Agro-ecology and Centers of Origin of Graft-transmissible Diseases of Citrus

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ABSTRACT. Citrus and other members of the Rutaceae appear to be susceptible to a relatively small range of viruses compared to several other families of cultivated plants. The occurrence of many virus diseases in citrus is correlated with cultivation from ancient times, vegetative propagation and worldwide exchange of germplasm. Knowledge on the centers of origin and diversification of virus and virus-like diseases could provide useful information to aid prevention of spread of new diseases.

The main centers of origin of citrus are in Asia, and there is evidence that tristeza, tatter leaf and satsuma dwarf viruses, and the greening bacterium originated in Asia. Later diversification of citrus occurred in other regions, and diseases such as impietratura, cristacortis, and stubborn may have originated in the Mediterranean region. The citrus leaf rugose and variegation ilarviruses were first found in North America and are related to other viruses present mainly there and in Europe, suggesting that one of these areas may be its center of origin.

Most virus and virus-like diseases of citrus are complex, and their agents difficult to identify. Only a few diseases are clearly associated with specific, well identified viruses (15), such as citrus tristeza closterovirus (CTV), citrus leaf rugose virus (CiLRV) and citrus variegation virus (CVV), both ilarviruses.

Other diseases have been found associated with a luteovirus (citrus vein enation, CVEV) (11), a rhabdovirus (citrus leprosis, CiLV) (15), a capillovirus (citrus tatter leaf, CiTLV) (33), and a neopvirus (Satsuma dwarf virus, SDV) (15). Citrus psorosis and ringspot are associated with unusual filamentous particles (13). Several viroids have been found in citrus (39), and different fastidious prokaryotes have been associated with diseases such as greening (CGD) (17), citrus stubborn (CSD) (34), and witches' broom disease of lime (WBDL) (18). The etiology of some other diseases such as impietratura, cristacortis and blight remains unresolved.

The purpose of this paper is to consider the susceptibility of citrus to these pathogens, and to consider probable centers of origin, with special reference to the citrus ilarviruses.

SUSCEPTIBILITY OF CITRUS TO VIRUS AND VIRUS-LIKE DISEASES

When comparing the field susceptibility of citrus to its pathogens, with that of many other cultivated plants it becomes evident that citrus is affected by a smaller range. Of the 35 groups of plant viruses, only 6 have definite or probable citrus infecting members. In addition there are the unclassified psorosis virus, the filamentous Algerian navel orange virus (20) and citrus yellow mottle virus (42). Only two other viruses have been reported to be able to infect citrus, tobacco necrosis virus (48) and potato mottle virus, a strain of potato virus X (25). *Citrus medica* has been indicated susceptible to cucumber mosaic virus (40), but this was a misinterpretation. The original report refers to African stock citron which is *Citrullus lanatus* var. *citroides*. The only viruses reported from other rutaceous plants are arabis mosaic and cherry leaf roll from *Ptelea trifoliata* (38, 36), tobacco ringspot from *Skimmia* sp. (44), alfalfa mosaic and the unidentified, soilborne, hardy primrose virus from *Ruta graveolens* (37, 41). Common rue can also be locally infected with tobacco rattle virus (35). Thus of the 700 or so plant viruses known (31), less than 3% are known to infect Rutaceae. Few viruses have been reported infecting other Geraniales close to Rutaceae, such as Meliaceae, Simaroubaceae and Burseraceae.

Field susceptibility of plants is often related to individual plant susceptibility and the inoculum potential. With citrus the inoculum usually comes

from other citrus, but may come from other non-citrus plants, as has been suggested for SDV (28) and stubborn (6).

While many virus diseases are insect transmitted, especially those of seed propagated herbaceous plants, few citrus diseases have such vectors. There is a similar situation with other trees and shrubs (30). Indeed only a few virus and virus-like diseases of citrus have important agro-ecological components, bound mainly to natural vectors and possibly to alternative hosts. The majority of graft-transmitted citrus diseases are connected with human activity, especially vegetative propagation, graft and pruning, a long history of cultivation and worldwide exchange of germplasm. Some citrus diseases have become very destructive, for example CTV, because in addition to being "largely a man-made problem" (5), they are actively insect transmitted.

CENTERS OF ORIGIN AND DIVERSIFICATION OF CITRUS VIRUS AND VIRUS-LIKE DISEASES

While the origins of many plant viruses are very old, probably around 300 million years ago, the majority of virus diseases of cultivated plants have originated relatively recently, mostly during the last few centuries (29). Some citrus diseases such as WBDL in Oman and citrus variegated chlorosis (CVCD) in Brazil, appear to be only a decade or so old.

Some plant and animal ssRNA viruses share sequence homology among nonstructural proteins as well as other similarities, suggesting a common origin (22). Evolution of viruses may have occurred 200 to 300 million years ago, periods very important for the coevolution of plants, insects, and nematodes. Variation rates in viral RNA can be quite rapid. Replication errors are of the order of 10^{-3} to 10^{-5}, against 10^{-8} to 10^{-11} for chromosomal DNA. This leads to production of mutant viruses (see 29). Experimentally obtained mutants are well known for some plant viruses. Generally mutants are picked up, and maintained through new host plants, new vectors or altered climatic conditions. For citrus, the chances of acquiring mutants are higher for viruses with vectors or alternative hosts, such as CTV and SDV. Mutants can also be selected and maintained after graft transmission to different species or cultivars. Weeds may be the original sources of vector borne diseases such as stubborn and witches' broom, and possibly citrus variegated chlorosis. Some vector borne diseases may originally have been diseases of the vector, for example leprosis and greening.

In seed propagated herbaceous plants a newly acquired disease agent may not move to other plants if it is not seed or pollen transmitted and may be lost if a vector does not spread it to other plants. With the vegetative propagation of citrus, an occasional infection, which may not cause noticeable symptoms, can be spread by grafting. Many citrus species are symptomlessly infected by viruses, but transmission to sensitive types can result in severe symptoms. The chance of survival is higher for viruses that have vectors or alternative hosts.

While present quarantine regulations, variety improvement programs and eradication schemes may reduce the probability of new diseases appearing and spreading, it is difficult to prevent them altogether. Most citrus diseases probably coevolved with citrus in its centers of origin and diversification, which generally are also the centers of origin of their diseases. In the case of introduction of citrus in new areas, it may be useful to study the susceptibility of citrus to the virus and virus-like disease agents prevailing in that region, that could possibly infect citrus plants.

The centers of origin of most cultivated citrus species are in Asia (49). CTV, CiTLV and CGD probably originated in China (5, 46, 10), and SDV in Japan (28). SDV may have an older association with China laurestine (*Viburnum odoratissimum*) since is symptomless in this species, generally

an indication of an old association. CiTLV is a capillovirus serologically related to apple stem grooving virus (33), and readily mechanically transmissible to non-rutaceous plants. It has been found in Japan infecting lily symptomlessly (26).

Some other virus-like diseases of citrus, mainly citrus leathery leaf (3), citrus mosaic disease (2), and citrus rubbery wood (1), probably originated and are still present only in India. The first two have been reported to be aphid-transmitted and if introduced in other countries they might spread rapidly.

Diversification of citrus has occurred outside Asia as worldwide spread occurred. Lemon and sweet orange had secondary centers in the Mediterranean Region (49) and grapefruit, in the West Indies (21). Concave gum, cristacortis and impietratura my have originated in Mediterranean countries. The same may be in the case of CSD (6). Citrus ilarviruses also probably originated outside Asia, and they warrant special attention.

POSSIBLE ORIGIN OF CITRUS ILARVIRUSES

It has been estimated that about 13% of the virus and virus-like diseases of woody plants in Italy are caused by ilarviruses, while they constitute only about 2% of the diseases of seed propagated herbaceous plants (30).

Ilarviruses share a number of important properties: i) They mainly cause diseases in trees and shrubs - of the 16 distinct ilarviruses (32), 10 have mainly woody natural hosts; ii) Except tobacco streak virus, they all have narrow natural, but wide experimental, host ranges; iii) They are frequently symptomless above 26 C; iv) They are frequently pollen and seed transmitted, but have no active vectors, and this often reduces their importance as plant pathogens; v) some can be mechanically transmitted through infected pollen with the help of thrips (24).

Citrus ilarviruses are spread by vegetative propagation (47) Normal pollen transmission has not been detected, but seed (12) and anthers (23) do carry CVV. It should be possible, as happens for other ilarviruses, that infected pollen and thrips can transmit citrus ilarviruses. Even if this event is rare, it could explain the origin of ilarvirus diseases in citrus.

CVV and CiLRV both belong to ilarvirus subgroup 2 (43) together with Tulare apple mosaic (TAMV), elm mottle and asparagus virus II, all serologically related. Perhaps in the evolution of these viruses some variants arrived in citrus through pollen with the help of thrips or bees, and once in citrus have been propagated by man.

If this is how CVV and CiLRV were introduced into citrus, then it is possible that the agents of other diseases such as cristacortis, which is present in the pollen (45), impietratura and concave gum were introduced in the same manner. This may explain why there appears to be no natural means for further transmission of these agents.

Ilarviruses may be more common in wild plants than reported, because often they are latent or cause symptoms only during a short period of the year (generally in spring under temperate conditions). Parietaria mottle virus has been present in the author's garden for many years, causing symptoms only for a short period, before it was described (7).

The origin of a new disease in one plant through infected pollen from a different species may be a rare event that requires a second means of spread, such as vegetative propagation, for maintenance of the new disease. TAMV, first described in 1955, and isolated from a single apple tree in Tulare County, California, has never been found again in apples (16), but a most similar virus was isolated in France, 20 yr later, associated with hazelnut mosaic (8).

CVV was first found in California (14) and CiLRV in Florida (19). The former has been found mainly in lemon growing areas. They are both serologically related to all the members of subgroup II of ilarviruses, present mainly

in North America and Europe. This suggests that CiLRV and CVV are not of Asiatic origin and probably originated in North America or in the Mediterranean region.

DISCUSSION

While members of the Rutaceae are not highly susceptible to a wide range of viruses, many of the diseases of citrus are threatening and destructive. This is especially true for vector borne diseases such as tristeza, greening and stubborn. New potentially destructive diseases have recently appeared, CVCD in Brazil (9) and WBDL in Oman (18), both probably insect transmitted. Today diseases without vectors can be well controlled through quarantine measures and certification schemes.

From the past history of citrus virus and virus-like diseases, we may learn lessons for the future management of disease prevention, which should be based mainly on exclusion (27). One important type of exclusion is to avoid the origin, or at least avoid the spread of a new disease.

Citrus cultivation throughout the world is increasing. Aubert (4) forecasts that during the last decade of the twentieth century there will be a need for 340 million new trees in South East Asia alone. Since this is in the main centers of origin for citrus, it is possible that new diseases could arise.

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