Vitis 23, 225—229 (1984)

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# Powdery mildew of *Vitis*: Papillae (wall appositions) as a host response to infection

by

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## L'oïdium de la vigne: Papillae (appositions du paroi) comme un répons de l'hôte au infection

Résumé : — L'oïdium, provoqué par *Uncinula necator* (SCHW.) BURR., de la vigne, par l'exemple du cultivar Rosette, produit papillae (appositions du paroi) en dedans des parois periclinales des cellules. On a vu les papillae dans des cellules épidermiques et subépidermiques des feuilles, des pétioles, des rafles et des rameaux verts. La fluorescence avec bleu d'aniline a démontré que les papillae consistent en callose (polysaccharides). Au microscope électronique à transmission, elles sont sombreuses aux électrons et elles se composent de vésicules.

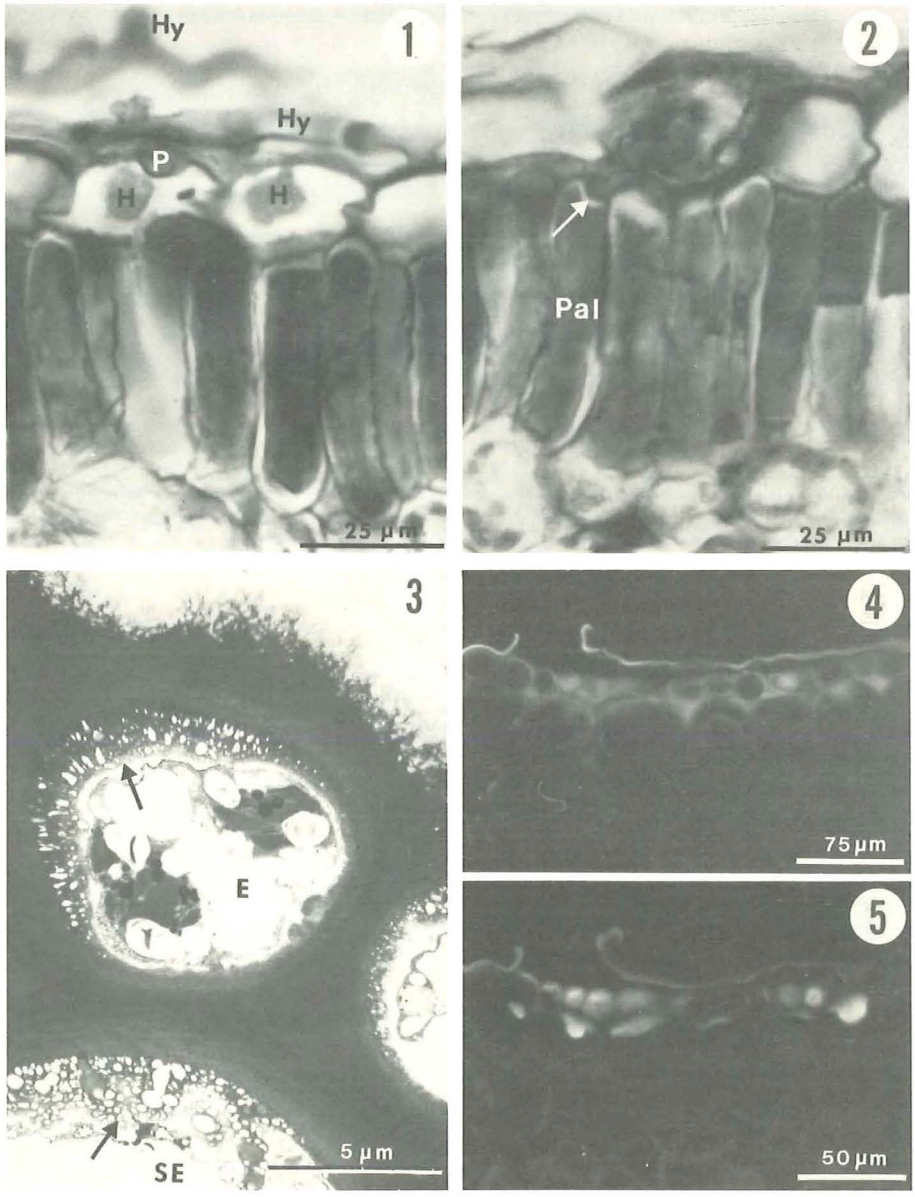
## Introduction

Powdery mildew diseases are typified by fungal pathogens which grow predominantly over the surface of the host plant. Prior to penetration of an epidermal cell, a specialized infection pad, termed an appressorium, forms at the hyphal apex. The appressorium produces a peg which penetrates the cuticle and the wall, allowing part of the fungus to grow into the host cell, forming a haustorium through which the fungus absorbs nutrients. The host cell characteristically produces at or near the peg a thickened area inside the wall. This area is called a papilla or wall apposition, and is generally composed of callose (polysaccharides), although, in some species, lignins are involved (AIST 1976). In this paper, the nipple-like growths are called papillae and the adjacent wall thickenings appositions, even though we recognize that their origin and composition are the same.

Haustoria of *Uncinula necator* (SCHW.) BURR., the cause of powdery mildew of *Vitis,* were first observed by VISIANI in 1851 (SMITH 1900). Haustoria and ingrowths of the host cell wall in infected grape leaves and berries were described by DE BARY in 1887 (SMITH 1900). In order to confirm or amend DE BARY's account, this paper will describe papillae and other wall appositions in epidermal and subepidermal cells of the infected grape cultivar Rosette.

## Materials and methods

We collected leaves, petioles, cluster rachises and green shoots from either non-sprayed Rosette vines or vines sprayed with appropriately scheduled fungicides during the growing season of 1980 in Naples, NY, USA. Specimens were prepared for light microscopic examination by fixation in FAA (formalin, acetic acid and 70 % ethanol v/v 5 : 5 : 85), dehydration and paraffin infiltration using a graduated series of ethanol :




Figs. 1 and 2: Transverse sections of Rosette grape leaves infected with *Uncinula necator* (SCHW.) BURR., stained with safranin and fast green and viewed with a light microscope. 24 June 1980. — Fig. 1: Hyphae (Hy) of *U. necator,* two epidermal cells each containing a haustorium (H), one cell having also a papilla (P). — Fig. 2: Papilla (arrow) in palisade cell (Pal).

Fig. 3: Ultrastructure of wall appositions (arrows) in epidermal (E) and subepidermal (SE) cells of infected Rosette petiole; transmission electron microscope. 30 September 1980.

1-butanol mixtures, and microtoming at 12 µm. Sections were stained in safranin and fast green for general anatomical study, or phloroglucinol-HCl for lignins, or aniline blue for fluorescence microscopy to detect callose (CURRIER 1957). Similar plant materials were plastic-embedded for transmission electron microscopy according to a previously published schedule (HOCH *et al.* 1980).

## Results

Following the appearance of mycelium on the adaxial surface of unsprayed mature leaves, haustoria and papillae were found in adaxial epidermal cells (Fig. 1), and papillae alone in palisade cells (Fig. 2). Haustoria and papillae stained green with safranin and fast green. The collapse of infected cells led to the necrotic spots seen later on adaxial leaf surfaces (LAKSO *et al.* 1982).

Infected petioles, cluster rachises and green shoots also had necrotic spots, where walls and papillae were thick and brown, up to 5 cells below the surface. Safranin staining of the papillae and other wall appositions was darker red than that of vessel walls. The phloroglucinol test for lignin, however, was negative throughout sectioned material except in fiber and vessel walls. Ultrastructurally, wall appositions in petiole cells were electron-dense except for numerous vesicles adjacent to the cell wall (Fig. 3). When examined by fluorescence microscopy, cuticle and epidermal cells of the petiole showed background fluorescence (Fig. 4). Strongly fluorescent wall appositions and papillae were evident in epidermal and subepidermal cells after staining with aniline blue (Fig. 5).

Samples from vines sprayed with fungicide showed no surface mycelia, haustoria, or papillae.

## Discussion

We have added three new observations to DE BARY's description:

(1) Papillae occur not only in epidermal but also in subepidermal cells, up to 5 cells deep in petioles and other cylindrical organs. They are similar to the structures termed

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Figs. 4 and 5: Transverse section of infected Rosette petiole viewed with a fluorescence microscope. 30 September 1980. — Fig. 4: Background fluorescence in epidermal cells. — Fig. 5: Same area stained with aniline blue. Papillae and wall appositions in epidermal and subepidermal cells fluoresce strongly.

Figs. 1 et 2: Coupes transversales des feuilles du cultivar Rosette infecté par *Uncinula necator* (SCHW.) BURR. Elles se teindrent avec safranin et fast green. Elles sont observées au microscope optique. 24 juin 1980. — Fig. 1: Hyphes (Hy) de *U. necator*, deux cellules épidermiques renferment deux haustoria (H), une cellule renferme une papilla (P) aussi. — Fig. 2. Papilla (flèche) dans une cellule pallisadique (Pal).

Fig. 3: Appositions (flèches) du paroi des cellules épidermiques (E) et subépidermiques (SE) de la pétiole infectée de Rosette, au microscope électronique à transmission. 30 septembre 1980.

Figs. 4 et 5: Coupe transversale de la pétiole infectée de Rosette au microscope à fluorescence. 30 septembre 1980. — Fig. 4: Fluorescence du fond dans des cellules epidermiques. — Fig. 5: La même aire teinte avec bleu d'aniline Papillae et appositions du paroi dans des cellules épidermiques et subépidermiques fluorescent très bien.

by BOUBALS (1961) "nécroses d'appressoria" or "appressoria nécrosés" in epidermal cells of the leaves of Vitaceae (see his Figs. 34—42). He thought that they might be the cause of powdery mildew resistance in some genera of the Vitaceae but not in cultivars of *Vitis*. We did not investigate the relationship between papillae and powdery mildew resistance in grapevines.

A haustorium was sometimes seen with or without a papilla in the same epidermal cell, but no hypha was seen in or between epidermal cells. AIST (1976) noted that papillae may form in response to chemical stimulation from wounding or pathogenic invasion.

(2) Both papillae and wall appositions are composed of callose (polysaccharides) without lignin. We found a change in staining reaction of papillae from safranin-negative in leaves to safranin-positive in cylindrical organs such as petioles.

(3) The ultrastructure of wall appositions is characterized by vesicles in the electron-dense material.

## Summary

Powdery mildew, caused by *Uncinula necator* (SCHW.) BURR., of grapevines, as exemplified by cv. Rosette, induces papillae (wall appositions) inside periclinal cell walls. Papillae occur in epidermal and subepidermal cells of leaves, petioles, cluster rachises and green shoots. Aniline blue fluorescence tests showed the papillae to be composed of callose (polysaccharides). Ultrastructurally, they are characterized by vesicles in the electron-dense material.

## Acknowledgement

The authors thank H. C. HOCH, Department of Plant Pathology, New York State Agricultural Experiment Station, for interpretation and Figs. 3—5.

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*Eingegangen am 4. 1. 1984*

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