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Title

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Permalink

<https://escholarship.org/uc/item/1c17z8m3>

Journal

International Organization of Citrus Virologists Conference Proceedings
(1957-2010), 1(1)

ISSN

2313-5123

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Publication Date

1957

DOI

10.5070/C51c17z8m3

Peer reviewed

HOST REACTIONS OF CITRUS TO TRISTEZA VIRUS IN SOUTH AFRICA

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INTRODUCTION

With the discovery, in 1947 (11), that the "incompatibility reactions" between the rootstock of sour orange, *Citrus aurantium* Linn., and most scion varieties of citrus in South Africa are caused by tristeza virus, it became apparent that the causal virus must have been present there since about 1896. That date marks the beginning of commercial citrus culture in South Africa, when trees of several standard varieties were budded on sour orange rootstock and planted in various parts of the country. With the exception of commercial lemon clones, *C. limon* (Linn.) Burm., these trees all died. Subsequent importations of sweet orange, *C. sinensis* (Linn.) Osbeck, on sour orange from the United States of America suffered the same fate. Sour orange was then replaced by Rough lemon, *C. jambhiri* Lushington, which to this day has remained South Africa's main rootstock for practically all its commercial varieties of citrus.

Later work by McClean (8, 9) has shown that tristeza occurs in practically all citrus plants grown out-of-doors in South Africa. Under normal circumstances the disease is perpetuated by clonal propagation from infected parent trees to Rough lemon or other rootstocks, which may have also become infected by means of the viruliferous aphid *Toxoptera citricidus* (Kirk.) even before the budding operation in the nursery took place. It may therefore be said that South Africa's citrus industry has developed in spite of the presence of tristeza, largely as a result of the high degree of tolerance possessed by its chief scion varieties, mainly sweet orange, when combined with Rough lemon and other tolerant rootstocks.

Somewhat conflicting views are held by various research workers as to the origin of tristeza and its subsequent spread to practically all commercial citrus-growing countries (1, 17). Failure in South Africa some 60 years ago of sour orange as a rootstock for most *Citrus* species is perhaps the earliest recorded evidence of the presence of the virus (18), although it does not necessarily follow that South Africa is the country of origin. The Far East, natural habitat of most cultivated species of *Citrus*, appears to have even stronger claims (16, 17). History records that the first citrus trees in South Africa came from the island of St. Helena in 1654, but as early as 1656 there was reference to the progress of citrus trees obtained from India (18). Unfortunately, no further details of the latter introduction are available. It is conceivable, however, that tristeza, accompanied perhaps by its efficient insect vector *Toxoptera citricidus*, reached South Africa from India shortly after the colonization of the Cape of Good Hope by the Dutch began in 1652. The disease is thought to have spread gradually northward to all citrus-growing territories in Africa south of the Sahara, and to have been introduced from South Africa into South America around 1930 in consignments of sweet orange trees budded on Rough lemon rootstock, which are now known to be latent carriers of the virus (12, 17).

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FACTORS COMPLICATING THE HOST REACTIONS OF CITRUS TO TRISTEZA

A simple or clear-cut evaluation of the influence of tristeza *per se* on the various *Citrus* species and varieties grown in South Africa is virtually impossible, since the position is complicated by a number of factors which, either independently or collectively, exert influences on growth, fruit production, and over-all tree physiology. Of these, the following are regarded as being the more important.

Absence of Tristeza-free Orchard Trees. In view of the wide distribution of the virus and its main insect vector in South Africa, there are no tristeza-free orchards available for comparison with infected orchards. Comparisons are restricted to greenhouse plants and to nucellar material that remains free of the virus for only a short while after being planted out in the open. Complications arising from such comparisons will be referred to later in this paper.

Complex Nature of the Virus. Tristeza is a virus complex, and the infection occurring naturally in citrus orchards of even a single variety may vary quantitatively (1) as well as qualitatively (10), and hence is by no means uniform, not even in a single tree. Grant and Higgins (3) recently reported mixtures of tristeza virus strains within the same plant, resulting in varying degrees of protective effects. All these considerations complicate any attempt to evaluate host reactions of different citrus varieties to tristeza infection in the field.

Vector Transmission. Since no uniform tristeza infection occurs in South African citrus orchards, it follows that vector transmission of the disease, especially in the case of virus-free nucellar scion and rootstock material prior to budding, will not result in uniform infection either. This would constitute a further source of variability in virus infection, although it is difficult to assess its possible significance under field conditions.

Variation in Rootstock Material. The Rough lemon known in South Africa must be regarded as consisting of several different strains, rather than as a single or uniform horticultural clone. Rated as a species highly tolerant to tristeza, it is conceivable that different strains used as rootstocks may exhibit differences in this respect, thereby complicating the problem. The Citrus and Subtropical Horticultural Research Station at Nelspruit has no less than 68 selections of Rough lemon under trial, and reports that four of these have already proved to be failures in the nursery as rootstocks for Valencia orange (6). South Africa's "sweet Rough lemon" performs well as a rootstock for sweet orange for several years, but such trees gradually decline and eventually go out of production (8).

Strain Differences in Scion Varieties. It is a fact that bud variation has given rise to strain differences in commercial citrus clones. This feature could likewise exert genetic influence in regard to tolerance shown by the variety to tristeza in the field (12). Considerable variation has been observed in the occurrence of stem-pitting symptoms in Valencia trees in the same orchard. In greenhouse inoculation trials, also, considerable variation has been observed in the reactions of budded trees propagated from nucellar Valencia orange seedlings originating from different parent trees and bud-inoculated with the same source of tristeza. Such differences in host reactions to apparently the same tristeza infection may be due partly to differences in tolerance within the variety or rootstock used.

Coexistence of Tristeza with Other Viruses. In addition to general but variable tristeza infection, it is known that exocortis and xyloporosis are likewise fairly generally distributed in some citrus clones in South Africa (A. P. D. McClean in private communication; unpublished results). While it is believed that these two viruses do not harmfully influence most scions on Rough lemon and sweet orange rootstocks, their coexistence with tristeza in certain clones does result in further variability in virus infection in South African citrus, thereby further complicating the matter.

Root Diseases. South Africa's principal rootstock, the Rough lemon, is fairly susceptible to attacks by dry root rot, caused by *Diplodia natalensis* Pole-Evans, and by brown-rot gummosis, caused by *Phytophthora citrophthora* (Sm. & Sm.) Leonian. According to Loest (5), both are of considerable importance in South Africa, but it is virtually impossible to dissociate their influence in the field from the ever-present tristeza disease. Whereas dry root rot occurs mainly in the summer rainfall areas of the Transvaal, brown-rot gummosis prevails chiefly in the Eastern Cape Province and other areas where the rainy season coincides with the cooler winter and the spring months (5).

Soil and Climatic Conditions. In South Africa, citrus is grown under soil and climatic conditions that are known to exert considerable influence on nutritional factors, rate of growth, and over-all tree physiology. Soil and climate probably bear no direct relation to tristeza influence, but constitute part of the very complex set of conditions under which this virus operates in the citrus orchards of South Africa.

MAJOR HOST REACTIONS OF SOUTH AFRICAN CITRUS TO TRISTEZA

Against the existing complex background, the major host reactions of commercial *Citrus* species to tristeza in South Africa may be summarized as follows.

Sweet Orange, *Citrus sinensis* (Linn.) Osbeck. Despite the presence of tristeza virus with which they had to grow up, South African sweet orange orchards, consisting largely of Washington Navel and Valencia on Rough lemon rootstock, are for the most part highly productive. Supported by results obtained in controlled greenhouse inoculations, it may therefore be concluded that sweet orange on its own roots or on tolerant rootstocks like Rough lemon; sweet orange; trifoliolate orange, *Poncirus trifoliata* (Linn.) Raf.; Rangpur lime, *C. limonia* Osbeck; and possibly others, possesses a high degree of tolerance to tristeza. Failure of sweet orange on rootstocks such as sour orange; grapefruit, *C. paradisi* Macf.; Mexican lime, *C. aurantifolia* (Christm.) Swing.; and commercial lemon provides one of the most spectacular host reactions to tristeza in South Africa. Indifferent reactions or even failures experienced on rootstocks like trifoliolate orange, sweet orange, and Rangpur lime, on the other hand, may result from the presence of other viruses such as exocortis and xyloporosis in the sweet orange scions.

One cannot say with certainty that tristeza has no harmful influences at all on sweet orange budded to tolerant stocks, since there are no tristeza-free orchards available for comparison. In greenhouse trials, bud inoculations with a virulent strain of tristeza resulted in considerable dwarfing of nucellar Valencia seedlings obtained from one parent tree, but had negligible influence on seedlings of another parent tree. Many sweet orange trees of different varieties on Rough lemon rootstock show visual symptoms of stem-pitting in young twigs, and it has been suggested that tristeza may play some part in the relatively short commercial life of sweet orange trees in South Africa (12). Orange varieties like Pera, Mediterranean Sweet, and others are characterized by lack of vigor; further, it is not unlikely that South Africa's "greening disease" (8, 12), which recently made its appearance also on trees of both the Frost and Olinda nucellar Valencia selections, may be a manifestation of tristeza.

Oberholzer and Hofmeyr (12) point to the exceptional performance of century-old seedlings of sweet orange, which, it would seem, have been exposed to the same tristeza infections as the plantings of Valencia and other commercial varieties of sweet orange. In view of this, they are optimistic regarding the future prospects of nucellar lines of commercial sweet orange clones, especially on rootstocks more suitable than Rough lemon. Meanwhile, South Africa enjoys the assurance that sweet orange varieties of good parentage, budded on tristeza-tolerant rootstocks, will develop into commercially productive orchards even in the presence of tristeza virus.

Naartjie: Mandarin-tangerine, *Citrus reticulata* Blanco. Seedling naartjie trees constituted some of the earliest citrus plantings in South Africa, and in many parts of the country century-old seedling trees are still to be found in good health and production (12). At the turn of the century, attention was given to the planting of commercial varieties like Natal Tightskin and Beauty of Glen Retreat, since these were better suited for export markets.

With the exception of certain mandarin varieties, such as Empress, serious decline problems are experienced with many naartjie varieties on tristeza-tolerant rootstocks like Rough lemon, sweet orange, and certain naartjies (12). In contrast, seedling trees, in general, succeed much better, so that many growers now plant seedling orchards. Unfortunately, it is still too early to assess the prospects of nucellar seedlings of varieties like Natal Tightskin and Beauty of Glen Retreat, old lines of which suffer severe decline when grown on tristeza-tolerant rootstocks.

All naartjie material that has so far been tested in South Africa appears to carry a severe strain of tristeza virus, and hence fails as a top on intolerant rootstocks such as sour orange and commercial lemon. Whether this virus bears any relation to the serious decline experienced on tristeza-tolerant rootstocks is, however, unknown at present. Limited inoculation trials in the greenhouse have shown that the common naartjie varieties possess a high degree of tolerance against tristeza; moreover, it has been impossible to distinguish between tristeza infection of declining trees and that present in productive and healthy century-old seedlings in the field. Results like those reported by Olson *et al.* (14) from Mexico, where some declining naartjie trees were found to be free of tristeza, lead one to believe that other factors are probably responsible for such decline phenomena. The fact that Empress and Cleopatra mandarins are being regarded as promising future rootstocks for citrus in tristeza-infected countries (6, 12) is further proof of their good tolerance against this disease.

Grapefruit, *Citrus paradisi* Macf. Grapefruit plantings in South Africa, totaling about 300,000 trees on Rough lemon rootstock, consist mainly of Marsh Seedless and Cecily (a seedless bud sport of Walters) in the Eastern Cape Province, with relatively small plantings of Marsh Seedless, Triumph, and Jackson (a seedless bud sport of Triumph) in the Eastern Transvaal.

Most grapefruit orchards start off promisingly, but soon show decline symptoms, followed by a gradual downward trend in production of fruit of marketable size. The majority of orchards show severe decline by their fifteenth year and usually cease to be profitable at the age of 20 years (13), whereas a small number of orchards have maintained excellent vigor and good cropping even at an age of 25 to 30 years (8, 13). From trees of such orchards a rather mild strain of tristeza has been isolated (8). Typical symptoms on severely diseased trees include the following: extensive twig dieback, small mottled leaves, profuse suckering of rootstock just below the union, and typical stem-pitting symptoms in the scion (8, 13). In severe cases, the wood becomes extremely brittle, with brown coloration due to gum formation. The majority of fruits are undersized and worthless.

Field observations supported by controlled greenhouse inoculations have left little doubt that tristeza is largely responsible for grapefruit decline in South Africa as a result of injury to the grapefruit scion. All grapefruit varieties appear to be more or less equally sensitive to the disease, regardless of the use of tolerant rootstocks. Judged by the reactions of West Indian lime and grapefruit seedling test plants, diseased grapefruit trees invariably carry tristeza virus that causes stem-pitting (9).

Some optimism in respect to future grapefruit culture has resulted from the discovery of mild strains of tristeza in old and relatively healthy-appearing Marsh Seedless and Cecily grapefruit trees in South Africa (9, 12). It is hoped that the presence of mild

strains of the virus may afford some protection against invasion by the more virulent strains, but no confirmatory evidence of this is available so far. Grapefruit scions carrying such mild strains of tristeza virus succeed surprisingly well on sour orange rootstocks, thus indicating that such infection is relatively harmless to sour orange tissue.

McClellan (9) and Oberholzer and Hofmeyr (12) have pointed out the potential value of nucellar material in relation to future grapefruit culture in tristeza-infected areas. Very promising results have been obtained with trees of tristeza-free Frost nucellar selections of Marsh Seedless and Red Blush selections (imported from California in 1948) that were experimentally inoculated with a mild strain of tristeza virus before they were planted in the field in 1952 (12). Up to the present such trees show no effects of exposure to infection with the naturally occurring virus strains, but they are still too young to warrant any conclusions regarding the matter of mild virus strains protecting against more severe strains.

Results obtained by the Nelspruit Research Station (7) indicate that grapefruit may offer promise as a future rootstock for lemons in South Africa.

Lemon, *Citrus limon* (Linn.) Burm. Lemon production from some 250,000 trees, chiefly Eureka budded to Rough lemon, is confined largely to the Eastern Transvaal, which has a summer rainfall and mild winter temperatures. Generally speaking, young orchards show great initial vigor and early, heavy cropping. Gradually, however, there is severe decline similar to that experienced in California and not unlike that previously described for naartjies and grapefruit, with the result that most lemon orchards present a rather dismal picture at the age of 15 years or more (7, 12).

At the present stage of our knowledge, it is difficult to determine the relation of tristeza to lemon decline in South Africa, although Oberholzer and Hofmeyr (12) have concluded that this virus cannot be held responsible for such decline. Early experiences in this country have shown that the commercial lemon is one of the very few species to show satisfactory horticultural compatibility with the sour orange, such trees exhibiting no more decline than those on tristeza-tolerant Rough lemon or sweet orange. McClellan and van der Plank (10) suggest that lemon clones, as well as grapefruit and sour orange, pick up only the stem-pitting component of tristeza to which they are reasonably tolerant. This would explain why lemon varieties succeed reasonably well on sour orange and grapefruit stocks (7, 12); it also lends some support to the suggestion that tristeza is not the major cause of lemon decline in South Africa (12).

Vigorous old lines as well as nucellar lemons are being tested on other rootstocks such as grapefruit and Sampson tangelo, *C. paradisi* X *C. reticulata*, as a means of controlling lemon decline (7). The Frost nucellar Eureka has shown considerable promise, but we need more information before definite conclusions can be drawn. Finally, it is thought, but not yet demonstrated, that regular pruning especially aimed at avoiding overcropping of trees may be very beneficial in correcting lemon tree decline.

When used as rootstocks, lemon varieties such as Lisbon and Eureka generally react in much the same way as sour orange (discussed below).

Sour or Seville Orange, *Citrus aurantium* Linn. Some of the most pronounced and severe reactions to tristeza in South Africa occur under the following circumstances: (a) when field sources of sweet orange, naartjie, and grapefruit are grown on sour orange rootstock; (b) when nucellar seedlings of sour orange are bud-inoculated with infected sweet orange and naartjie tissue; and (c) when buds of field sources of sweet orange and naartjie are inserted into virus-free nucellar budlings of these two species on sour orange rootstock. These severe and well-known reactions

have been described in detail by workers in South Africa, Australia, Java, Argentina, Brazil, and the United States and are undoubtedly the result of direct injury to the phloem tissues of the sour orange by tristeza (15).

Variety and rootstock trials at the Nelspruit Research Station, together with small commercial plantings in several parts of South Africa, show that various strains of sour orange grow well as seedlings. However, when budded to sour orange, sweet orange, or Rough lemon, they show stunting and decline symptoms not unlike those described for grapefruit, excepting that stem-pitting symptoms are rarely found in the wood or bark of sour orange.

Oberholzer and Hofmeyr (12) have suggested that sour orange be re-evaluated as a rootstock for vigorous nucellar and old-line lemon clones, especially under conditions conducive to root and trunk diseases. In Pretoria the author has succeeded in growing fairly vigorous, healthy-appearing nursery trees of Cecily grapefruit carrying a mild strain of tristeza virus, on sour orange rootstock.

Lime, *Citrus aurantifolia* (Christm.) Swing. Limes have not been cultivated on any commercial scale in South Africa. The acid limes, especially the West Indian or Mexican types, are nontolerant to tristeza, and usually suffer rather severe injury and dieback as scions on Rough lemon and sweet orange. No seedling material is available for field study, but it is safe to assume that such material would suffer the same fate as has been reported of seedling-lime orchards in Ghana (4). Decline symptoms follow the same general pattern as those already described for grapefruit. Seedlings of West Indian lime are used as standard test plants for detecting the presence of tristeza in citrus material. Experiments are still in progress to determine whether mild strains of tristeza will have any protective influence in Mexican lime seedlings against invasion by severe strains of the virus.

Trifoliolate Orange, *Poncirus trifoliata* (Linn.) Raf. Information available in regard to trifoliolate orange is confined largely to one strain of *P. trifoliata* in rootstock trials conducted by the Nelspruit Research Station. When grown on Rough lemon rootstock it exhibits typical dwarfing and pronounced overgrowth by the scion at the bud union, but otherwise appears normal.

Experiments at Nelspruit show that trifoliolate fails as a rootstock for most varieties of sweet orange (Valencia excepted), naartjie, grapefruit, and lemon. The presence of exocortis in at least some of the Nelspruit rootstock trials may partly explain these disappointing results. Oberholzer and Hofmeyr (12) emphasized the importance of re-evaluating *P. trifoliata* as a future rootstock for nucellar and old-line material known to be free of exocortis. Such studies have been in progress in Australia for some time (2) and are likely to be of great value to future rootstock work in South Africa.

Citron, *Citrus medica* Linn. At present the citron is not grown on a commercial scale in South Africa. At the Nelspruit Research Station, Etrog and Corsican varieties are usually dwarfed and stunted on Rough lemon rootstock, with dieback and severe stem-pitting symptoms in the scion. It is concluded that the citron is nontolerant to tristeza. At present it is not known whether the citron material available in South Africa is free of the other viruses of citrus.

Kumquat, *Fortunella Swingle.* Kumquats, like citrons, are not grown commercially in South Africa. At the Nelspruit Research Station, kumquat tops on a variety of rootstocks are quite variable, generally failing on Rough lemon, Natal naartjie, and sweet lime, *C. limettioides* Tanaka, but succeeding rather better on Yuzu, *C. junos* Tanaka; calamondin, *C. mitis* Blanco; and *P. trifoliata*. On *P. trifoliata* rootstock some varieties of kumquat give rise to hardy dwarf trees which are sometimes grown for garden use. Little information appears to be available on the behavior of kumquats as rootstocks for other species. Its reaction to tristeza infection is little understood.

Tangelo, *Citrus paradisi* X *C. reticulata*. Included in the variety and rootstock plantings of the Nelspruit Research Station are several imported American varieties of tangelo, such as Minneola, Orlando, Sampson, and Thornton. When grown on Rough lemon and sweet orange rootstocks, they show typical tristeza symptoms such as stem pitting, dieback, and leaf abnormalities, but in general suffer less than grapefruit and acid limes on these rootstocks. As mentioned earlier, Sampson tangelo offers promise as a rootstock for lemons and grapefruit. As with so many other rootstocks, the tangelos, too, need re-evaluation for scion varieties known to be free of exocortis and xyloporosis.

Miscellaneous Citrus Species. The very extensive collection at the Nelspruit Research Station contains numerous other species, hybrids, and types whose reactions to tristeza are not definitely known.

Rootstock trials conducted by the Nelspruit Research Station show that both sweet lime and Rangpur lime fail as rootstocks for most scion varieties, no doubt due partly to the presence of xyloporosis and exocortis in many citrus varieties. Both of these limes therefore need re-evaluation as rootstocks for nucellar clones and old-line clones of citrus known to be free of these two viruses. Sweet lime and Rangpur lime grown on Rough lemon rootstock usually exhibit stunting and fairly severe decline. In view of the probable coexistence of tristeza with xyloporosis and exocortis, it is at present impossible to determine the relation of tristeza to such decline phenomena.

Types such as Japanese citron, Yuzu, calamondin, and others need re-evaluation as rootstocks for scion varieties known to be free of xyloporosis and exocortis.

SUMMARY AND CONCLUSIONS

A critical analysis has been presented of the major host reactions of South African citrus to infection by tristeza virus. It is emphasized that the problem is complicated by many factors which, independently or in combination with tristeza, make a clear-cut evaluation of the influences of the virus *per se* almost impossible. The major factors are the following.

- 1) Because of the widespread distribution of both the virus and its major insect vector, no tristeza-free orchards are available for comparison with infected orchards.
- 2) The complex nature of the virus itself and the lack of uniformity in infection occurring naturally in orchards of the various species and varieties are complicating factors. Further, buds of a single parent tree may carry different strains of tristeza virus.
- 3) The existence of virus strains differing in virulence and occurring singly or in mixtures of two or more strains makes it certain that vector transmission of the virus to rootstocks or other field-grown nucellar material is not uniform.
- 4) Variations in rootstock material may result in differences in tolerance to the virus, which, in turn, may influence the host reactions of orchard trees budded on such stocks.
- 5) Genetical differences in citrus clones, arising through bud variations, may likewise result in different degrees of tolerance to tristeza. Hence it is logical to expect that nursery trees of a given variety may sometimes vary in degree of tolerance to the virus.
- 6) Coexistence of tristeza with the exocortis and xyloporosis viruses in some orchard trees complicates the problem. Furthermore, there are indications that orchard trees of one and the same variety are not uniformly infected with exocortis and/or xyloporosis.
- 7) Rough lemon rootstock is fairly susceptible to several root diseases which are of considerable importance to the general health of our citrus orchards. As a result of climatic conditions, there is considerable variation in the type of root disease prevalent in the different citrus regions of South Africa.
- 8) While probably exerting no direct influences with respect to host reactions to

tristeza, the exceedingly wide range of soil and climatic conditions under which citrus is grown in South Africa is bound to influence growth, nutrition, and over-all tree physiology.

With the foregoing limitations in mind, the author lists the following as representing the major host reactions of citrus to tristeza virus in South Africa.

A) The relatively healthy condition and good general performance of nucellar seedlings of sweet orange, Rough lemon, sour orange, and some naartjie varieties, and of most sweet oranges, Rough lemon, and some naartjies as scions on tristeza-tolerant Rough lemon and sweet orange rootstocks are attributed directly to the high degree of tolerance possessed by such material. At present it is not known whether tristeza bears any relation to decline phenomena encountered in certain varieties of sweet orange and naartjie when grown on tristeza-tolerant Rough lemon and sweet orange rootstocks.

B) Severe injury, usually resulting in serious decline and relatively short economic life of grapefruit, citron, and Mexican lime on Rough lemon rootstock, is apparently due to the direct effect of the virus on the sensitive tissues of the three scion species referred to. The presence of mild strains of the tristeza virus may afford varied degrees of protection against invasion and injury by more severe strains of the virus.

C) General failure of sour orange, grapefruit, commercial lemon, and certain tangelos as rootstocks for sweet orange and naartjie is apparently due to severe injury by tristeza present in the scion variety to the intolerant rootstock tissues of the species concerned. On the other hand, scions of grapefruit and commercial lemon, especially those carrying relatively mild strains of tristeza, succeed fairly well on the above-mentioned rootstock types.

D) Critical analysis of the available evidence makes it doubtful whether tristeza plays any major role in the serious decline problems experienced with Eureka and Lisbon lemons budded to all common rootstocks in South Africa.

ACKNOWLEDGMENTS

The author is indebted to Dr. R. H. Marloth and Mr. W. J. Basson for placing at his disposal results obtained in rootstock and variety trials conducted by the Citrus and Subtropical Horticultural Research Station, Nelspruit, Union of South Africa. Appreciation is also expressed to Dr. A. P. D. McClean and Mr. A. H. P. Engelbrecht, Division of Plant Pathology, Department of Agriculture, Pretoria, for information supplied in regard to the occurrence of exocortis and xyloporosis viruses in South African citrus.

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