

# Symptoms of Virus Infection in Cactus

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## Abstract

Work with cactus viruses is now approximately a century old. The first definitive indication came in 1951 in Europe. In 1961 virus was also detected in cultivated cactus in the USA, and in 1965 in wild cactus in Arizona.

Some infections are symptomless, but both external and internal symptoms do occur. Externally they consist of chlorotic circles, rings and spots on the pads of prickly pear cactus (*Opuntia* spp.) to a reddening of the fronds of the Christmas cactus (*Zygocactus* sp.). Occasionally more extreme symptoms, such as bending, marked yellowing and dieback of stems occur.

Cactus viruses characteristically induce the production of large cigar- or spindle-shaped Giemsa-stainable inclusions, mainly in the outer cell layers of infected plants. Such inclusions are readily distinguishable from the crystal clusters and spherical inclusions of calcium oxalate found uniformly in epidermal layers of *Opuntia* spp. In addition, virus infection may produce interrupted spindles, as well as corkscrews, rings, threads, polyhedra and X-bodies.

The stomatal apparatus is particularly sensitive to virus infection in some cactus species. Guard cells are conspicuously spindle-free, they fuse with each other and with accessory cells, and they produce outgrowths or "tumors". Whether these changes influence stomatal function in general or the unusual diurnal behavior of stomata in cactus and other succulents would be interesting subjects for research.

A virus of barrel cactus (*Ferrocactus* sp.) induces severe deformation and dwarfing in tissues formed after infection. Whether the flange-shaped anomalies (cristae) of this and other cactus are virus-caused is unclear. Although virus-like particles have been found in witches' broom specimens of *Opuntia tuna*, a spiroplasma is the probable cause of the excessive shoot formation.

## HISTORICAL

The study of cactus viruses is more than 100 years old. The family *Cactaceae* is essentially native to the New World, but early explorers were intrigued by their strange shapes, and many were introduced into cultivation in Europe, and from there to other continents both in and out of cultivation.

By the late 19<sup>th</sup> century they were already a favorite subject of scientific investigation. Hans Molisch (1885) reported the microscopic presence of proteinaceous cellular inclusions in *Epiphyllum*, an observation which became the harbinger of numerous investigations on the nature and role of such inclusion bodies in many cultivated cacti in Europe.

For example, Rosenzopf (1951) demonstrated that the inclusions could be transmitted by grafting to previously inclusion-free *Epiphyllum* cladodes.

Amelunxen (1958) provided the first definitive proof that the spindle- or cigar-shaped inclusions were viral in nature in cultivated *Opuntia monacantha*, and that indeed, the virus was a member of the potexvirus group.

We also observed similar inclusions in *O. monacantha* in cultivation in the USA, as well as virus particles similar in size to tobacco mosaic virus (TMV) in the electron microscope (Sammons and Chessin, 1961).

The first cactus virus in the wild was reported from Arizona, again with TMV-like

particles (Chessin, 1965).

## SYMPTOMS

### External

Since virus infection in higher plants is most often noted in leaves, it is not surprising that the cacti, which typically lose their true leaves soon after they are formed, seldom exhibit marked external symptoms of infection. However, thanks chiefly to the flowering of cactus virus research in Europe after WWII, we can state that a great variety of external symptoms do occur.

**1. Chlorosis.** Chlorotic spotting, especially when accompanied by rings and arcs in the flat-padded prickly pears, is highly diagnostic for the presence of the Sammons' Opuntia Virus (SOV), (Milbrath et al., 1973; Chessin et al., 1965). Some care must be used in such diagnosis since the chinch bug can produce similar markings shortly after feeding on prickly pears. However, it leaves a conspicuous exudate plug where it feeds (Milbrath et al. 1973). Other unidentified insects may be responsible for the small chlorotic streaks which radiate from feeding sites. Both are readily distinguishable from the SOV-induced markings. Severe infection with virus in *Rhipsalis cereuscula* when grafted onto *Pereskia aculeata* results in the production of yellow-green shoots on the latter (Weber and Kenda, 1951). This can be distinguished from the normal yellowing in this plant which precedes the aging process. Presumably, the other leafy cactus genus, *Pereskopsis*, might respond similarly. When spindle-free plants of *O. brasiliensis* were infected with sap from spindle-containing specimens, a generalized yellow-spotting or fine mosaic developed on the injected pad (Chessin et al. 1963).

**2. Reddening.** The counterpart of the anthocyanins, the betalains or betacyanins, are only found in two orders of flowering plants, the *Caryophyllales* and the *Cactales*. Here, they appear to play a role similar to the anthocyanins in their response to stress. Chemically they differ from the anthocyanins chiefly in their containing nitrogen.

Virus infection of *Epiphyllum truncatum* and *E. bridgesii* produced reddish brown spots which may also have contained a betalain (Weber, 1953). A most striking example of virus-induced reddening was observed in my laboratory in the epiphytic-like Christmas cactus, *Zygocactus*. A wide range of degree of reddening was noted in different plants, possibly related to severity of infection. All had spindle-shaped inclusions in their superficial tissues (Giri and Chessin, 1975).

**3. Effects on Growth.** A fairly common symptom of severe virus infection in the flat-padded cacti is a crimping or depression of the pad immediately under the virus-induced spots or flecks. This was true in *O. brasiliensis* (Chessin et al., 1963), underneath the characteristic chlorotic markings in *Platyopuntia* spp. (Milbrath et al., 1973) and under the yellow-brown spots or streaks in *Epiphyllum truncatum* (Weber, 1953).

*Zygocactus* and *Epiphyllum* seem particularly prone to cladode limpness after severe infection. The *Zygocactus* exhibited this symptom accompanying marked reddening (Giri and Chessin, 1975) while *E. bridgesii* cladode withering was associated with reduced root growth. Interestingly, a marked inhibition of flowering was also observed (Weber, 1953). Another unusual effect on growth was the "bending" of the end of the stem of virus-infected *Pereskopsis pititache* (Weber, 1953).

**4. Necrosis.** The yellow-brown spotting in Weber's experiments on virus-infected *Epiphyllum* may be considered a type of necrotic response (Weber, 1953). A more clearcut example was provided in the work with *O. brasiliensis* (Chessin et al., 1963). A cladode inoculated almost 2 years previously produced young pads with very severe yellowing at the distal end, followed by necrosis of the yellowed portion. The extremely long incubation period for development of the necrosis discouraged attempts at repetition.

A recent report (Mertelik and Mokra, 1998) mentioned the occurrence of tomato spotted wilt virus (TSWV) in cultivated *Opuntia*. Although the symptoms in that plant were not described, photos sent to me by Dr. Mertelik indicate severe blistering and necrotic rings as a result of virus infection.

## Internal Symptoms

**1. Cellular Inclusions** I have already referred to the diagnostic value of the proteinaceous spindle-shaped inclusions in the cells of virus-infected cacti (Rosenzopf, 1951; Amelunxen, 1958). Such inclusions are typical of all cactus viruses which belong to the potexvirus group, as well as of SOV. Such inclusions are also produced when test plants such as *Chenopodium quinoa* are inoculated from virus-containing cacti (Milicic and Udjbinac, 1961).

The spindles can be stained red with acid fuchsin although this results in their breakdown into fibrils (Reiter, 1953). They are also stainable with the Giemsa stain which leaves them intact much longer, and is confirmatory of their nucleoprotein makeup (Chessin et al., 1963). The viral nature of the spindles was also demonstrated by their stainability with specific fluorescent antibodies by Stefanac et al., (1967).

A great variety of other kinds of cellular inclusions have been reported from virus-infected cacti, although definitive proof of their viral causation is not as strong as with those of spindle shape.

These include “corkscrews” after treatment of tissues with KI and Fleming’s fixative (Weber, 1951); “interrupted” spindles in *O. subulata* (Weber and Kenda, 1952); fine threads and rings in *Epiphyllum* (Molisch, 1885); and polyhedra of different shapes (Weber, 1953b). Most of the observations were the product of the earlier European work.

**2. The Stomatal Apparatus.** Another contribution to cactus virology also emerged from intense efforts by several European contributors during the 1950s. This involved certain anatomical anomalies of the stomatal apparatus which was brought to my attention in recent years. I am unaware of any follow-up research on this subject since then.

The major effects included the conspicuous absence of spindles in the guard cells and their deformation and twinning, the production of guard cell “tumors”, and the fusion of their membranes with each other and with those of accessory cells (Weber and Kenda, 1953). It would be of great interest to determine whether such abnormalities influence the unusual diurnal stomatal function typical of cacti and other succulent plants.

**3. The Barrel Cactus Virus.** I treat this virus separately because aside from the potexviruses of *Platyopuntia* and the isometric virus of the saguaro cactus, *Cereus giganteus* (Milbrath & Nelson, 1972) it occurs only in the wild and exhibits most unusual external symptoms.

To date, its occurrence has been verified for the California barrel *Ferrocactus acanthodes* only in the Clark mountains of eastern California (Attathom et al, 1978a). More recently I have observed several specimens of this striking cactus with symptoms similar to those previously described, in the Saguaro National Monument near Tucson and in the T’Ono O’Odham Reservation between Tucson and Ajo, Arizona, also out of cultivation.

Infected plants are severely deformed, showing a sudden and uniformly abrupt shrinkage of the conspicuous cylindrical vegetative body, usually several feet above ground level.

The onset of this symptom is associated with the initiation of flowering. Since pollen from infected plants is infectious, the authors suggest that the virus is spread during pollination, since other means of spread would not be expected to be confined to the post-flowering phase.

The authors described an assembly of external symptoms including branched terminal buds; distorted, malformed and randomly distributed areoles; twisted, malformed spines; a systemic mottle and necrosis; and depressed necrotic spots.

Characteristic spindle-shaped inclusions were produced when infected plant samples, including pollen were inoculated to leaves of *Chenopodium amaranticolor* and *C. quinoa*. By implication, the spindles were present in infected *F. acanthodes* as well.

Serological and EM studies suggested that the virus was an isolate of Cactus Virus X (Attathom et al., 1978b).

### Miscellaneous Considerations

Several types of growth abnormalities have for long encouraged speculation as to their possible viral etiology.

A massive deviation from the normal cylindrical growth of the saguaro, variously described as cristate or a fasciation, may have a number of causes. But there is no proof that a virus is involved in this case.

Published research has, however, been done on the causal mechanism of witches' brooming of *Opuntia tuna monstrosa*. Both virus and mycoplasma have been detected in such plants. Treatment with 100 ppm of tetracycline hydrochloride resulted in the temporary disappearance of the mycoplasmas and the witches' brooming, but not of the virus particles. Apparently the mycoplasma but not the viruses (one isometric and the other anisometric) was responsible for the symptoms (Maramorosch et al, 1972).

### CONCLUDING REMARKS

Cacti have become increasingly popular and can be expected to be part of the burgeoning international trade in ornamental plants.

Viruses are found worldwide in cultivated cacti, and have also been detected in the wild in the southwestern USA in prickly pears (*Platyopuntia* spp), the giant saguaro (*Cereus giganteus*), and the California barrel cactus, *Ferrocactus acanthodes*.

Some symptoms of infection are highly diagnostic, such as the chlorotic markings induced by SOV in prickly pears, and the cigar- or spindle-shaped cellular inclusions associated with all known anisometric cactus viruses.

Much work needs to be done in the application of modern molecular techniques to the characterization of cactus viruses, and in the study of the mechanism of the anomalies in the stomatal apparatus of some virus-infected cacti; and of their possible relation to the withering and limpness observed in such plants.

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