknown inciting agent. The inheritance of susceptibility is well illustrated in wheat, where many varieties differ in resistance to rust or bunt fungi, and where the fungus inciting the symptoms can be easily detected. On the other hand, if an undemonstrable virus is responsible, it may not be clear whether susceptibility to the virus or direct inheritance of a disorder is involved.

When several or many genes control a heritable character, proof of inheritance is difficult. For example, the mode of inheritance of trifoliate versus unifoliate leaves in hybrids of *Citrus* x *Poncirus* is not certain, even though the 3-leaf condition is regularly dominant in F_1 hybrids. Populations of F_2 plants from open pollination show far more 3-leaved zygotic plants than would be expected from a single, dominant gene.

Indirect evidence.—It is difficult to use Mendelian segregation to prove inheritance of citrus disorders. Many zygotic seedlings do not survive, and populations for study are incomplete. The occurrence of nucellar seedlings further complicates the problem. The time and land required to raise sufficient zygotic individuals of several successive generations to an age where most disorders become apparent is excessive. Therefore, classifying disorders as inherited usually becomes a matter of determining whether affected plants express characteristics and behavior of inherited disorders, and a matter of eliminating other possible causes.

An inherited disorder should normally be expected to exhibit the following characteristics: it should be limited to certain varieties or clones of a crop, in some cases being traceable to a single source plant; it should not be transmissible from affected to normal plants either by propagative parts or by external agents; and it should not spread in the field. In citrus, all nucellar lines from affected clones should show the disorder. Histochemical tests for viruses should be negative. The disorder should appear on many soil types and under many cultural and climatic conditions, although it might not develop under certain climatic conditions.

In the aggregate, these characteristics point strongly toward inheritance, but they do not completely eliminate the possibility that a virus is involved. If a virus were present in all members of a variety and if all other varieties were tolerant or immune, evidence of transmission would be difficult to obtain. A virus disease can fail to spread in the field due to the lack of a vector. Viruses in plants are not known to be 100 per cent seed transmitted; if, however, 100 per cent transmission did occur, the disease, like an inherited disorder, would be present in all nucellar clones. A disorder due to a virus might also falsely appear to be inherited if all nucellar seedlings should immediately become infected.

Malnutrition or injuries due either to deficiencies or excesses of various elements and compounds can cause symptoms resembling those of inherited disorders. If the disease occurs in orchards on different soil types, and in orchards irrigated with water of various salt contents, and if other varieties and species of the crop growing nearby do not show symptoms, the possibility of faulty nutrition is greatly reduced.

Parasitic organisms, such as bacteria, fungi, and nematodes, can usually be eliminated as causal factors if none are found associated with early symptoms of the disease. There remains the possibility that organisms on one part of the plant could indirectly induce what appear to be primary symptoms in another part.

Examples of Inherited Disorders of Plants

There are numerous examples of simple inheritance of disorders that are virus-like. In tomato, the single recessive gene, sun dwarf, produces a stunting and corking of the internodes when the plants are grown in light of high intensity (8). Another recessive gene in tomato, curly mottled, causes a curling and mottling of the leaves that is very similar to symptoms caused by tobacco mosaic virus (8). Symptoms are produced only under certain environmental conditions. A disorder of maize being investigated by J. W. Cameron is genetically controlled, yet has some virus-like characters. In one line of sweet corn, the leaves develop numerous chlorotic spots early in the life of the plant. The spots enlarge longitudinally, and necrosis follows until a third or more of the leaf surface dies. Other varieties of sweet corn, grown adjacent to this line, do not develop these spots. When the affected line is crossed with other varieties, the F_1 hybrids never develop the spotting, but F_2 populations from selfing segregate in a ratio of 3 normals to 1 spotted, indicating that the character is recessive.

In woody plants, genetic information is often incomplete, but there are examples of disorders which are probably inherited. Noninfectious bud failure in almonds occurs in the varieties Peerless and Nonpareil. This disorder also occurs in Jordanola, a hybrid between Nonpareil and a nonaffected variety. Seedlings from Jordanola x Ne Plus Ultra, another unaffected variety, also carry the disorder. Attempts to transmit the disease have failed (15). It seems likely that the genes controlling bud failure are passed from variety to variety.

Sweet cherry crinkle leaf occurs in some trees of the Bing and Black Tartarian varieties, and transmission has not been obtained (5). Symptoms occur in scattered portions of trees as if frequent somatic mutations were responsible. The incidence of crinkle leaf shoots is frequent in old wood of trees low in vigor. Some hybrid seedlings have developed crinkle leaf when one parent was affected and one was normal.

Some Apparently Inherited Disorders of Citrus

Apparently-inherited disorders of citrus may be divided into two main types: those which are independent of rootstock-scion interaction, and those which are not. The former includes lemon sieve-tube necrosis and wood pocket, and the latter includes various incompatibilities.

LEMON SIEVE-TUBE NECROSIS.—This disorder of the scion portion of the lemon tree trunk is one of several diseases having decline as an ultimate symptom. It affects all Eureka lemon trees as well as some strains of Lisbon and Villafranca (12). A characteristic symptom is necrosis of older sieve tubes, which may begin when trees are 3 or 4 years old; after several more years, necrosis may increase and involve even the youngest sieve tubes. As a result of the blockage of translocation, reserve starch is used from the xylem; unless new phloem forms, the feeder roots die. Entire blocks of trees in apparent good health may suddenly decline or wilt from this disorder.

Lemon sieve-tube necrosis has many of the distinguishing characteristics of inherited disorders. Only certain clones are affected. It occurs in all Eureka trees regardless of rootstock, and is found throughout the diverse environmental conditions of southern California's coastal and semicoastal areas. Most of the trees in a planting are affected simultaneously. One Lisbon lemon strain and 10 Eureka lemon clones derived from nucellar seedlings have been examined; all of them, like the clone from which derived, are affected by lemon sieve-tube necrosis. Symptoms have not been produced in closely related disease-free clones by budding and grafting, nor has it been possible to demonstrate a consistent relation of any known virus to this disorder (2, 14). Strains of lemons that are consistently free of sieve-tube necrosis do not develop it when used as rootstocks for affected clones; this indicates nontransmissibility. There is no evidence that soil fungi, nematodes, or soil fertility are involved.

Wood pocket.—This is a disorder which affects a few strains of Lisbon lemons and the Tahiti lime (1, 7). Chlorotic blotching occurs on one or both sides of the midrib of the leaves, and pockets of dead bark and wood appear on the limbs and trunks. Warm interior climates favor symptom production. Although this disorder was thought to be a virus disease when first described (4), it is now believed to be an inherited disorder for the following reasons. It occurs in both zygotic and nucellar seedlings; although present for 41 years in diseased lemon tops, it has not moved down into healthy lemon interstocks; efforts to transmit the disease by grafting to lemons during a 9-year period have failed (1); indexing for known virus diseases has shown no one virus to be consistently present in affected trees; and in lemons the disease is clonally limited. The variable pattern of symptoms suggests that wood pocket may be due to an unstable gene or a chimeral condition (1).

Other disorders.—Disorders which may be inherited are: crinkle-scurf of Valencia orange (6); chimeric breakdown of Tahiti lime fruits (7); and a seed-perpetuated disorder of trifoliate orange with symptoms resembling those of exocortis (3).

Incompatibilities.—When Eureka lemons and certain Lisbon lemon clones are grown on sour orange rootstocks, the trees go through cycles of decline and recovery, beginning at about 12 to 15 years of age. The decline is due to necrosis of sieve tubes immediately below the bud union; hence the name sour orange rootstock necrosis (10, 11). After 8 years, symptoms of this disease were not transmitted by grafts from affected lemon strains to strains compatible with sour orange rootstocks. Frost nucellar Eureka trees are affected but certain Lisbon lemon strains are consistently free of the disease. The disease occurs in many areas, and affected strains decline when growing next to nonaffected strains.

Experimental and commercial attempts to grow Eureka lemons on the trifoliate orange and on Troyer citrange (sweet orange x trifoliate) have failed because of a degeneration of tissues at the bud union. Eureka trees on Troyer rootstock decline when 3 or more years old (13). Other lemon varieties incompatible with Troyer are Genoa and 2 varieties developed from crossing a hybrid of Genoa with an unnamed clone of Lisbon lemon. Sweet orange is a compatible rootstock for lemons, so it is apparently the trifoliate orange that carries an incompatibility factor.

Orlando and Minneola tangelos (tangerine x grapefruit) are apparently compatible with Troyer citrange. When these varieties were crossed with a grapefruit hybrid called Sukega by R. K. Soost, progeny were obtained which were not compatible with Troyer. Some hybrids obtained from crosses of the Frua tangerine with Sukega and of the Sunrise tangelo with Sukega were also incompatible with Troyer. Although it is not known whether Frua and Sunrise are compatible with Troyer it appears that the Sukega carries germ plasm for incompatibility.

Discussion

Classifying apparently-inherited disorders with virus diseases has been a convenient way of handling them, but such classification has not always motivated satisfactory investigations. Some citrus diseases have not been transmitted nor has it been possible to prove them to be inherited, but this should not prevent them from being placed in the category where they most likely belong. Classification of diseases has not always awaited procedures for proving their cause. The existence of citrus virus diseases is accepted, but Koch's postulates have not been carried out. Although graft transmission proves that an infectious agent is present, it gives no evidence of the nature of the agent. Classifying disorders as inherited should be based upon the disorders having characteristics like those of known inherited disorders. Likewise, evidence for virus is largely a matter of the disease having characteristics of known virus diseases. These are similarity of symptoms of the disease to other virus diseases, the manner in which the disease spreads, transmission by an insect vector, absence of parasitic organisms, and histochemical evidence for virus in affected tissue. Recognition that a disease is probably caused by virus stimulates appropriate investigation and control measures, and recognition that a disorder is probably inherited would direct more attention to its investigation and control.

Certain methods used to control virus diseases can be applied to inherited disorders. For example, affected scion varieties, rootstocks, or scion-rootstock combinations can be avoided. In a cherry budwood certification program, stone fruit virologists are eliminating some apparently-inherited disorders that arise spontaneously. If all members of a variety are affected, and if there is no satisfactory substitute variety, this approach is not possible. Cultural practices, such as pruning, may be used at times to alleviate the effects of a disorder, or varieties may be selectively grown in environments where the disorder does not occur.

Anatomical studies can sometimes detect the presence of slowly developing disorders many years before they become limiting to the health of the tree, thus aiding in the selection of new varieties and scion-rootstock combinations by early elimination of undesirable ones. Breeding may sometimes eliminate inherited disorders, although with tree crops this is a slow and tedious process.

Additional techniques should be sought to alleviate inherited disorders, but this might require more knowledge about the physiological and biochemical effects of the disorders. Perhaps the application of some compound, which the plant cannot synthesize, would enable it to grow normally; or some chemical might be used to neutralize a toxic substance.

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