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SIMILARITIES AND DIFFERENCES BETWEEN TRISTEZA IN NORTH AND SOUTH AMERICA[1]

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INTRODUCTION

In the two decades following 1930, twenty million citrus trees perished from tristeza in Argentina and Brazil. The epiphytotic was so sudden, so unprecedented, and so destructive that citrus growers the world over looked on in sympathy and alarm. Sympathetic growers were mostly those of countries where sweet orange, grapefruit, and mandarin trees had long been failures when grafted on sour orange, and where, as a consequence, no commercial acreages of these combinations existed. On the other hand, there was probably more alarm than sympathy wherever these same graft combinations had always done well, and where, as a result, sour orange was still much in use.

In countries like South Africa, the question of whether tristeza was the same as the stem-pitting disease of grapefruit (*34*) was, to a large extent, a matter of academic interest. But in areas of the world where sour orange was in favor, the same question was of much concern to growers. In the United States, for example, there was considerable solicitude as to whether California's quick decline was the same as South America's tristeza; for if these two diseases were to be proved identical, it could mean that the holocaust in South America might be repeated here. There was much clutching, as at straws, for differences that would show quick decline and tristeza to be separate entities.

Ten years have passed since Fawcett and Wallace (*18*) suggested a relationship between South America's tristeza and California's quick decline. Since then the bulk of the literature on these two diseases has been published, and today we are in a much better position to evaluate the question of affinities. It is the purpose of this paper to assemble evidence of relationships, to review briefly the already well-known facts of similarity, and to discuss in detail some findings by the author that point to differences.

The terms "South American tristeza" and "North American tristeza," coined to facilitate this discussion, are in need of definition. By the former term is meant that disease which has been called *podredumbre de las raicillas* by the Argentines, and *tristeza* by the Brazilians. These two diseases may justifiably be combined because of their close correspondence in matters of severity, host range, insect vector relationships, and the evidence that the causal virus was introduced into both countries in shipments of infected nursery trees.

The term "North American tristeza" is meant to include the disease known in California as *quick decline*, and that known in Florida as *tristeza*. Reasons for treating these two diseases as a single entity are presented by Grant and Schneider (*27*), and consist of agreement in matters of host range, histological symptoms, and wood-pitting and vein-clearing reactions in Key lime seedlings.

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SIMILARITIES

Evidence pointing to a close relationship between South American tristeza and North American tristeza consists mainly of facts that can be grouped under five headings: host range, morphological and histological symptoms, graft and insect transmissibility, incubation period within the host, and control.

1. Host Range. The fact grasped first and most readily about tristeza, wherever it occurred, was that it destroyed trees on sour orange rootstock. The very simplicity of this generalization did much, especially in the minds of growers, to equate the diseases found in various parts of the world.

As a matter of fact, the correspondence goes much further and includes numerous rootstocks in addition to sour orange. Certain varieties of the following groups have been found to be susceptible to tristeza in both North America (*6*) and South America (*16, 21, 23, 24*): sour orange, grapefruit, tangelo (e.g., Thornton), shaddock, lemon (e.g., Eureka and Lisbon), lime, citremon, and *Citrus macroptera.* Although the varieties included within these groups may differ from one investigator to another, the breadth of agreement indicates that in rootstocks the range of susceptible species is alike for both North American and South American tristeza.

Further agreement is found among species that are tolerant. In both North America (*6, 8*) and South America (*16, 23*), certain varieties of sweet orange, mandarin, tangelo (e.g., San Jacinto), and lemon (e.g., Rough lemon) have not been found to be susceptible to tristeza when used as rootstocks. This list might be extended to show even greater agreement, were it not for the likelihood that certain varieties in one hemisphere have been judged susceptible when they were in reality showing symptoms of other diseases.

Further similarities in host ranges of North and South American tristeza are found in the susceptibility of certain seedlings. Thus in both hemispheres the Key or West Indian lime is susceptible and manifests symptoms of vein clearing and wood pitting (California, *38;* Brazil, *10*). Seedlings of sour orange and Eureka lemon also show evidence of infection in both areas (*12, 39*).

Still other similarities between North and South American tristeza are to be found in the tolerance and susceptibility of certain stock-scion combinations. Thus, in both hemispheres (California, *6*; Argentina, *17*), tolerance is shown by sweet orange, sour orange, mandarin, and lemon when budded on sweet orange; and susceptibility when sweet orange, mandarin, and grapefruit are budded on sour orange (California, *6;* Florida, *8;* Argentina, *17;* Brazil, *9*). Furthermore, various three-way graft combinations react in the same manner. Tolerant are such combinations as lemon/sour/sweet, lemon/sweet/sour, and sour/sweet/sour; and susceptible, such a combination as grapefruit/sweet/sour (California, *5;* Brazil, *3*).

Finally, in both areas protection from tristeza can be obtained whenever acid lemons are top-worked onto a susceptible combination such as sweet orange on sour orange (California, *6;* Brazil, *2, 12, 20*).

2. Morphological and Histological Symptoms. In both hemispheres the external symptoms of tristeza in commercially grown varieties of citrus are equally lacking in specificity. Such few specific symptoms as do exist—vein clearing, leaf dwarfing and cupping, and vein corking in certain indicator species—are similar in both areas.

Histological symptoms of tristeza are alike in Brazil, California, and Florida (*27, 37*).

3. Graft and Insect Transmissibility. In both North and South America, tristeza has been shown to be graft-transmissible (California, *18;* Florida, *27;* Brazil, *2*).

Both North and South American tristeza are also transmitted by aphids (California, *14;* Brazil, *33*). Species involved differ, however, from one hemisphere to the other. In South America, *Toxoptera citricidus* (Kirk.) is reported to be the vector, and in North

America, *Toxoptera aurantii* (B. de Fonsc.), *Aphis gossypii* Glover, and *A. spiraecola* Patch. *T. citricidus* is not known in North America, and none of the three North American vectors has been reported to transmit tristeza virus in South America, probably because these species have not been tested or used in numbers large enough to compensate for their inefficiency.

4. Incubation Period Within the Host. Wherever indicator plants have been insect-inoculated with tristeza, the disease has appeared in approximately 30 days' time (Brazil, *2;* California, *38*). The same incubation period holds in both areas when transmission is by grafting and indicator plants are the West Indian lime.

5. Control. In both North and South America (California, *7;* Argentina, *15*), it has been learned that trees in decline because of tristeza cannot be saved by applications of fertilizers. It has also been found in both areas that susceptible combinations such as sweet orange on sour orange rootstock can be protected from tristeza by top-working to lemons (Brazil, *2, 12, 20;* California, *6*). Furthermore, the use of budwood known to be free of the causal virus will, in the absence of insect vectors, always insure against spread of the disease in nurseries.

DIFFERENCES

The similarities enumerated above suggest strongly that tristeza in South America is the same as the disease of that name in North America. Certain differences do exist, but they are not as conspicuous as many of the similarities are. Nevertheless, such differences may have certain theoretical and economic consequences.

1. Host Range. Studies of host range in Brazil and Argentina (*11, 28*) revealed that *Aeglopsis chevalieri* Swingle, when insect-inoculated with tristeza virus, responded quickly and sharply with vein clearing in the foliage, wood pitting in the stems, and stunting of the plant as a whole. In fact, in Argentina (*28*) reactions in *A. chevalieri* were so conspicuous (fig. 1) and so rapid that this species was deemed to be a better indicator plant than Key lime.

In Florida, on the contrary, *Aeglopsis chevalieri* has proved quite unsusceptible (*28*). Seeds of this species, derived from the same parent tree that supplied seeds for the Argentine trials, were planted and grown under insect-free conditions. Forty of the resultant seedlings were selected for uniformity and divided into four groups of 10 plants each. Each group was budded with a different source of tristeza virus. Plants in Group 1 received infected budwood from a 4-year-old Valencia orange tree on sour orange that was nearly dead from tristeza. Plants in Group 2 were budded from a 23-year-old navel × Temple hybrid on sour orange root—a tree that is still alive, though in poor condition after having been infected, apparently, for the 27 years of its existence. Plants in Group 3 were budded from a 12-year-old Ruby Red grapefruit tree on sour orange that still produced commercially acceptable crops of fruit. Plants in Group 4 were budded from a 12-year-old Lue Gim Gong sweet orange tree on sour orange root, which, though still alive, has long been defunct commercially.

It was intended by means of these four parent trees in various stages of decline, to obtain a sampling of virulence, should strain differences be accountable for the success or failure of the *Aeglopsis* test. Actual presence of tristeza virus in the various sources of budwood was confirmed by indexing tests on West Indian lime plants, in which vein-clearing symptoms typical of tristeza were obtained. Despite positive reactions in West Indian lime, none of the 40 *Aeglopsis* seedlings graft-inoculated from the same source has, in the course of 2½ years, developed symptoms of vein clearing, wood pitting, or stunting.

To determine whether failure to obtain reactions in *Aeglopsis chevalieri* might have been the result of inadequate sampling of virus strains, additional sources of tristeza-infected trees were indexed to *A. chevalieri.* These sources included budwood from

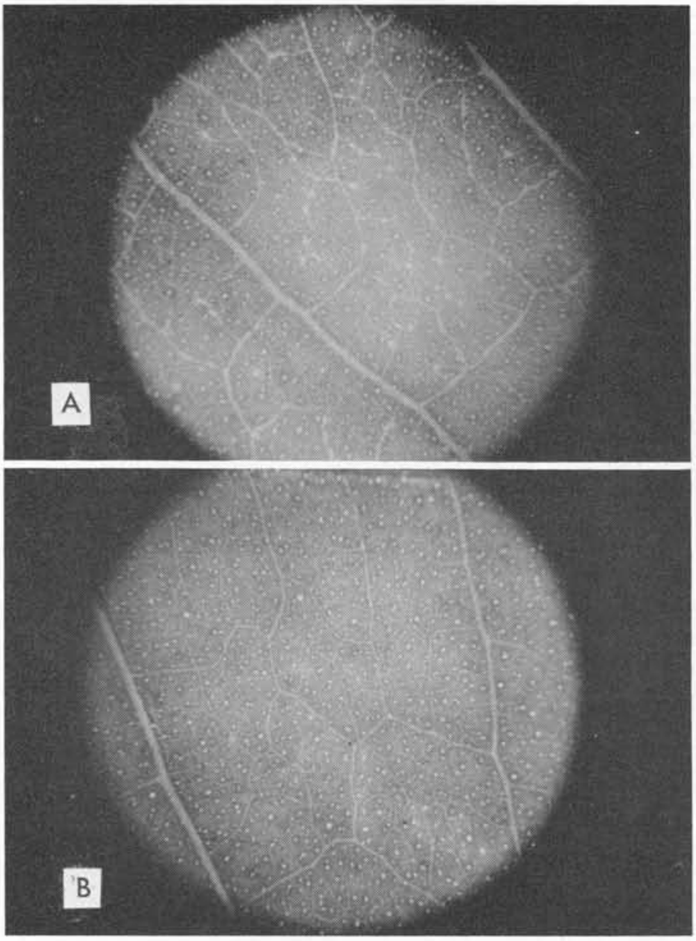

Fig. 1. A) Magnified portion of a leaf of *Aeglopsis chevalieri* taken from a plant that was insect-inoculated with South American tristeza virus. Note thickening of long portions of the veinlets and the intercalary beadlike swellings—characteristics that are also present in the vein clearing of Key limes inoculated with North American tristeza virus. B) Portion of a leaf of *A. chevalieri* from a noninoculated plant. (Both X 15.)

the Mauritius papeda (*Citrus hystrix* DC.), Meyer lemon, Duncan grapefruit, and Nagami kumquat. The kumquat budwood appears to have been infected with an unusual strain of the virus in that leaves on the parent tree showed vein clearing, and the wood showed conspicuous pitting. In addition, when budded into West Indian lime, the vein-clearing symptoms were so intense and so complete as to involve the entire veinal network in the clearing reaction. However, despite the diversity of sources and the apparent virulence of certain strains of Florida tristeza virus, no symptoms in *Aeglopsis* have appeared within 12 months after inoculation.

Additional sources of *Aeglopsis* have also been tested in the event that among the diversity of forms in this monotypic genus there might be varieties that are susceptible to Florida strains of tristeza virus. Varieties of *Aeglopsis* used in these later trials included a large-fruited type from French Morocco, a small-fruited type, also from Morocco, and a selection from the Ivory Coast. To date, a year after budding, none of these variants of *Aeglopsis* has shown symptoms of vein clearing, stunting, or wood pitting.

To determine the possibility that symptoms in *Aeglopsis chevalieri* in Florida might be masked because of environmental influences, 9 of the 40 *Aeglopsis* seedlings originally budded with the 4 different sources of Florida tristeza virus, were indexed to Key lime seedlings. Results for tristeza were negative, indicating that the *Aeglopsis* seedlings were not masked carriers of the virus. That union had occurred between the inoculum tissue and *Aeglopsis* seedlings was attested to by the fact that one of the original sources of tristeza virus also contained the virus of psorosis, and when these seedlings were tested, retrieval of psorosis virus was demonstrated by the appearance of symptoms of psorosis on leaves of the lime test plants.

Various other differences in the host range of North American and South American tristeza have been noted in the literature:

A) In California, only sweet orange trees on sour orange rootstocks are known with certainty to show the effects of quick decline from natural infection (*36*). In South America, on the other hand, tristeza is known to affect most top varieties on sour orange roots, including sweet orange, mandarin, grapefruit, and certain pummelos, tangelos, citranges, and limes (*15, 23*).

B) In California, the rootstock Palestine Sweet lemon has been reported to show some susceptibility to quick decline (*6*). This is in contrast to the situation in Argentina and Brazil, where *Lima de Persia*, considered by many to be the same as Palestine Sweet, was the mainstay of growers during the dark days of tristeza (*17, 23*). It would be interesting to know whether the California instance is complicated by the presence of xyloporosis virus to which this rootstock is known to be susceptible.

C) The uncertain reactions reported from California (*6*) as affecting sweet oranges on trifoliate orange and mandarin rootstocks, are in contrast to the clear-cut tolerances shown by these combinations in South America (*17, 23*). It is conceivable that the trifoliate orange and mandarin rootstocks showing uncertain reactions in the experimental rootstock tests in California may be infected with viruses other than the tristeza virus.

D) Morton citrange was found to be one of the rootstocks tolerant to tristeza in Brazil (*23*), but in California it was reported to be susceptible to stem pitting (*6*). In Florida we have also encountered pitting in Morton citrange rootstock, but have not been able to obtain vein-clearing reactions when wood from this source was indexed to West Indian lime.

2. Morphological and Histological Symptoms. Symptomatology and host range are two sides of the same coin. Some aspects of this coin, however, are better discerned in terms of symptoms than in terms of host range.

One of the most conspicuous differences between tristeza in Argentina and in Florida relates to the development of stem-pitting symptoms. Whereas both North and South American isolates commonly show pitting in the wood of twigs and small seedlings of such varieties as West Indian and Tahiti lime, Florida and Argentine tristeza acts differently in the trunks of grapefruit trees. In Argentina (*17, 29*), as well as in Brazil (*10*), South Africa (*34*), and Australia (*1*), a distinctive stem-pitting syndrome is found in trunks of grapefruit trees harboring tristeza virus.

External symptoms consist of longitudinal grooves that extend from the bud union into the main limbs. Affected trunks give the appearance of being sheathed in a mantle of vertically undulating ropes—an aspect that suggests the name "ropy trunk" for this symptom. When bark is removed from affected areas, the woody cylinder is seen to be heavily pitted, with the network of depressions appearing like the vermiculated tunnels of wood borers.

In Florida, ropy trunk has not been encountered, despite the fact that many grapefruit trees are known to contain tristeza virus. Moreover, only occasional grapefruit trees are observed in which there is even a pitting in the twigs. In California, also, grapefruit appears to be singularly unaffected by trunk pitting. According to one report (*4*), of 136 five-year-old Valencia trees on grapefruit rootstock, half of which were exposed to field inoculation by aphids, stem pitting was found in the grapefruit portion of only four trees. Even here it is questionable whether these trees were actually affected by the stem-pitting disease described by Oberholzer *et al.* (*34*). Varieties reported to have become pitted in California (e.g., trifoliate orange, 77 per cent) failed to show pitting in South America under conditions where stem pitting of grapefruit abounded (*17, 25*). In fact, in Argentina, the dissemination of stem-pitting disease was so general that all of 48 field-grown seedlings of grapefruit showed ropy-trunk symptoms by the time they were three years old.[3]

Further differences in pitting reactions occur in other varieties where comparisons are possible. Thus in California (*4*), sour limes when used as rootstocks for sweet orange, were reported to show stem pitting to the extent of only 14 per cent, whereas in Brazil 91 per cent were found to be pitted. These differences, however, might reflect differences in the varieties of limes used in the two trials and the periods of time the respective trees had been infected.

DISCUSSION

The foregoing recital of differences, if it does nothing else, obliges one to try to put the pieces together again—that is, to try to synthesize the parts into a whole. Various explanations have been offered to account for the diversities in behavior of tristeza. Some differences, as for instance those connected with rates of dissemination, can be attributed to differential activity among vectors. Other differences require a more inclusive rationale.

McClean and van der Plank (*32*) attempted an integration by proposing that tristeza was a complex made up of a seedling-yellows component and a stem-pitting component. They postulated further that the stem-pitting component when present alone or in combination with the seedling-yellows component induces the stem-pitting disease in grapefruit. When both components are present in seedlings of sour orange and Eureka lemon, a yellowing of new foliage develops; and when the complex is present in combinations such as sweet orange on sour orange, tristeza disease appears.

In the light of such an explanation, Knorr and Price (*30*) found it difficult to explain the absence, in Florida, of stem-pitting disease in grapefruit, or, for that matter, of seedling-yellows disease. None of their isolates of tristeza virus from sweet orange trees, when inoculated into sour orange and Eureka lemon seedlings, produced any acute yellowing or dwarfing—at least not to the marked extent described by Fraser (*19*), McClean and van der Plank (*32*), and Wallace (*39*).

The Florida situation would certainly seem to pose a paradox: although tristeza is not uncommon in Florida, neither the seedling-yellows component nor the component causing Oberholzer's stem-pitting disease appears to be present. One possible explanation is that the seedling-yellows component is present in Florida but by itself cannot produce seedling yellows, which develops only when the stem-pitting component is also present. If this is assumed, then it needs further to be assumed that only the seedling-yellows component of the complex, not the stem-pitting component, is present in Florida and that seedling-yellows virus by itself causes the mild form of tristeza to be found there. However, these assumptions are not supported by studies in Australia (*19*), California (*39*), and South Africa (*32*), which indicate that the seedling-yellows virus or

[3] L. C. Knorr. Unpublished data of the Tristeza Laboratory, Concordia, Entre Ríos, Argentina. 1952.

virus strain does not exist separately but is always mixed with other strains that cause stem pitting and vein flecking on lime but not the seedling-yellows reaction on lemon.

Knorr and Price (*30*) presented the hypothesis that tristeza, stem pitting, and seedling yellows are caused by a single virus that exists in the form of numerous strains. In support of this hypothesis they suggested the following:

1. Naturally infected trees can harbor two or more tristeza virus strains simultaneously, one or another of these strains predominating, depending upon the species or variety of citrus in which they occur.
2. The strain of virus predominating in sweet orange trees in Australia (*19*) and South Africa (*32*) is usually one that will induce seedling yellows in grapefruit, Eureka lemon, and sour orange seedlings.
3. The seedling-yellows virus strain is not well adapted to grapefruit.
4. In grapefruit trees infected with a mixture of strains from sweet orange, a virus strain better adapted to grapefruit soon predominates, this being a strain that causes the stem-pitting disease of grapefruit or one that is considerably less severe than the stem-pitting strain.
5. The loss of the seedling-yellows component in experimentally infected grapefruit seedlings which at one time showed seedling-yellows symptoms (*19, 31*), can better be explained by assuming the stem-pitting and seedling-yellows components to be strains of the same virus than that they are distinct and separate entities.
6. It is not necessary to assume that strains of tristeza virus exist; their existence has been demonstrated in South America (*13, 22*) and in the United States (*26, 35*). It is necessary to assume only that the strains of tristeza virus commonly found in the United States cause neither seedling yellows nor the stem-pitting disease of grapefruit.

At present, there seems to be insufficient experimental evidence to come to a final conclusion regarding relationships among the viruses reputed to cause seedling yellows, stem pitting, and tristeza (quick decline).

Cross-protection tests, to determine if the stem-pitting virus or mild strains of tristeza virus provide protection against the seedling-yellows virus, might afford some evidence of relationship. Grant and Costa (*22*) reported that a strain of tristeza virus which caused mild symptoms on sweet orange on sour orange trees protected against strains that were severe on this host combination. Similarly, Olson (*35*) demonstrated that a selected strain of tristeza that caused mild symptoms on seedlings of Mexican lime gave protection against a strain that caused severe symptoms on lime seedlings. The severe strain obtained by Olson from a Sueoka satsuma tree induced severe symptoms on grapefruit and sour orange seedlings, indicating that he was working with a strain of seedling yellows. If so, the protection afforded by the mild strain against the severe strain suggests virus-strain relationship. However, Fraser (reported elsewhere in this volume) states that in numerous tests, the stem-pitting virus strains studied by her in Australia have failed to protect small sweet orange on sour orange trees against seedling yellows (tristeza). The trees were first inoculated with strains of stem-pitting virus that varied from mild to severe, none of which caused symptoms of tristeza. Four months later, reinoculation from seedling-yellows sources resulted in tristeza symptoms.

Additional studies are required before the question of cross protection between stem-pitting and seedling-yellows viruses can be settled with finality. Even if no evidence can be obtained of cross protection between the two, this will not provide conclusive proof of nonrelationship. Evidence of relationship or the lack of relationship would be strengthened if serological techniques could be applied to these viruses. So far no such studies have been made.

There still remains need for much study of the viruses involved in the various disease types which heretofore have been grouped as one disease, namely, tristeza. Fraser (reported elsewhere in this volume) proposes that the seedling-yellows symptoms are caused only by a virus that causes tristeza, i.e., the decline or death of trees of sweet orange on sour orange rootstock, and that this virus is unrelated to the so-called stem-pitting virus which is present in all yellows infections. Acceptance of this hypothesis poses many puzzling questions. One of these which as yet is unexplained is that in California where many thousands of sweet orange trees have died from tristeza (*5*), no seedling-yellows virus has been found in any of the naturally infected trees (*39*).

To explain some of the contradictions in the findings of workers in different parts of the world in regard to the diseases described as tristeza, stem pitting of grapefruit, and seedling yellows, and to bring agreement as to the relationship of the viruses or virus strains involved in these diseases calls for further exploration. At present, it seems that the true and complete facts have not been revealed. Other possibilities must be explored—possibilities such as variations in growth conditions of the host, interactions between viruses in multiple infections, and influences inherent in reciprocal stock-scion relationships.

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