REACTION OF GRAPEVINES TO LEAFROLL VIRUS

A. C. Goheen

Leafroll, whose origin is obscure, is the most widely distributed of all grapevine viruses in California even though its natural spread by a vector has not been definitely established. In 1853 Fabre (4)* described a mysterious disease with leaf-roll-like symptoms in France. Scheu (17) refers to published reports of leafroll-like symptoms in the wild grapevines of Germany in the middle of the 19th century. Leafroll undoubtedly moved to California and many other grape-growing areas of the world with importation of infected European planting stocks. In 1902, the white Emperor disease, which we now know is leafroll, was first reported in a brief communication (19) in the Pacific Rural Press, a popular farm journal.

In 1936 Scheu (17) first demonstrated that leafroll was a virus disease, and ten years later Harmon and Snyder (11) showed that white Emperor disease was transmissible. Subsequently, Harmon and Weinberger (12) showed by graft inoculation tests to Emperor that a virus disease was present in many other grape varieties which produced the white Emperor disease in Emperor. Goheen, Harmon, and Weinberger (6) correlated white Emperor disease with Scheu's leafroll, noting that leafroll was widely distributed in many California grape varieties.

Leafroll, an insidious disease, does not produce dramatic symptoms in the vine, such as death or sterility. Its effects are reduced yields and diminished quality of fruit, and symptoms vary with variety, season and location.

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* Numbers in parentheses refer to "Literature Cited" at end of this paper.

For sure diagnosis the disease must be indexed on sensitive indicator vines. The symptoms and the methods of testing for leafroll virus were recently reviewed by Goheen and Hewitt (7).

In brief, leafroll symptoms on leaves of vinifera varieties consist of premature discoloration, with a tendency of older leaves on each cane to roll downward or burn during the late summer and fall. In spring and early summer, leafroll and healthy vines are similar, but the trunk, canes, and leaves of affected vines are smaller. Fruit produced on affected vines is less than that on healthy vines, and the sugar at harvest time is reduced. Fruit color is also affected, particularly with varieties that normally produce red-colored berries; the fruit remains greenish-white at harvest.

Infected American rootstock varieties do not show leafroll symptoms, but some bunch grape varieties are extremely sensitive to it and become severely dwarfed when infected.

In California, indexing for the presence of leafroll has been based on the indicator varieties, Emperor, Mission and Baco 22 A. The basis for the test in Emperor is fruit-color change; in Mission, leaf-color change; and in Baco 22 A, vine dwarfing. Time requirements for completion of the test in Emperor are 3 to 4 years; in Mission, 6 to 18 months; and in Baco 22 A, about 3 months. Although the Baco 22 A test is the most rapid it does not always detect mild strains of leafroll, because dwarfing is a relative condition and factors other than leafroll virus can produce poor growth in the indicator vines. For routine checking of moderate or severe leafroll strains, the Baco 22 A test is adequate; for critical evaluation of leafroll in selected clones, the Mission test is more accurate.

A comparison of diseased and healthy vines shows that leafroll influences several physiological processes, although the mechanisms whereby the virus interferes with these processes are not known. Thus, it has been shown that leafroll affects carbohydrate accumulation in different plant organs, cation uptake, pigment concentration, protein content and resistance of the vine to attack from the powdery mildew fungus. Disease symptoms appear to be morphological responses of the grapevine to disruption in physiological processes.

Several workers (2, 5, 17) found that vines with leafroll have less sugar in the fruit at harvest than do normal vines. Tests of leaves from leafroll and healthy plants demonstrate that carbohydrates accumulate as starches and sugar in far greater concentrations in the affected leaves (9). Accumulation of starch possibly brings about the downward rolling of the leaf margins; the brittleness of tissues noted in leaves on affected vines; and the leaf burning noted on some varieties.

Leafroll virus affects the distribution of cations within the grape plant. Cook and Goheen (3) found that the amount of calcium and potassium in leaf blades of leafroll-affected vines was significantly less than in leaf blades of healthy vines of the same variety. Potassium appeared to accumulate in the leafroll-affected petioles. Similar reduction in potassium content of the leaf blades in affected vines is reported by Millikan *et al.* (15). Hoefert and Gifford (13) noted that the first anatomical indication of leafroll infection is degeneration of phloem tissues in young leaves and developing stems. Sugar accumulation in leaves, along with a reduction of sugar in fruit of affected vines, suggests that leafroll virus must disrupt translocation. Since potassium becomes deficient in the leaf blades and appears to accumulate in the petioles of affected vines, it is evident that the leafroll virus, by some unknown means, blocks the movement of potassium ions from one end of the sieve tube chain to the other. These facts lend circumstantial support to Spanner's

(18) electro-osmotic theory of sugar translocation in plants.

The reduced potassium in affected leaf blades caused much confusion in early attempts to understand the nature of the leafroll disease. Ravaz, Dupont and Callaudeaux (16) found a marked deficiency of potassium in the analysis of leaves from rougeau-affected vines as compared to leaves from adjacent healthy vines. They assumed that the disease was caused by potassium deficiency, although they saw diseased and healthy vines growing side-by-side. For many years French viticulturists believed that rougeau, which is undoubtedly the same as leafroll, was caused by potassium deficiency induced by small variations in the soil, water supply, or crop load (14). In carefully controlled sand culture experiments, Cook and Goheen (3) found that a lack of potassium in leaf blades was a symptom of grape leafroll and not a cause of it. Their experiments demonstrated that symptoms produced in grapevines by true potassium deficiency, although similar, could be distinguished from leafroll symptoms with careful observation.

Sugars and cations are not the only substances the distribution of which in the plant is affected by leafroll virus. Anthocyan pigment concentrations are also affected. Fruit on infected vines of certain redfruit varieties does not color properly at harvest time (6, 10), while the leaves on these same vines color prematurely (6, 17). On the basis of comparative chromatographic analysis Albach, Kepner, and Webb (1) observed that the concentration of the anthocyan pigments in fruit from affected vines is less than that from healthy vines, although the same pigments are present in both. There are no published accounts of the comparative analysis of the pigments in the leaves of diseased and healthy vine.

Protein synthesis within the vine is also affected by leafroll. In a preliminary report Millikan, Pickett, and Hemphill (15) suggest that leafroll virus interferes with protein synthesis. During the early part of the growing season, leaf tissues from leafroll-affected vines appeared to have more protein content than healthy leaves; but by midseason the reverse seemed to be true.

Leafroll-affected grapevines appear to be more resistant to powdery mildew than do healthy vines of the same variety. Goheen and Schnathorst (9) found considerably fewer colonies of the fungus, *Uncinula necator*, on canes of affected vines of Carignane than on canes of adjacent healthy vines of the same variety. They demonstrated accumulation of starches and sugars in the affected leaves, and suggested that resistance was perhaps brought about by an increase in osmotic pressure associated with carbohydrate accumulation in any tissue of the affected vines that synthesizes sugar.

It is difficult to understand how a virus disease for which no insect vector is known can be as widespread as leafroll appears to be in California. Goheen and Hewitt (7) indicate that leafroll virus can infect several rootstock varieties without producing symptoms. Goheen, Hewitt, and Alley (8) suggest that the propagating methods for establishing new California vineyards, along with the use of leafroll-infected rootstocks, have been the principal cause of spread. A vector for leafroll may be found, but if so it will not spread the disease any more efficiently than has the practice of indiscriminate propagation of infected rootstocks. Conversely, if no natural vector occurs, the practice of vine selection and certification now used in California will eliminate leafroll disease completely.

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