Virus and Virus-Like Diseases of Citrus and Their Impact on Citrus Production and Germplasm Selection

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Abstract. Numerous virus and virus-like diseases affect citrus. Some of the virus, viroid and procaryotic causal agents have been well characterized, but most remain poorly defined. The vector-borne tristeza, greening and stubborn diseases are serious, widespread problems which often limit production in many areas. Virus and virus-like pathogens are transmitted by propagation, by insect vectors, by seed, and mechanically. In some cases the means of natural spread remain unknown. Symptoms vary according to pathogen strain, the host and environment. Graft inoculation of specific indicator plants is still the main identification procedure; however, rapid progress has been made recently with serology and nucleic acid analysis techniques. Control procedures include eradication, certification, use of tolerate or resistant varieties, cross protection, shoot-tip grafting, thermotherapy, and chemotherapy. The complexity of disease factors complicates the already difficult problem of developing useful new citrus varieties.

INTRODUCTION

Virus and virus-like diseases have had a major impact on citrus culture and often are a limiting factor for economic citrus production (38). These diseases may be lethal, e.g. citrus tristeza virus (CTV) in susceptible hosts (Fig. 1A). Over 50 million trees have been destroyed by CTV in the past 40-50 years, and greening has devastated citrus industries in several Asian countries. Less obvious but economically significant effects of virus-like diseases are the subtle, nonlethal responses such as reduced tree vigor and/or yield. In many cases, this damage is largely unrecognized or attributed to other causes such as nutrition, etc. Citrus virus and virus-like diseases may also limit the choice and distribution of certain citrus cultivars. For example, CTV-sensitive varieties are avoided in areas with severe forms of CTV. In some cases, grower prefer-ence has gradually developed without recognition of the disease factors affecting selection.

Continued economic production of citrus and development of new cultivars and germplasm resources require appropriate recognition of the impact of virus and virus-like diseases. This paper briefly outlines the more significant virus and virus-like pathogens of citrus, their transmission, detection, host interactions, and control. The term "virus-like" is used to include several pathogens once considered viruses, but now recognized to be viroids or procaryotes, as well as a number of uncharacterized agents presumed to be viruses on the basis of symptoms and transmissibility. Diseases which have been called virus-like without evidence for infectivity will not be covered in detail. Selected references are cited which can be consulted for additional detail.

VIRUS AND VIRUS-LIKE CITRUS PATHOGENS

Viruses. The most important well-characterized virus is citrus tristeza virus (CTV). This important virus presumably originated in Asia, but is now endemic in most major citrus-growing areas except portions of the Mediterranean Basin, portions of the U.S., Mexico and Cuba (5, 7, 38). Biologically different isolates of CTV occur which cause mild to very severe symptoms in different hosts. It is vectored with varying efficiency by several aphids (5). Two major disease conditions are produced by CTV. One is the classic CTV-induced decline of sweet orange, mandarin and grapefruit scions grafted on sour orange rootstocks. Necrosis of the phloem at the

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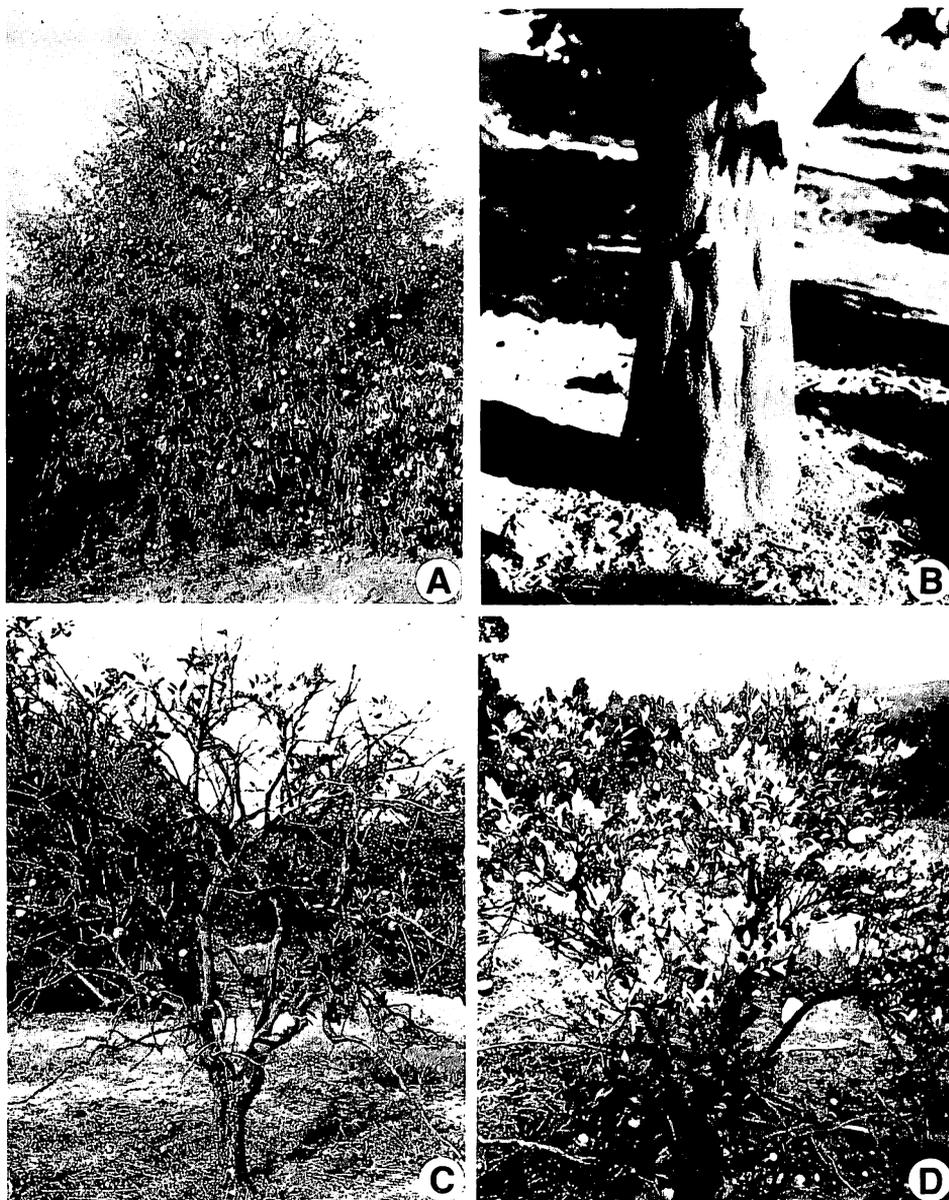
Fig. 1. Symptoms of several important virus and virus-like diseases. A) Severe quick decline symptoms in sweet orange tree on sour orange rootstock caused by citrus tristeza virus, B) tristeza-induced stem pitting in trunk of Marsh grapefruit, C) orange tree naturally infected with severe psorosis (ringspot) agent in Argentina, and D) greening symptoms in Tankan mandarin tree in Taiwan.

budunion restricts carbohydrate move-
ment to the roots and leads to tree
decline (38). Trees may decline slowly
or very suddenly (quick decline). The
other CTV-induced disease is stem
pitting, a severe problem in many
areas for limes, grapefruit (Fig. 1B),
and some sweet orange varieties, re-
gardless of rootstock (32, 38). Certain
rootstocks, such as Alemow, are also
severely affected. Stem pitting is not
lethal, but when severe it debilitates
the tree, reduces fruit size, and causes
extensive losses (32).

Other well-characterized citrus vi-
ruses include satsuma dwarf (SDV),
citrus variegation (CVV) and citrus
leaf rugose (CLRV) (7). SDV has been
a significant problem in some areas of
Japan and seems to spread slowly
there (24). Citrus mosaic, navel or-
ange infectious mottling, and Natsu-
daidai dwarf viruses are apparently
related to SDV (24). CVV and CLRV
are not currently regarded as major
problems for citrus production but
should be recognized and avoided
(23). Circumstantial evidence suggests
that natural spread of CLRV can oc-
cur in Florida (23).

The tatter leaf-citrange stunt causal
agent, presumably a rod-shaped, me-
chanically transmitted virus, is not
well characterized, and the presence
of more than one component has not
been completely clarified (24, 38). This
virus has been recovered in Japan and
the U.S. from citrus imported from
China (22, 24), but its distribution and
effects on production in China are not
well known. Although it is of limited
distribution in the U.S. and Japan and
natural spread has not been reported,
tatterleaf-citrange stunt causes con-
cern because of the devastating stock-
scion incompatibility it produces in
trees grafted on trifoliate orange or
citrange rootstocks. If a vector for tat-
ter leaf-citrange stunt exists in China,
use of susceptible rootstocks in other
areas may pose unrecognized risks.

The psorosis complex includes a
group of diseases with poorly charac-
terized causal agents. These diseases
are all associated with chlorotic leaf
patterns in young leaves which usu-
ally fade as the leaf matures plus var-
ious trunk and limb symptoms (15, 20,
21, 38).

One component of the psorosis com-
plex, psorosis B, is considered similar
to citrus ringspot by some workers
(36). The ringspot agent is mechan-
ically transmissible to herbaceous
plants, filterable through 0.22 μ mem-
branes and sediments in centrifugal
fields normal for other plant viruses,
but it is unstable and its particle mor-
phology has not been determined. Cit-
rus ringspot is of significant interest
because natural spread of unknown
means has been observed in Texas,
Argentina, and apparently in Florida
(9, 36, Timmer, unpublished). Bark-
scaling lesions debilitate affected trees
and cause decline (Fig. 1C). Currently,
a tree decline from ringspot is a major
problem in Argentina (9) and is re-
garded as a serious potential threat to
Texas and Florida.

Psorosis A causes less virulent leaf
symptoms and bark scaling than pso-
rosis B or ringspot and does not pro-
duce persistent leaf symptoms or fruit
symptoms. Concave gum and blind
pocket forms of psorosis are associated
with an "oak leaf" type of leaf pattern
and deformations of the trunk or ma-
jor limbs often with localized gum
impregnation (38). Cristacortis and
impietratura are somewhat similar dis-
eases which occur commonly in old-
line citrus in the Mediterranean area
(38) and have also been associated
with chlorotic leaf patterns (7, 10, 38).
Cristacortis causes stem pitting in
some varieties and impietratura in-
duces gum pockets in the fruit albedo.
Natural spread of these diseases has
been suspected, but remains unproven.

Woody gall (vein enation) is an
aphid-vectored virus which has not
been well characterized, but it is wide-

spread in many citrus-growing areas (38). It causes galling on the trunk of susceptible rootstocks such as rough lemon (38), but generally is not considered a major production problem.

A number of other virus-like diseases have been described, including leprosis, leaf curl, yellow vein, yellow corky vein, gummy pitting, dweet mottle, multiple sprouting, Tarocco pit, and a factor which causes stem pitting in Milam lemon and mandarin hybrids in Florida (20, 23, 38). These diseases generally are not well characterized and have been of limited distribution and importance.

Additional citrus viruses probably will be discovered. A mechanically transmitted agent has been found in some selections of navel orange imported into Florida many years ago. This presumed virus produces symptoms in several herbaceous hosts, but not recognizable symptoms in citrus (23). Other latent viruses may not be recognized until introduced into reactive germplasm.

Viroids. Citrus exocortis disease was originally considered to be caused by a virus, but extensive research has shown that it is caused by a viroid (34). The small, infectious RNA molecule has been extensively characterized biochemically, but as yet its mode of replication and mode of biological interaction with the host to produce symptoms are not known (34).

In susceptible cultivars, CEV causes stunting and chlorotic or necrotic bark and leaf symptoms associated with localized tissue necrosis in the cortex (15, 20, 38). Many citrus species and cultivars, including most commercial scion varieties, are symptomless. Symptoms are formed in trifoliate orange, sweet lime, Rangpur lime, Etrog citron, and some trifoliate orange hybrids as seedlings or in grafted combinations with these varieties as rootstocks. Shell bark symptoms in lemon trees have also been associated with CEV infection (15). The primary eco-nomic effect of CEV is dwarfing of trees grafted on susceptible rootstocks which is frequently associated with scaling of the rootstock bark.

Since CEV-sensitive rootstocks are used extensively worldwide, CEV has important implications for citrus production. The effects of CEV are rarely lethal and the degree of stunting varies with different isolates. Many different strains exist and use of milder forms of CEV has been proposed to produce dwarfed citrus trees for high-density plantings (15).

Although CEV is spread as a contaminant on mechanical pruning and hedging equipment, the hazards to full-size trees are not great, and the primary concern is with CEV infection in nurseries and young plantings.

Recent circumstantial evidence suggests that xyloporosis (cachexia) may also be caused by a viroid, although the causal agent has not been characterized (28). Xyloporosis affects several mandarins and mandarin hybrids, Rangpur lime and sweet lime. It may also cause mild symptoms on rough lemon. Symptoms include several forms of wood pitting plus formation of gum pockets with the bark (38). Severely affected trees are stunted and show chlorosis similar to that induced by other girdling diseases. A similar disease called fovea has been described in Murcott tangerines (21).

Procaryotic pathogens. Stubborn, once considered a virus disease, is now known to be caused by *Spiroplasma citri*, a wall-free procaryote with an extensive host range which can be vectored by several leaf hoppers (6, 7, 20, 26, 38). *S. citri* has been cultured and extensively characterized. Stubborn severely stunts trees which are infected when young, and severely reduces yield and fruit quality. It is a major problem in arid regions of California and North Africa, Turkey and Iran, but has not been a problem in cooler areas or humid tropical regions such as Florida. Control of stubborn is a

major problem in areas with high vector populations and reservoirs of inoculum in other hosts since orange, mandarin, mandarin hybrid and grapefruit cultivars are stongly affected. Lemons, limes and trifoliate orange show some tolerance, but, in general, use of host tolerance for control is not promising.

The causal agent of greening is a walled, gracilicute-like procaryotic organism (6, 7) which has not yet been cultured or characterized. A number of diseases have been described which are apparently all synonymous with greening. These include leaf mottling (Philippines), citrus vein phloem degeneration (Indonesia), citrus dieback (India), and likubin and yellow shoot (China) (7, 19, 37, 38, 40). High and low temperature forms of greening have been reported and two species of citrus psylla, *Trioza erytreae* Del Guercio and *Diaphorina citri* Kuway, are vectors. Trees affected with greening initially show various leaf mottle patterns characteristic of phloem degeneration and have small, poorly colored fruit. Initial symptoms may be confined to one or more limbs, and the Chinese name of yellow shoot (Huanglongbing) (Fig. 1D) is descriptive (40). Affected trees subsequently die back and may also be attacked by secondary pathogens (38). The greening pathogen does not move rapidly within the plant and the extent of decline in individual trees is apparently related to extent of the initial infection and subsequent vector activity.

Devastating losses have occurred to commercial citrus plantings in China, Indonesia, India and the Philippines, where the greening agent has been introduced and significant populations of the vector exist. Commercial citrus production rapidly becomes impossible without control efforts in severely affected areas. Most citrus scion varieties are severely affected and varietal tolerance is not an effective control.

A procaryotic pathogen has been suggested as the cause of Australian citrus dieback, but the association remains unproven (14).

Declines of unknown etiology. Blight is a serious decline problem of citrus in Florida associated with a pronounced xylem dysfunction (7, 35). Trees are not affected until 6 or more years old. Blight occurs on all common rootstocks, but rough lemon, Rangpur lime and trifoliate orange are especially susceptible. Blighted trees have delayed growth flushes, do not take up water by trunk injection, often accumulate Zn in the trunk, and form numerous amorphous plugs in the xylem (7). Similar diseases have been reported in Brazil (declinio), Argentina (declinamiento), Cuba, and South Africa. Several pathogens including CTV and fastidious, xylem-limited bacteria have been suggested as possible causes, but no cause has been definitely established. Blight has not been propagated or bud transmitted, but may have been transmitted recently by root grafts.

TRANSMISSION

Knowledge of transmission of citrus virus and virus-like diseases is important for developing adequate control strategies. Most citrus virus and virus-like agents are readily transmitted or perpetuated by grafting, and long-distance movement of citrus virus and virus-like pathogens has often occurred through propagation (5). Phloem-restricted pathogens such as the causal agents of tristeza, stubborn and greening are graft transmitted only when phloem is present in the inoculum and a vascular union is completed between donor and receptor tissues. Several pathogens such as tatterleaf and citrange stunt may be graft-transmitted inconsistently because of irregular distribution.

Seed transmission of psorosis has been demonstrated in trifoliate orange and several citranges, but is rare in other cultivars (38). No other citrus viruses are known to be seed trans-

mitted, but seed transmission of greening has been suggested (40).

Several virus and virus-like pathogens are vectored by various insects. Tristeza and woody gall viruses are vectored by several species of aphids (5, 38), stubborn by several leaf hoppers (8, 26), and greening by two psyllas (1, 7). The most efficient vector of CTV, *Toxoptera citricida* Kirk., and the vectors of stubborn and greening are not present in some major citrus-growing areas such as Florida, and quarantines are valuable to reduce hazard of importing these pests.

Natural spread of satsuma dwarf, citrus ringspot and citrus leaf rugose has been observed, but the vector(s) remains unknown. The extensive natural spread of ringspot in Argentina is a problem of major concern (9).

A number of viruses can be transmitted by sap (mechanical) inoculation (7, 15, 23, 24, 39) and this is commonly used for experimental purposes. Transmission of CEV as a contaminant on cutting tools has been important in the dissemination of this pathogen (29). Contamination is a possible explanation for the observed movement of several other virus pathogens in the field, and has been demonstrated experimentally (29).

No transmission of citrus virus or virus-like pathogens by nematodes has been demonstrated. Spread of satsuma dwarf is apparently soil associated; the vector is unknown (24).

VIRUS-HOST INTERACTION

The relationship between pathogen and host is often poorly understood, especially for poorly characterized pathogens, yet this relationship is often highly important for understanding virus diseases and for developing adequate controls. More information is becoming available on the interaction of viruses with their citrus hosts with development of sophisticated, quantitative assay procedures for several citrus pathogens (4, 7, 14, 16, 17, 30, 31).

Symptom severity may be independent of the degree of virus replication. Essentially symptomless plants may support extensive virus replication, whereas plants with strong symptoms may contain only a low titer of virus. However, symptoms of CEV infection apparently are correlated positively with viroid titer.

The symptomless condition is sometimes confused with resistance when evaluating new germplasm. In resistant or immune plants, the pathogen fails to replicate or does so only at a low rate (12). In contrast, tolerant plants are susceptible to infection and support virus replication. Recently, some useful modifications in terminology of plant response to virus infection have been proposed (12).

Virus isolates can also vary specifically in their effect on individual hosts, and generalizations on pathogen severity based on a single host may be misleading. For example, a CTV isolate may be mild in some hosts and severe in others (3, 38).

Viruses replicate in their citrus hosts primarily during flushes of new growth, and virus concentration often drops rapidly as tissues mature (18). The net concentration of virus present is the differential between concurrent synthesis and degradation processes and is affected by environmental conditions. Some pathogens reach highest concentrations or maintain their concentration longer under cool conditions, whereas warm conditions favor replication of CEV and stubborn. The dynamics of replication are important to indexing, transmission, and control of virus-like pathogens.

Some pathogens are consistently restricted to particular tissues such as phloem, and such tissues are the reservoir of these agents for isolation or transmission.

Some pathogens such as tater leaf-citrange stunt and ringspot invade their hosts erratically with no clear tissue association. Some parts of the

plant may be infected and show symptoms while nearby tissues remain virus-free and the pattern may vary from flush to flush. We have also experienced erratic results in recovering CTV from systemically infected grapefruit trees (18), but variations in replication of CTV in this host are not well understood.

The consideration of host-pathogen interaction is further complicated by the use of numerous rootstock-scion combinations. Germplasm resistant or tolerant to a given virus as a seedling may form a disease-susceptible combination when grafted on certain rootstocks and/or scions. Sweet orange is usually considered CTV tolerant, but when grafted on sour orange, it forms a tree susceptible to CTV-induced decline. Trifoliate orange is resistant to infection by tatter leaf-citrange stunt, and sweet orange is a tolerant host of this pathogen, but sweet orange trees grafted on trifoliate orange rootstocks are severely affected. Thus, new germplasm sources need to be evaluated for virus reaction in the anticipated stock/scion combinations, and designations of resistance and susceptibility must be used precisely for the components and the combination plant.

IDENTIFICATION

The classic means of identifying virus and virus-like infection in citrus are symptoms exhibited in the field or in graft-inoculated citrus indicator plants (11). Although extensive improvement in use of citrus indicator plants has been made, especially for CTV and CEV, these procedures still require extensive time, good plant material and skilled personnel. Identification of mild isolates and interpretation of mixed virus infections are also problems. Development of rapid, sensitive identification procedures has often been the key to rapid progress on pathogen characterization and disease control.

Herbaceous indicators have been used for some mechanically transmitted citrus viruses (7, 11, 24, 39) and can speed and improve specificity of identification. Herbaceous indicators may also detect unsuspected, latent infections not revealed by citrus indicators (23).

Electron microscopy has been used effectively for identifying CTV infections, and the immune or serologically specific electron microscopy procedure is especially effective (16, 17). Electron microscopy of thin sections was also important for diagnosis and characterization of the causal agents of stubborn and greening infections (6).

Light microscopy of stained viral inclusions has been used effectively for CTV detection and provides a convenient, rapid procedure requiring a minimum of facilities or equipment (17). Use of fluorescent antibody techniques also appears promising (16).

Extensive progress has been made in serological detection of citrus viruses and S. citri (4, 16, 18, 31). Good antisera have been prepared to CTV, SDV, citrus variegation, citrus leaf rugose, and S. citri. Use of these sera in various labeled antibody procedures, especially enzyme-linked immunosorbent assay (ELISA), provides sensitive, specific and rapid identification. The ELISA procedure has been used extensively for CTV detection in a number of countries, and over 1 million trees have been tested. Further improvement in serological procedures is anticipated. Monoclonal antibodies have been prepared recently to 3 citrus viruses, and further work is in progress to develop specific antibodies to additional citrus pathogens.

Recently, diagnosis of virus infection based on direct detection of the pathogen nucleic acid (2) or analysis of replicative forms of these nucleic acids (dsRNA) in tissue extracts (13) has been reported. Complementary DNA (c-DNA) has been prepared to nucleic acid fragments of CEV and CTV and cloned (30, 37). Cloned c-

DNA, radioactively labeled, has been used experimentally in dot-blot hybridization procedures for identification of these pathogens.

While extremely rapid progress is being made in detection procedures, problems still remain in correlating biochemical and serological analysis with specific biological properties. For example, CTV antisera developed so far are not strain specific and do not indicate the biological properties of the isolate detected (16).

CONTROL

Many strategies have been used to control virus and virus-like diseases of citrus. The selection and probable success of a particular strategy must be evaluated from knowledge of the disease, its cause and its mode of dissemination.

Eradication or suppression programs are used in some situations where infection is limited and can be detected and eliminated. This approach is currently used against CTV in Israel and parts of California where the level of CTV infection is low and has been facilitated by ELISA (16).

Use of virus-free budwood and budwood certification programs are highly effective for viruses which are spread primarily by propagation, such as much of the psorosis complex, exocortis, and xyloporosis. Virus-free budwood can be obtained by growing nucellar seedlings, by heat therapy and shoot-tip grafting. The latter procedure is an excellent approach to rapidly obtaining virus-free, horticulturally characterized plants (25), and will be useful in safe transfer of germplasm between countries. In some cases, a combination of heat therapy and shoot-tip grafting is necessary to eliminate all pathogens (27). Certification is also useful to control accidental introduction of vector-borne pathogens, but it is not effective after the pathogens become well established and extensively vectored unless combined with other procedures.

Tolerant or resistant varieties have been used effectively to control CTV decline when field infection is widespread (38). Rough lemon, Rangpur lime, trifoliate orange, Cleopatra mandarin, and various trifoliate orange hybrids are rootstock substitutes for sour orange which allow commercial citrus production in the presence of CTV. Development of additional new tristeza-tolerant stocks is also feasible, but a major problem is to combine CTV resistance or tolerance with all the other factors needed.

Overcoming severe, CTV-induced stem pitting poses an even greater challenge since horticulturally acceptable substitutes tolerant to pitting are not yet available (32). A long-range potential exists to incorporate the CTV resistance found in trifoliate orange into scion varieties through a multistep hybridization program (16).

Mild strain cross protection has been used as one more immediate solution to the CTV stem-pitting problem, and millions of "protected" Pera orange trees are currently grown in Brazil (13). Beneficial effects have also been obtained in lime and grapefruit through cross protection (3, 15, 38). Accurate, reliable use of cross protection requires extensive research and some precautions to prevent undesirable effects. Other factors such as vector management or reduction of inoculum potential may be needed to maintain the benefits of cross protection under severe challenge pressure.

Stubborn and greening also pose difficult control problems because they are naturally vectored, and adequate sources of host tolerance or resistance are not available and may be difficult to develop.

Antibiotic treatments have been used to obtain temporary remission of symptoms and are used commercially against greening (33). This approach, however, is not a permanent solution and involves other problems, including cost, phytotoxicity, avoidance of

residues and development of antibiotic-resistant strains.

Limited distribution of these procaryote pathogens within the host suggests that strain cross protection probably would not work even if attenuated forms of these agents were found or developed.

The key to control of these diseases probably is the inefficiency of the vectors and, in the case of greening, that the inoculum reservoir is apparently only infected citrus. Preliminary results suggest that a combination approach to control which incorporates 1) use of disease-free budwood and rootstocks for propagating new plantings, 2) elimination of existing infected trees from areas around new plantings, 3) suppression of vector populations during periods favorable for transmission, and 4) periodic inspection and roguing of any diseased plants from new plantings, can be effective in containing greening and allow reestablishment of commercial citrus in affected areas (19). Unfortunately, this program is difficult to establish in areas with small-plot agriculture, uneducated growers and limited technical resources.

The presence of alternate hosts for *S. citri* presents additional headaches for control of stubborn. It appears that the greatest stubborn hazard is to young plantings, and it is important to establish and maintain these disease-free for a few years to minimize damage (8). Use of trap plants and other vector management techniques are also under investigation.

Clearly, development of new citrus germplasm sources tolerant or resistant to CTV, stubborn and greening, or repellant to their vectors, would be highly desirable to ameliorate the limiting effects these diseases have on citrus production. Unfortunately, these diseases may occur concurrently with each other and with other non-virus diseases. Thus, selection for resistance to a single factor may have little prac-

tical value. Rough lemon, Rangpur lime, Carrizo citrange and trifoliate orange are all highly tolerant or resistant to CTV when used as rootstocks, but their use in Florida is jeopardized by their susceptibility to blight. Sweet orange is tolerant to both blight and CTV, but is highly susceptible to *Phytophthora*. Therefore, development of new germplasm resources must be done with consideration for all limiting factors present. New hybrids should also be evaluated for resistance to potential disease problems wherever possible, and this can often be facilitated by some international cooperation.

Further research is urgently needed on several virus-like diseases such as ringspot and tatter leaf-citrange stunt and on undefined declines such as blight, to better assess approaches to their control. Better information about modes of transmission is especially important for those pathogens where natural spread is occurring or suspected and undefined, e.g., ringspot, satsuma dwarf and CLRV.

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Florida Citrus Packinghouse Operations and Handling

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There are over 100 commercial citrus packinghouses in Florida, that in a season without freezing weather or other serious difficulties will pack over 72 million 4/5 bushel cartons (over 1,472,00 metric tons) of fruit.

Additionally, several hundred gift fruit packinghouses and roadside stands sell over 16 million cartons (over 327,000 metric tons). These businesses range from very small roadside stands to the world's largest citrus packinghouse (over 3 million cartons annually). Only 14% of the citrus grown in Florida is sold as fresh fruit, but that 14% is about twice the amount of citrus presently produced in China.

An industry this large is very diverse and difficult to describe in a few words. The publications cited in this paper provide a more complete understanding of the problems for fresh fruit and methods used in Florida citrus.

MATURITY STANDARDS

Citrus fruits grown in subtropical climates are very different from those grown in arid desert climates. China and Florida are both considered to have humid subtropical climates. Some of the characteristics of fruit grown in humid subtropic and arid desert climates are shown in Figure 1. Florida citrus and much of that grown in China has the characteristics of subtropical citrus: blemished and scarred peel that tends to be pale or even green, but a thin peel with a high juice and high sugar. A region such as Florida growing citrus in a subtropical cli-

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