Physiology and Biochemistry

Photosynthesis, Transpiration, and Water Use Efficiency of Mature Grape Leaves Infected with *Uncinula necator* (Powdery Mildew)

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ABSTRACT

Lakso, A. N., Pratt, C., Pearson, R. C., Pool, R. M., Seem, R. C., and Welser, M. J. 1982. Photosynthesis, transpiration, and water use efficiency of mature grape leaves infected with *Uncinula necator* (powdery mildew). Phytopathology 72: 232-236.

Photosynthesis and transpiration of mature leaves of susceptible *Vitis vinifera* 'White Riesling' and less susceptible *V. labruscana* 'Concord' were related to levels of infection by *Uncinula necator* that developed in the field. Photosynthetic rate was reduced more in White Riesling than in Concord at similar levels of *U. necator* infection and of *U. necator*-induced tissue necrosis, due primarily to greater palisade layer destruction in White Riesling than in Concord leaves. Because transpiration was relatively unaffected by infection, water use efficiency in both cultivars decreased with increasing infection. In Concord, visual ratings of tissue necrosis provided better estimates of photosynthesis reduction than did visual ratings of *U. necator* infection. In White Riesling, both methods gave similar estimates of damage.

Knowledge of the physiological effects of pest and disease attack has become increasingly important as improved strategies for integrated pest management and pesticide optimization develop. Unfortunately, these areas are complex and relatively little is known about the wide range of interactions between host, pathogen, and environment.

Carbon metabolism and water relations are critical areas of concern in understanding the effects of disease on plants. Recent reviews by Daly (4), Duniway (6), and Ayres (1,2) have summarized many of the known effects. Foliar obligate parasites (primarily rusts and mildews) reduce net photosynthesis, although in some

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cases a mild stimulation of photosynthesis has been found at early stages of infection (2,4). Whether this reduction is due to direct tissue destruction or to indirect effects of fungal metabolites or growth factors is not clear. Transpiration of plants infected with rusts and mildews can be quite variable (2,7,11,12).

Few studies on the physiological effects of powdery mildews have been conducted on perennial crops, except that of Ellis et al (7), which examined the detrimental effects of powdery mildew on apple leaf photosynthesis and transpiration. Infection of immature grape leaves by *Uncinula necator* (Schw.) Burr. reduces leaf area (5,10,14), but little is known about the response of mature grape leaves.

This study was undertaken to compare the effects of *U. necator* on photosynthesis and water relations of mature grape leaves of two cultivars with differing susceptibility and to evaluate the extent to which visual rating of *U. necator* mycelium correlates with *U. necator*-induced tissue necrosis (3) and physiological injury.

MATERIALS AND METHODS

Field-grown *Vitis vinifera* L. 'White Riesling,' a cultivar susceptible to *U. necator,* and *V. labruscana* Bailey 'Concord,' a less susceptible cultivar, were used in all studies. In early September, shoots were excised near their base by cutting under water and were transferred to the laboratory. Mature leaves were selected to represent a range from healthy to visually uninfected to severely infected conditions.

Net photosynthetic (Pn) and transpiration (E) rates of a 12-cm^2 area of attached leaves on excised shoots were determined with an open flow infrared gas analysis system (Beckman Instruments, model 864, Fullerton, CA 92634) having a dewpoint hygrometer (General Eastern, model 1100AP, Watertown, MA 02172) and a thin traplike assimilation chamber (because grape leaves are hypostomatous, the chamber enclosed only the abaxial surface of the leaf). The shoot and the assimilation chamber were enclosed in a growth chamber. A tungsten lamp light source was used to give the standard conditions of analysis: leaf temperature, 25 ± 1 C; photosynthetically active radiation, 800 $\mu E/m^2/sec$; leaf-air vapor pressure gradient, 17 ± 2 mb; and flow rate, 1.5 L/min.

U. necator infection and *U. necator*-induced tissue necrosis were rated visually with the Barratt-Horsfall system for rating affected leaf area and converting to percent affected leaf area using Elanco tables (13). Readings were made on the 12-cm^2 area on which Pn and E were measured.

Histological preparations were made in mid-September from mature leaves with varying degrees of *U. necator*-induced symptoms. Lamina pieces were fixed in formalin/acetic acid/ethanol (5:5:85, v/v), dehydrated in 1-butanol, embedded in paraffin, and microtomed at 12 μm. After removal of the paraffin with xylene, unstained sections mounted in 70% ethanol or immersion oil and sections stained in safranin and fast green were examined. The first method gave the clearest distinction between living and necrotic tissues in photomicrographs.

RESULTS

The relationship between visual estimates of percent infected area with *U. necator* and percent necrotic area indicated that for a given area covered by *U. necator,* leaf tissue necrosis was more

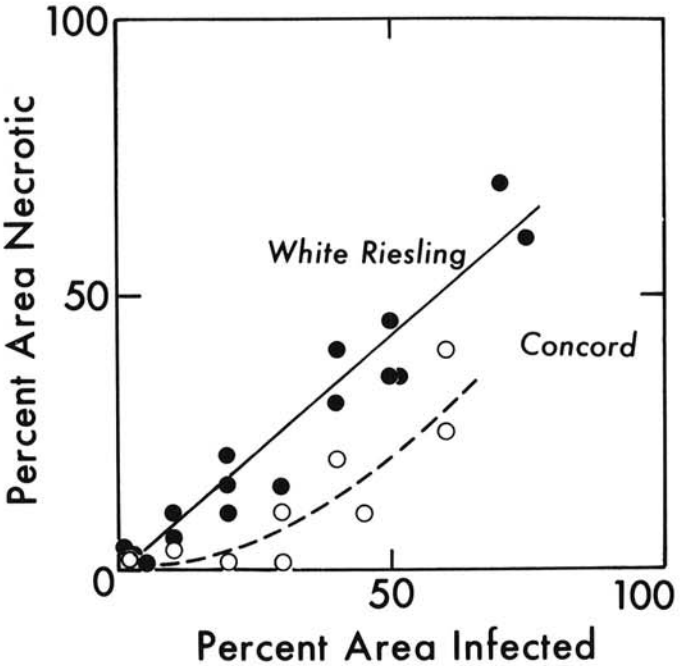

Fig. 1. Relationship between *Uncinula necator* infection (I) and *U. necator*-induced necrosis (N) in mature field-grown White Riesling and Concord grape leaves. Regressions and correlations are: White Riesling, $N = 0.86I - 1.52$, $r = 0.97$; Concord, $\sqrt{N} = 0.09I - 0.05$, $r = 0.93$.

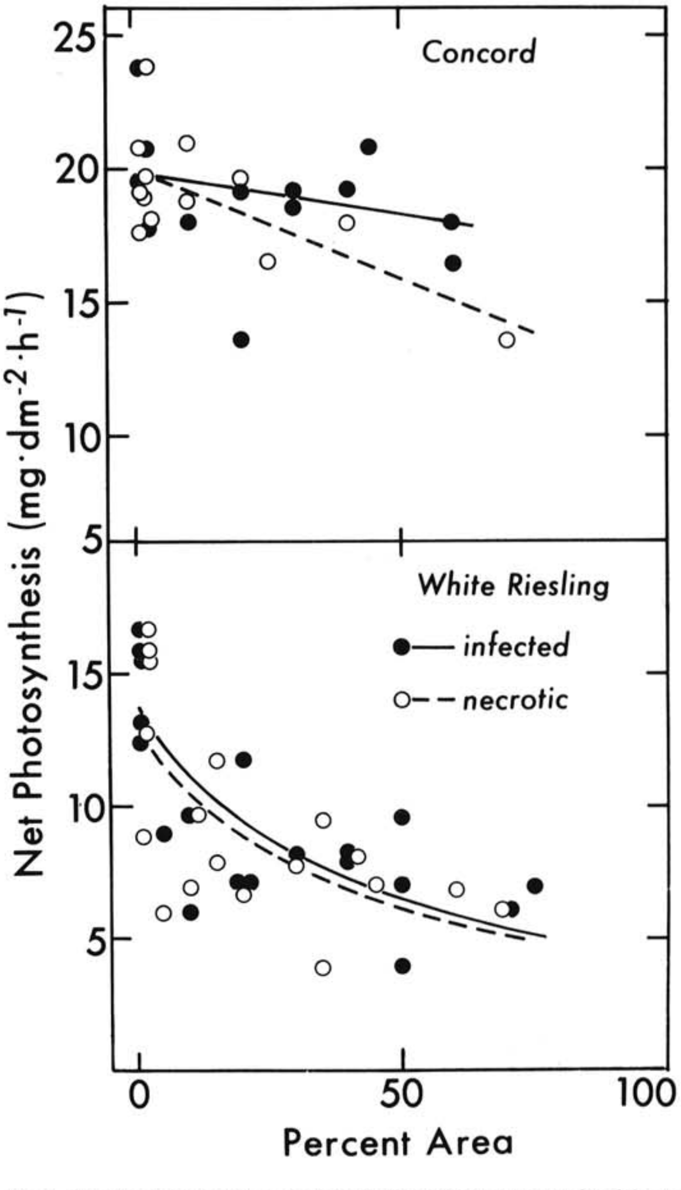

Fig. 2. Relationship between net photosynthesis (Pn) and area of leaf tissue infected (I) by *Uncinula necator* or with *U. necator*-induced necrosis (N) in mature White Riesling and Concord grape leaves. Regressions and correlations are: Concord, $Pn = -0.03I + 19.6$, $r = -0.27$; Concord, $Pn = -0.08N + 19.9$, $r = -0.70$; White Riesling, $Pn = -1.00\sqrt{I} + 13.8$, $r = -0.78$; White Riesling, $Pn = -0.97\sqrt{N} + 13.1$, $r = -0.72$.

extensive horizontally in White Riesling than in Concord (Fig. 1).

Pn reduction was also greater in White Riesling than in Concord (Fig. 2). In Concord, Pn correlated better with tissue necrosis than with "area infected," whereas both correlations were similar in White Riesling because of the high correlation between tissue necrosis and area infected in that cultivar. In contrast, E was not markedly affected by increasing infection or tissue necrosis, but showed extreme variability (Fig. 3).

Water use efficiency (WUE = mg of CO_2 fixed per gram of H_2O transpired per millibar of vapor pressure deficit) was reduced for both cultivars with increasing infection or necrosis (Fig. 4). As with Pn, WUE correlated better with infection and necrosis in White Riesling than in Concord.

Differences in both horizontal and vertical distribution of necrotic cells were found within and between infected leaves. Even small strips, 0.58 mm long, contained areas of: no necrosis, moderate necrosis (dead upper epidermal cells), and severe necrosis (dead upper epidermal and palisade cells) (Fig. 5). The third type of necrosis was rarely found in Concord leaves except in severely necrotic areas (Fig. 5A). In White Riesling (Fig. 5B), palisade layer necrosis occurred in both moderately and severely necrotic leaves. Necrosis of the palisade cells is the only type that would be expected to directly affect photosynthesis. Concord leaves were hairy and thicker (mainly with respect to palisade parenchyma) than the glabrous White Riesling leaves.

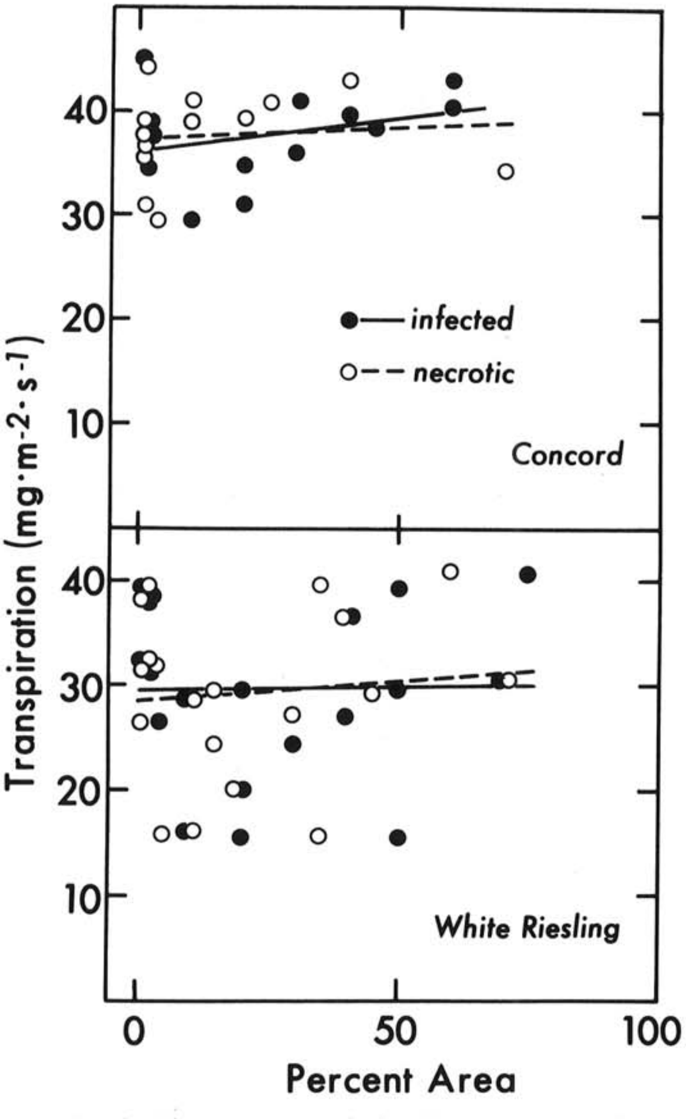

Fig. 3. Relationships between transpiration (E) and area of leaf tissue infected (I) by *Uncinula necator* or with *U. necator*-induced necrosis (N) in mature White Riesling and Concord grape leaves. Transpiration was measured only from the lower epidermis. Regressions and correlations are: Concord, E = 0.07I + 35.9, r = 0.33; Concord, E = 0.02N + 37.2, r = 0.10; White Riesling, E = −0.0006I + 29.1, r = −0.002; White Riesling, E = 0.04N + 28.5, r = 0.11.

DISCUSSION

The reductions in Pn and WUE were similar to those reported by Hewitt and Ayres (9), who found reductions in Pn in hypostomatous oak leaves infected on the upper surface with *Microsphaera alphitoides* (oak powdery mildew). Transpiration, measured from both leaf surfaces by Hewitt and Ayres (9), increased with time after inoculation, producing a reduced WUE in the infected leaves. The lack of effect on transpiration in our study contrasts with the reductions in E due to powdery mildew infections in barley, apple, and soybean (1,7,11). We found no evidence of stomatal plugging, as reported for downy mildew (*Plasmopara viticola*) infection of grape leaves (12). The E measured in our study was that through the lower epidermis and would not include water vapor loss associated with penetration of the upper epidermis by hyphae. No evidence of lower epidermis destruction was found because *U. necator* infection was limited to the upper epidermis in the leaves evaluated.

The results point out that visual estimates of *U. necator* infection may not always indicate very well the effects on grape leaf physiology. For example, a disease development level of 50%

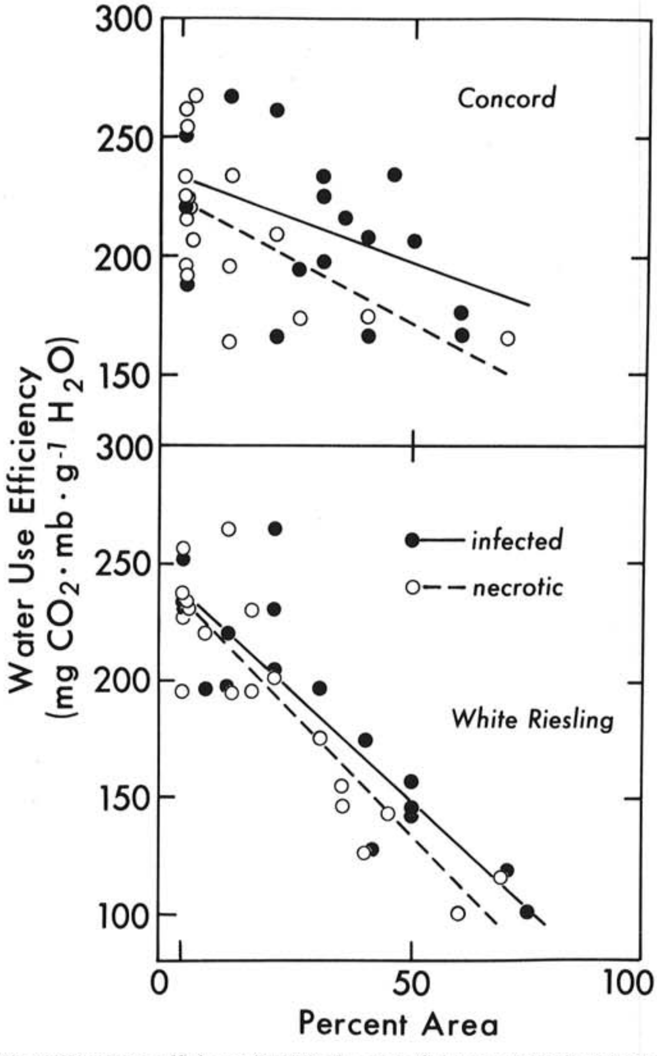

Fig. 4. Water use efficiency (WUE) of mature field-grown White Riesling and Concord grape leaves in relation to leaf area infected (I) with *Uncinula necator* and with *U. necator*-induced necrosis (N). Regressions and correlations are: Concord, WUE = −0.71I + 231, r = −0.45; Concord, WUE = −1.01N + 222, r = −0.59; White Riesling, WUE = −1.79I + 238, r = −0.90; White Riesling, WUE = −2.06N + 235, r = −0.91.

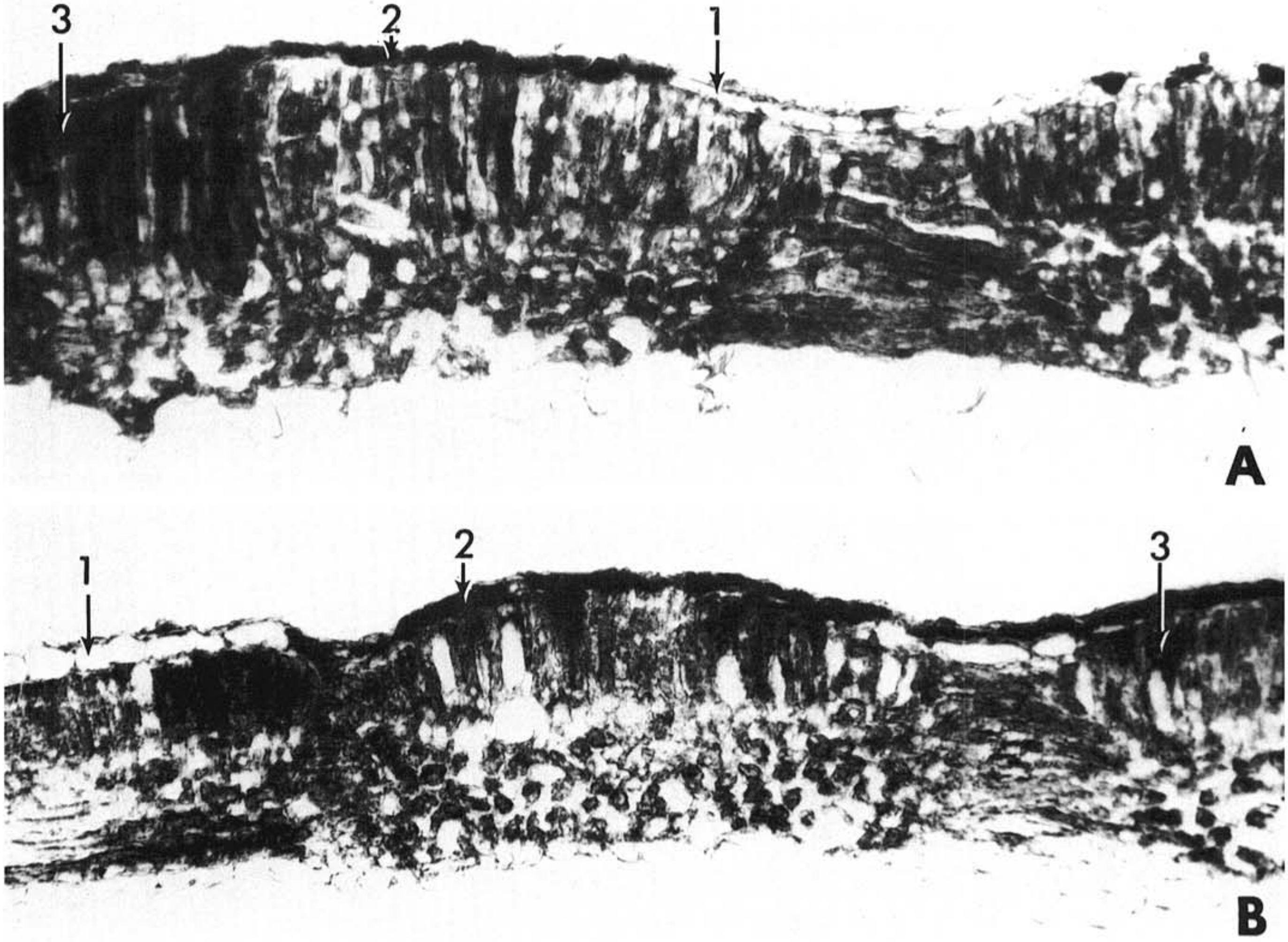

Fig. 5. Transverse, unstained sections of mature leaves of Concord (A) and White Riesling (B) grape cultivars field-rated as severely injured by *Uncinula necator*, showing three levels of damage: 1, no necrosis; 2, necrosis of upper epidermis; 3, necrosis of upper epidermis and palisade cells, × 337.

infected area in White Riesling leaves corresponded to about 45% necrotic area, 50% reduction in Pn, no effect on E, and a 38% reduction in WUE. By contrast, in Concord leaves, a 50% infected area corresponded to 20% necrotic area, 8% reduction in Pn, 8% increase in E, and 15% reduction in WUE.

This demonstrates that visual estimates of *U. necator* infection in mature leaves may be acceptable estimates of physiological damage in certain cultivars (White Riesling in this study). However, they may be poor indicators of physiological damage in other cultivars (ie, Concord). Unfortunately, no easy method with which to evaluate physiological damage for mass screening is apparent. In addition, this study evaluated infection of *U. necator* on mature leaves; cultivar screening based on the obvious effects of *U. necator* infection on immature tissue should also be examined closely.

Yarwood (15) has indicated that many mildews cause necrosis at the point of penetration and that this necrosis may extend to uninvaded cells close to the invaded cells. He further cites necrosis of ripening green grape fruits and grape shoots caused by *U. necator* as a good example of this phenomenon. Palisade layer destruction in the leaves in our study did not appear to be due to direct invasive by the fungus, and perhaps this reaction was a hypersensitive one as described by Yarwood.

The results of this study point out the possible inaccuracies of using visual ratings of disease development alone to predict the physiological damage to a plant. Habeshaw (8) similarly found different photosynthetic responses to powdery mildew and leaf blotch in barley cultivars. Workers in integrated pest management programs and disease-resistance breeding programs thus need to closely examine their evaluation procedures to ensure that they accurately estimate the relevant plant responses.

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