Association of Bacterialike Organisms With a New Potato Disease

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We would like to thank I. Harpaz, Dean, Faculty of Agriculture, for many helpful suggestions and for critically reviewing the manuscript.

Accepted for publication 15 December 1975.

ABSTRACT

KLEIN, M., S. ZIMMERMAN-GRIES, and B. SNEH. 1976. Association of bacterialike organisms with a new potato disease. Phytopathology 66: 564-569.

A new disease of potatoes, termed leaflet stunt, is described. The disease, which has so far been found only in Israel, is characterized mainly by deformation and stunting of leaflets. Bacterialike bodies were found only in phloem cells of infected plants, but not in healthy plants. Each body is bounded by two sets of membranes. In transverse section these bodies have a spherical shape, but when sectioned longitudinally rod-shaped particles measuring 1.0 - 2.40 × 0.2 - 0.3 μm are discerned. Beaded forms enclosed by a plasma membrane are sometimes detected inside the particle. Unlike most bacterialike organisms recently claimed to cause yellows type diseases in trees or grape-vines, the outer membranous wall of the organism found in phloem cells of infected potatoes is generally thin and unrippled. According to its ultrastructure, the organism found in infected potatoes resembles the clover-club leaf pathogen rather than those of four other plant diseases, in which xylem but not phloem tissues are claimed to be inhabited by the suspected causal organisms.

Additional key words: yellows diseases, potato.

Plants of the family Solanaceae are known to be attacked by agents of the yellows group of diseases. Mycoplasmalike organisms (MLO) are assumed to be the etiological agents of stolbur and stolbur P diseases of tomatoes in Mediterranean countries (12, 15, 16); Panjan et al. (21) reported the occurrence of such organisms in potato plants previously grafted with shoots from stolbur-infected tomato plants in Yugoslavia. Mycoplasmalike organisms were shown to be transmissible by dodder from stolbur and parastolbur-infected tomato plants to *Vinca rosea* (23). Pleomorphic bodies, such as MLO, also were observed in vascular bundles of phloem of *Nicotiana glauca* and tomato plants infected with the potato witches' broom agent in Czecoslovakia (2, 11). Stolbur of potatoes was also recorded from Israel (32).

The present paper describes a disease of the above-mentioned group causing stunting of leaflets in potatoes and discusses its presumed causative agent.

MATERIALS AND METHODS

Infected materials.—Potato plants (cultivar Up to Date) with stunted leaflets were first observed on July, 1972, in the Golan Heights. Several such plants, at their flowering, were potted in 12-cm diameter clay pots and brought into a temperature-controlled (23-25 C) glasshouse for observation. The plants were used as grafting tissue sources for transfer onto members of the Solanaceae, and for ultrastructure studies with the electron microscope. Stunted *Datura stramonium* L. plants which grew spontaneously in the vicinity of cultivated potato plants in the Golan Heights were collected in summer 1974 for the same purpose. The glasshouse was routinely fumigated against insects and mites with dimethyl 2,2-dichlorovinyl phosphate.

Transmission.—Conventional mechanical sap inoculations were tested on the following test plants: *Chenopodium amaranticolor* Coste and Reyn., *C. quinoa* Willd., *Citrullus vulgaris* Schrad., *Cucumis sativus* L., *Cucurbita pepo* L., *Datura stramonium* L., *Gomphrena globosa* L., *Nicotiana debneyii* L., *N. glutinosa* L., resistant Hicks and Samsun cultivars of *N. tabacum* L., and *Physalis floridana* Rydb. For vector transmission trials, the aphids *Myzus persicae* Sulz., *Aphis gossypii* Glov., and the whitefly *Bemisia tabaci* Gennadius were used either in a persistent or in nonpersistent manner. Several hundred insects previously grown on healthy *Datura* plants were starved for about 2 hours and caged afterwards in small groups on stunted graft-infected *Datura* plants for short acquisition feedings of 30-60 seconds. The insects were allowed to feed afterwards in groups of ten on individually-caged healthy young *Datura* seedlings which were in the two-leaf stage. Forty-eight hours later the test plants were sprayed with phosphamidon to kill all surviving insects. Separate groups of insects were allowed to acquire the suspected pathogen from infected *Datura* for different periods, ranging from 30 minutes to more than 48 hours. They were then put on healthy *Datura* seedlings, either immediately following their accession period or following different periods (from 24 to 96 hours) on intermediate healthy *Datura* hosts. Inoculation feeding lasted 24 hours and was terminated by an insecticide application. An

equal number of insects, which had been treated in the same way, were used as controls.

Grafting.—Stunted potatoes and *Datura* scions were grafted by the side-graft technique onto various of the Solanaceae, as listed in the RESULTS section.

Electron microscopy.—Ultrathin sections were cut from young petioles of naturally infected potato and *Datura stramonium* plants and of tomatoes and *Datura* plants 75 days following grafting with naturally infected material. Similar material from healthy plants and from plants which had been grafted with healthy shoots were used as controls. All material was fixed in phosphate-buffered 5% glutaraldehyde (0.1 M phosphate buffer, pH 7.2) for 3 hours at room temperature, rinsed in buffer, and postfixed for 2 hours in 1% osmium tetroxide in the same buffer. It was then rinsed again and dehydrated in graded ethanol solutions followed by prophylene oxide and embedded in Epon. Ultrathin sections, of about 40 nm, were cut with glass knives on a Reichert type-8802A ultratome. The sections were stained for 10 minutes in a 50% alcohol solution of a saturated aqueous solution of uranyl acetate followed by a 3-minute treatment with Reynolds' lead citrate solution. Electron micrographs were taken in a Jem T7 (JEOL, JAPAN) electron microscope at 100 KV.

RESULTS

Field observations revealed that the rate of infection of original Irish as well as a local stock of the cultivar Up to Date potato was fairly small. It did not increase since 1972, remaining as low as 0.8 to 1.0% of plants counted in the field.

Disease symptoms.—*Naturally infected plants of potato cultivar Up to Date.*—The growth of infected plants is only slightly stunted. Symptoms appear mainly in leaves, becoming very clear close to flowering. The leaflets become gradually deformed, though the unpaired leaflet and the first paired ones usually remain unaffected in size and shape. The rest, however, are very small in comparison with leaflets of healthy plants, showing a marked degree of inequality between the two members of each pair (Fig. 1). The color of the youngest leaflets changes from dark green to yellow green, or yellow. No effects on flowers could be observed in the field.

Naturally infected Datura stramonium plants.—Infected *Datura stramonium* plants, growing spontaneously in the vicinity of cultivated potato plots, developed leaves smaller than normal, with a clear yellowing in the interveinal region. Flowers were somewhat deformed, but capsules seemed to be normal in shape.

Graft-inoculated plants.—1) Tomato. — Tomato plants, of cultivar Marmande, grafted with shoots taken from naturally infected potato and *Datura* plants, developed very small and narrow yellow leaves. Some very small, degenerated flowers were produced, but they dropped off very soon without setting any fruit.

2) Eggplant. — Leaves of grafted eggplants (cultivar Black Beauty) were transiently rolled, but flowering was unaffected. Six months after grafting, symptoms could be noticed only on apical young leaves, and fully developed leaves showed no symptoms.

3) Tobacco (*Nicotiana tabacum* 'Samsun'). — Results of grafting trials indicated only some minor growth change and an insignificant reduction in leaf size and color intensity.

4) *Datura stramonium* (Cornell type). — A little-leaf symptom was particularly noticeable on grafted *Datura* plants (Shoots: *Datura* or potato) maintained in the glasshouse (Fig. 2). Most of the leaves were dwarfed, and the biggest leaf was still far from normal average size. The internodes were short, giving the whole plant a dense appearance. Flowers of infected plants were stunted (Fig. 3). Their length, base diameter, and fully opened flower were up to 54 mm, 5 mm, and 15 mm, respectively, whereas the respective measures in healthy plants grown at the same conditions were 110, 12-15, and 50-55 mm. Capsules that developed from the stunted flowers ceased to grow earlier than those set on healthy plants. They were either spikeless or with a small number of spikes as compared to many and systematically arranged spikes in healthy plants (Fig. 4).

Etiology.—Disease symptoms resemble those incited by *Fusarium* spp. However, no vascular discoloration, which is typical of *Fusarium* infection, could be observed.

The pathogen of the potato leaflet stunting disease could not be transmitted by mechanical sap inoculation to any of the above-mentioned test plants.

Potato leaflets stunt could not be vector-transmitted neither by *Myzus persicae* nor by *Aphis gossypii* either in a persistent or nonpersistent manner. Negative results were also obtained by the whitefly, *Bemisia tabaci* using infected *Datura stramonium* as source plants.

Plants grown from seeds taken from capsules of infected *Datura* showed no disease symptoms.

Electron microscopy.—Transverse sections of infected petioles of the three species examined, revealed numerous spherical bacterialike bodies of different sizes scattered throughout most of the phloem elements. Part of the elements were filled with these bodies whereas in others they could scarcely be seen. Several of such phloem elements from tomato petioles and a few adjacent cells can be seen in Fig. 5. Finely fibrous and granulated matrix is scattered between the spherical particles. Companion cells were normal in shape and normally vacuolated, as well as the mesophyll cells. A discrete cell wall surrounds each particle, and encloses a second membrane several nanometers deeper. Wrinkles are scant and many walls are ruptured. The granules are assumed to be ribosomes of the suspected pathogen. The central region of most particles is weakly stained (Fig. 6). Sometimes a very dense group of spherical and rod-shaped particles occupies the phloem elements (Fig. 7). The length of the rod-shaped particles is about 1.7 μm, with a width of about 280 nm. Some small spherical bodies seem to originate from such rod-shaped particles whose diameter is about the same as the width of the cell from which it seems to be derived. Similar spherical bodies about 280 nm in diameter or less, are enclosed in pairs within a single cell wall. Those interior bodies exhibit their own bounding membranes. The rod-shaped particles very often demonstrate an unhomogenous distribution of the cytoplasm and organelles. This is clearly seen in Fig. 8-A. The two-set membrane system is clearly demonstrated in Fig. 8-B. Degeneration of these bacterialike organisms may take place in old sieve elements discerned by the coagulation of the cytoplasm and the vanishing of

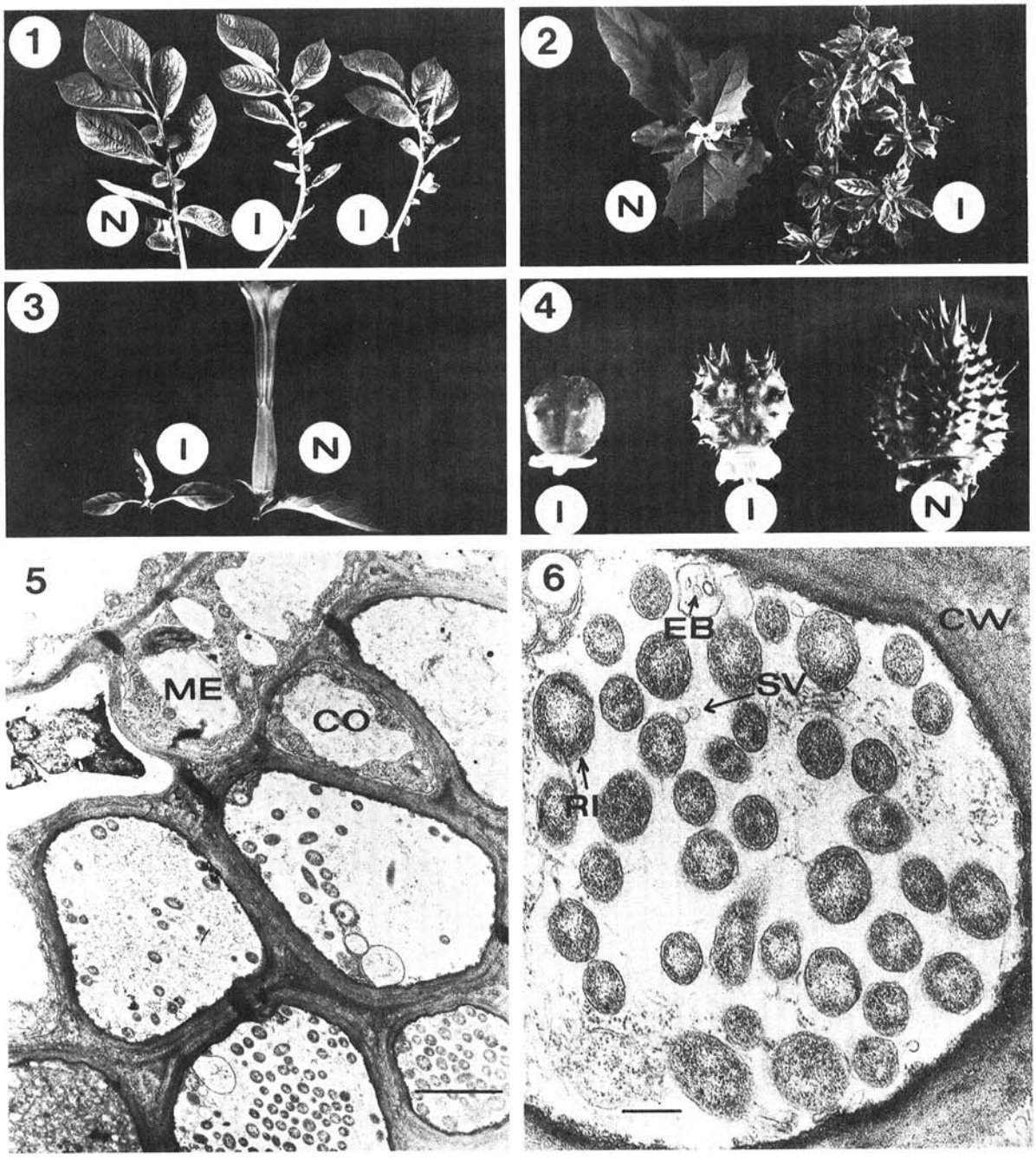

Fig. 1-6. (1-4) Symptoms of potato leaflet stunt (PLS) on infected plants. **1)** Leaves from naturally-infected Up to Date (cultivar) potato plant. Deformation of the leaflets as well as their small size can be seen on the two leaves from an infected plant (I). The leaf on the left (N) was taken from a healthy plant grown adjacent to the infected one. **2)** "Little leaf" symptoms on a *Datura stramonium* plant grafted with a PLS-diseased potato (I). In addition to the small size of the leaves, they show yellowing at the interveinal areas. Note size and color homogenicity of healthy leaves on the plant at the right (N). **3)** A small deformed flower from PLS-infected *Datura* plant (I) in comparison with a healthy flower (N). **4)** Symptoms of PLS on capsules of *Datura* grafted with infected potato scions. N:normal capsule. I:capsule of infected scion. (5-6) Electron micrographs of PLS-infected tomato plant. **5)** Transverse section of phloem elements, a low-magnification micrograph. Bacterialike organisms seen in the elements are spherical due to their being transversly sectioned. No particles could be seen occupying companion (CO) or mesophyll (ME) cells. CW-Cell Wall. Scale bar = 2 μm. **6)** Phloem cell from the petiole of a plant grafted with PLS-diseased potato, showing spherical, bacterialike, bodies of various sizes. Each body is bounded by a double set of membranes. The outer membrane is sometimes rippled (RI), or both membranes may be ruptured (arrow). Large empty bodies (EB) and small vesicles (SV) are often found in such plant cells, especially close to the cell wall (CW) of their host. Scale bar = 400 nm.

ribosomelike structures (Fig. 9). Vesicles of various shape and size are fully distributed in such plant cells.

Healthy control material was invariably free of such bacterialike bodies.

DISCUSSION

The disease known by stunting of leaflets in potatoes which will from now on be called potato leaflet stunt (PLS) is new in Israel, and has been found only in the upper northern regions of the country. To the best of our knowledge, no such disease has been reported to occur in potato anywhere. The syndrome occurring naturally in *Datura* and potato apparently is caused by the same pathogen. This was proven by reciprocal graft transmission trials on several solanaceous species as well as by the ultrastructural study.

Potato leaflet stunt is not a physiological disease, since its agent is transmissible at least by grafting. This new disorder resembles the yellows group of diseases, but it is distinct from all types of stolbur (27), parastolbur (26), witches' broom (31), purple top wilt (4), and purple top roll diseases (19), either symptomatologically or by the peculiar ultrastructure of the suspected causal agent. Unlike most of the diseases mentioned above, no phyllodoid flowers were observed in PLS-infected plants.

Pleomorphic bodies, resembling mycoplasma, were

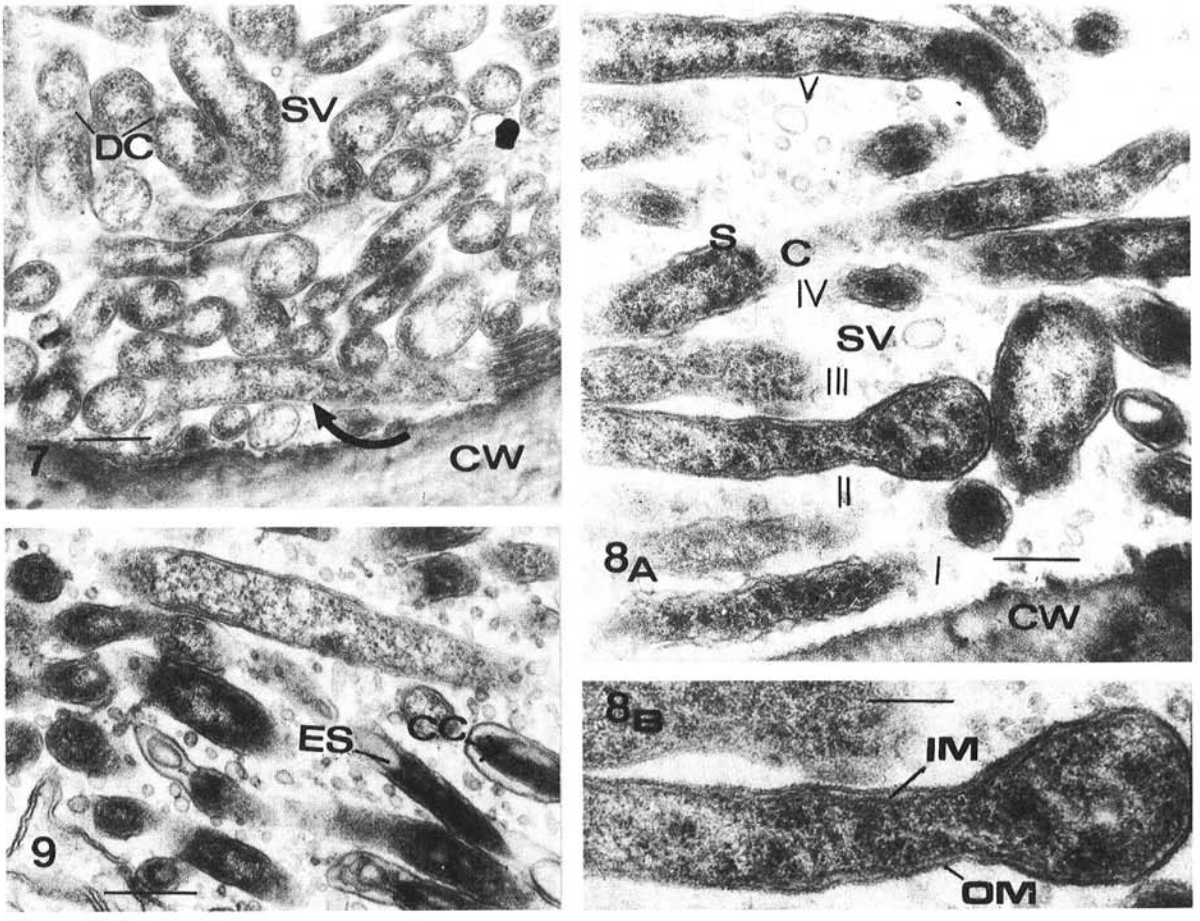

Fig. 7-9. Sections of phloem elements showing the alien bodies within. **7)** Dense population of bacterialike bodies in phloem element from a petiole of *Datura stramonium* grafted with PLS-diseased potato. The bodies were sectioned in various positions. Few paired bodies (DB) can be seen. Few small spherical bodies appear to have originated and budded from a peculiar large body (arrow). Many small vesicles (SV) are scattered among the bacterialike particles. Scale bar = 400 nm. **8-A)** Part of a transverse section of an element from a petiole of PLS-infected tomato plant. The electron dense areas within particle V apparently developed as a result of cytoplasm accumulation, which in some cases causes either swellings (S), or contractions (C) in particles II and IV. In particles III and IV, this dense cytoplasm appears to be enclosed by a membrane. The membranes of particle I seem to be ruptured. Scale bar = 300 nm. **8-B)** An enlargement of particle II in Fig. 8-A to show its fine ultrastructure. The outer membrane (OM) is triple-layered, and has an overall width of about 8 nm, inner membrane (IM) also triple-layered, of about 5 nm in width, with a gap of approximately 10 nm in between; ribosomelike structures, and DNA-like strands are visible. Scale bar = 600 nm. **9)** Bacterialike bodies in mature phloem element showing apparent degenerative nature. This is characterized by coagulation of cytoplasm (CC) followed by formation of empty spaces (ES) within the various bodies. Small vesicles in and outside the bodies are believed to have been released from the degenerated bodies, or else result from sectioning the empty edges. Scale bar = 400 nm.

detected in phloem elements of solanaceous plants infected with yellows diseases (2, 7, 11, 12, 15, 16, 21, 23). However, in the present case of potato leaflet stunt, the suspected pathogen resembles a bacterium rather than a mycoplasma since it is enveloped by a double membrane. Other yellows diseases in plants, characterized by closely structured causal organisms are claimed to be caused by rickettsialike pathogens. These are the clover club leaf disease (30), *Sida cordifolia* little leaf disease (8), Pierces' disease of grapevine (5, 9), peach phony disease (10, 20), apple proliferation disease (22), and sugarcane ratoon stunt (14). Of the seven diseases mentioned above (including PLS) only in one instance, namely Pierces' disease, was the organism actually cultured in-vitro and its pathogenicity convincingly demonstrated (1). It should, however, be pointed out that the Pierces' disease pathogen was in fact found to be a Gram-positive bacterium, which adds another element of confusion to the distinction between bacteria and rickettsiae in ultrathin sections of diseased plant tissue [see also Moll and Martin (18)].

The suspected causal agent of the PLS disease resembles *Rickettsia rickettsii* cells (28), due to thin cell wall which both organisms have. Detachment of a plasma membrane from the cell wall is common in both cases. Such cells, however, are apparently nonviable. Another rickettsia, *R. canada,* shows two major types of structures in its tick vector (3). Most individuals of this rickettsia have a thick densely stained cell wall, whereas the remainder show a relatively thin, weakly stained cell wall. The PLS organism resembles the latter type of *R. canada,* being therefore also similar to the organism suspected of causing the club leaf disease of clover (30). The PLS organism is also reminiscent of organisms found in phloem cells of *Sida cordifolia* plants with little-leaf disease symptoms (8). Two additional features suggest that the three diseases may be grouped together: (i) the site where the suspected causal organism was seen, and (ii) the similiarity of the syndrome. The suspected organisms inhabit only phloem cells in all three cases, and their pathogenic effect seems to be manifested mainly by leaf stunt.

Beaded rod-shaped particles as well as single-membrane "small structures" are commonly seen in ultrathin sections of clover club leaf and PLS-diseased plants. Although no comparative data are available for the little-leaf disease of *Sida cordifolia,* the latter may be related to the other two, due to its peculiar cell wall and the symptoms it causes in the host plant.

The structure of the PLS organisms found in *Datura,* tomato, and potato plants was quite similar, being always bound by thin and weakly-stained walls. These walls were more like those of the clover club leaf organisms found in crimson clover than in periwinkle (30). Such morphological dissimilarity suggests that the host plant may affect the structure of these rickettsialike organisms.

In four of the above-mentioned diseases, namely Pierces' disease of grapevine, peach phony disease, apple proliferation disease, and sugarcane ratoon stunt, the organisms were seen in xylem cells but not in the phloem. All have a very thick and rippled outer wall. It seems, therefore, that there are two separate groups of organisms which cause all these diseases.

The possibility that PLS is caused by an organism belonging to the Chlamydiae is not ruled out. In several cases, the suspected agent resembles initial bodies of Chlamydiae (6). Species of these organisms have a high frequency of budding, releasing miniature membrane-bound structures (25). Small vesicles, similar to the miniature bodies known in Chlamydiae, could be seen in phloem cells of clover club leaf infected plants (30) as well as in the PLS disease. The formation of small structures on the periphery of large cells of chlamydia and their liberation, increase following the introduction of penicillin into the culture media of L-cells (17). The clover club leaf disease is, thus far, the only yellows type disease in plants to be affected by the application of penicillin (29). Some indication of the efficiency of this antibiotic against the PLS agent was in fact obtained in recent chemotherapeutic treatments. Unfortunately, however, the PLS syndrome often disappears temporarily, even in untreated infected plants. Small rounded vesicles are known also to be present in MLO cultures. This may increase in over-aged cultures (13), and in response to administration of therapeutic agents (24). No vesicles of this type could be seen when the suspected agent of the plant disease seems to have a heavy, rigid cell wall (5, 9, 10, 20, 22). Apparently, the stability of the wall prevents disruption of a portion of the organism to cause vesicles. The real nature of the PLS causative organism could not be interpreted from the recent work. This will have to wait at least until a vector is found.

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