

Confusion Over the Etiology of Graywall or Internal Browning of Tomato

In the *Compendium of Tomato Diseases* (8), edited by J. B. Jones, John Paul Jones, R. E. Stall, and T. A. Zitter and meant to serve as a definitive reference to diseases of this crop, graywall is included in Part III, "Diseases of Undetermined Etiology." Stall (10) prepared this section and in his brief introduction states that: "Graywall was adopted for the name of a disease of tomato fruit in Florida. There is much uncertainty about its cause and distribution around the world. Blotchy ripening in greenhouse tomatoes in the northern United States and southern Canada and 'cloud' in tomatoes in New Zealand are probably graywall. Similar symptoms also occur in field tomatoes with blotchy ripening in New York and California and in tomatoes with internal necrosis in New Jersey and Pennsylvania, but these two diseases probably should not be considered graywall and are not included in this description."

With regard to the economic importance of this disease, Stall continues: "Graywall can be devastating, because affected tomatoes are unmarketable, and the malady occurs after all of the cost of production has been expended. The percentage of fruit affected is dependent on the environment and cultivar of tomato. However, it is not unusual to find 40% of the fruit of a susceptible cultivar affected."

Stall goes on to say that graywall "is expressed as black to dark brown necrotic tissue in the walls of the tomato fruit. The necrosis is sometimes present in the cross-walls but seldom in the center column of the fruit. Most frequently, only the outer walls are affected." Plates 67A and 67B show external and internal symptoms of graywall. It should be noted that these illustrations are strikingly similar to those considered by some (2,3) to be typical of TMV-induced internally browned fruit. While the illustrations of Boyle and Wharton (3) and Boyle and Bergman (2) are of internally browned green fruit, similarly affected fruit were allowed to ripen and resulted in symptoms identical to those illustrated in Plates 67A and 67B in the compendium (Boyle, unpublished).

Zitter (14) prepared the section on tomato mosaic and tobacco mosaic and explains that the two viruses (ToMV and TMV) are "mentioned together because they differ only slightly in host, serological, and cross-protection reactions." He describes the "most characteristic symptoms of the disease caused by common strains" as "mottled areas of light and

dark green on the leaves (Plate 51A)." He describes other effects on vegetative plant growth, then notes: "In general, symptoms vary greatly in intensity according to viral strain, cultivar, time of infections (both calendar year and stage of plant growth), light intensity, and temperature."

It is of interest to note that Zitter apparently considers ToMV or TMV of little importance with regard to effect on fruit, for he states: "Although the fruit does not ordinarily have marked disfigurement, it may show uneven ripening and be reduced in size and number. Yellow rings may occur if it ripens at high temperatures (Plate 51B). Various strains have been described and named largely on the basis of fruit symptoms; strains include corky ring, crusty fruit, yellow, and Aucuba."

"At times the fruit may develop a symptom referred to as internal browning or brownwall. This symptom is evident in mature but unripened fruit and usually involves the fleshy parenchyma, whose cells often collapse. The symptom is attributed to a 'shock' reaction following ToMV infection."

Neither Stall (10) nor Zitter (14) cites publications that explain the etiology of internal browning or graywall. It would seem neither Zitter nor Stall understands the unique role TMV plays in the etiology of this disease.

The first experimental reproduction of internal browning was reported by Boyle and Wharton (3). They stated: "Attempts to reproduce the internal browning symptom by inoculation of *young* [italics mine] tomato plants with tobacco mosaic virus isolates from internally browned fruit were unsuccessful; however, when large, healthy tomato plants were inoculated mechanically with the same isolates just as the first fruit were beginning to ripen, a high percentage (up to 93 per cent) produced internally browned fruit." Table 3 summarized the results of this experiment, and it is to be noted that of the 5,379 fruit produced on 77 plants, 14% were internally browned. These fruit were harvested and cut within 25 days after plants were inoculated. This report was corroborated by Broadbent (4), by Jenkins et al (7), and by Murakishi (9), who, in an obfuscating publication, attempted to differentiate between internal browning and graywall.

In an effort to better understand the disease and perhaps end the confusion that had arisen from the numerous studies on internal browning, graywall, and blotchy ripening, Boyle and Berg-

man (2) published the results of a series of experiments made from 1956 to 1963 involving the critical examination of more than 400,000 fruit in which "the etiology of tomato internal browning has been confirmed by the successful and repeated reproduction of the disease in plants inoculated with tobacco mosaic virus (TMV). In the few cases where the disease occurred in noninoculated plants, the presence of TMV was demonstrated. Chance infections in noninoculated controls were minimal when disease evaluations were made on immature fruits, completely harvested, approximately 25 days after TMV was introduced into the experiments; e.g., in 1959, 7 of 278 noninoculated plants produced 0.2% internally browned fruits of a total of 21,399 fruits. By contrast, 263 of 276 inoculated plants produced 13% internally browned fruits of a total of 21,583."

"Factors shown to markedly affect the incidence and severity of disease are soil moisture and cultivar susceptibility."

While a graduate student in horticulture at Penn State, Taylor completed a study of the influence of some environmental and nutritional factors of internal browning of tomato, and his thesis and the subsequent station bulletin (13) challenged the etiological importance of TMV in the internal browning disease. It is of interest to note that in 1969 Taylor, now a professor of vegetable crops at Rutgers University, published, with others (12), on the influence of time of tobacco mosaic virus inoculation and stage of fruit maturity on the incidence of tomato internal browning. They stated (12): "Field and greenhouse studies support earlier reports by others that tobacco mosaic virus (TMV) infections can cause the tomato internal browning disease (IB)."

In 1982, I (1) reported that internal browning and graywall are diseases of the same etiology. On visits to Florida in 1968, 1980, and 1981, I collected approximately 50 fruit from the Homestead and Naples areas that R. A. Conover, greenwrap producers, and other workers in the tomato industry considered typical graywall (5,11). TMV was consistently isolated from these fruit. Four Florida TMV isolates were used to inoculate and reproduce typical internal browning, i.e., graywall symptoms, in field-grown Rutgers and Floradade plants. Noninoculated plants were free of internal browning/graywall (1).

The key to determining the etiology of internal browning/graywall is to recognize that the syndrome is not the

same as that associated with TMV infections of tomato plants before fruit is set. *Internal browning (i.e., graywall) is not a developmental disease.* It is a disease that results from infection of large plants with fruit already set. Some of the fruit on these plants will be affected as a result of virus synthesis and translocation into them. Many factors affect the response of any given plant, for example, plant vigor, cultivar susceptibility, and virus isolate. *However, time of infection is the salient point of host response, not severity of virus strain,* as suggested in 1950 by Holmes (6). Observations of Conover (5) that graywall was most common in the third picking in one season can now readily be explained by the fact that TMV was mechanically transmitted by the pickers in the first and second pickings while looking for and harvesting ripe fruit. Observations that plants that had produced graywall fruit but later produced normal fruit are understandable when one accepts the fact that fruit necrosis occurs following the synthesis and translocation of virus into only some of the developing fruit. The fruit that are going to be affected are affected at this time. Other fruit develop normally, and fruit subsequently set and produced on infected plants are not affected.

It is unfortunate that Stall (10) in his treatment of graywall in the compendium did not at least cite the literature that explains the etiology of this disease. It is also unfortunate that Zitter (14) in his treatment of tomato mosaic and tobacco mosaic neglects to deal with the malady internal browning/graywall or the literature pertaining to it.

I am preparing a manuscript that will summarize the literature, deal with synonymy, and explain and clarify the contradictions that have resulted in the present confusion with regard to ripening disorders of tomato fruit. The purpose of this letter is to point out the synonymy and common etiology of the maladies known as internal browning and graywall.

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Dr. Stall replies: Dr. Boyle devotes much of his letter to reviewing his work with internal browning of tomato fruit that is caused by tobacco mosaic virus (TMV). This apparently is good work, and Dr. Zitter mentioned the malady in his description of symptoms caused by TMV. Dr. Boyle also criticizes our treatment of the disease in the *Compendium of Tomato Diseases* (American Phytopathological Society, St. Paul, MN), which consists of brief descriptions of symptoms, causal agents, and control measures for tomato diseases, with a few significant references—not a review of the literature—for each disease. This reply is also not a literature review.

Dr. Boyle and I differ in lumping together internal browning (as caused by TMV) and graywall of tomato. I prefer to keep the two diseases separate, mainly because in several studies there was not a constant association of TMV with the graywall disease. Stoner and Hogan (5) were aware of the reports by Haensler (1) and Holmes (2) regarding association of TMV with internal browning of tomato when they published their work on graywall. Stoner and Hogan (5) clearly determined that a virus was not associated with the plants that developed fruit with graywall. This work was accepted by workers in Florida as well done and is probably still the primary basis for the prevalent view that internal browning and graywall are not synonymous. Murakishi (3) also considered the graywall and internal browning diseases as distinct after the graywall symptom developed in fruit of plants that indexed

TMV-free. He used the presence or absence of TMV to distinguish the two diseases because he could not consistently separate the two diseases by symptoms. L. J. Alexander, C. B. Hall, and I (4) also concluded that TMV was not the primary cause of the graywall disease in Florida. Fruit from Dr. Alexander's TMV-resistant tomato breeding line developed graywall in our tests even though the plants are considered to be immune to the virus. Graywall also developed in fruit of plants of a Florida breeding line that were not infected with TMV. The plants in the tests were assayed periodically for TMV by mechanical inoculations of two local lesion hosts with leaf extracts.

Probably the most compelling argument for the separation of the two diseases comes from cultivar development and field plantings. Graywall has ceased to be a problem for tomato production in Florida in recent years because of the introduction of cultivars that are resistant to graywall. These cultivars are susceptible to TMV. Floridade is a cultivar highly resistant to graywall, but Floridade was mentioned by Dr. Boyle in his letter as being susceptible to internal browning in an inoculation experiment with TMV. Murakishi (3) also reported that some cultivars were resistant to graywall and susceptible to internal browning.

TMV can undoubtedly be isolated from tomato plants that have developed fruit with graywall, as suggested by Dr. Boyle. TMV seems to be ubiquitous in tomato production. Also, reproduction of symptoms similar to graywall with the isolated strains of TMV may well be possible. However, one must satisfy the first element of Koch's postulates, which is to demonstrate constant association of TMV with the graywall symptom, before establishing that internal browning and graywall are synonymous. TMV is not a constant associate with graywall in many research efforts. Thus, I prefer to consider graywall and internal browning, as caused by TMV, to be two distinct diseases.

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Dr. Zitter replies: I wish to reply to Dr. Boyle's letter concerning the confusion over the etiology of graywall and internal browning, also referred to as uneven ripening, bronzing, or simply browning, depending on which reference is read. Most authors consider blotchy ripening to be a physiological problem, and thus it is appropriate that it was discussed by Dr. Stall in the graywall section of the compendium. My reply is from the perspective of the detail that could be provided to describe tomato mosaic virus and tobacco mosaic virus infection on tomato. I wrote the section with the knowledge that Dr. Stall was writing a separate section on graywall, and to avoid confusion I did not include reference to graywall in the virus section.

Although the compendia series are meant to be definitive references for crop diseases, authors and editors operate under severe space constraints. Information and references should present a balanced overview of each disease, a "snapshot" of information that can best be applied to current disease problems in an international setting. The compendia are not intended to replace textbooks such as those by Sherf and MacNab (3), which has a section on common mosaic (tobacco mosaic virus) of

tomato, and Fletcher (1), which has a section on tomato mosaic virus. The USDA Agricultural Handbook No. 28 (2) has an entire section on internal browning complex, complete with five references cited by Dr. Boyle. In the handbook's section on causal factors of the internal browning complex (page 29) is the statement that: "Research has clearly shown that tobacco mosaic virus alone does not produce symptoms, but may increase the percentage of fruits affected and intensify the symptoms if the virus is present in plants also affected by other predisposing factors." On page 148 of his book (1), Fletcher refers to bronzing (also known as internal browning) "as being attributed to TMV." On page 674 of their book (3), Sherf and MacNab state that: "'Internal browning,' described in the United States, and 'bronzing,' described in Great Britain, refer to similar fruit symptoms caused by TMV." In the fourth paragraph of the section of the compendium on tomato mosaic and tobacco mosaic (page 39), I indicate that ToMV may be associated with internal browning but I also list other contributing factors. Thus, after more than 35 years of discussion, there remains less than total agreement over the etiology of graywall or internal

browning of tomato.

I have addressed the lack of reference to the internal browning malady in the virus section of the compendium from the standpoint of lack of space and the ambiguity that remains to this day. I am fully aware of Dr. Boyle's previous publications and those of my major professor, Dr. Murakishi. Although my thesis dissertation did not address internal browning of tomato, I did in fact work with TMV strains that were associated with internal browning research, including the JSB-1 isolate from Dr. Boyle and the HRB (Holmes rib-grass) strain from Dr. Holmes.

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