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Original Article

Cucurbit Downy Mildew (*Pseudoperonospora cubensis)*

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Abstract

Downy mildew of cucurbits, caused by Pseudoperonospora cubensis, is a globally significant disease with major impact on cucurbit production. The pathogen induces sudden and widespread foliar epidemics that lead to considerable yield losses, particularly in cucumber and melon crops. This review outlines the taxonomy, biology, host specificity, distribution, life cycle, and epidemiological characteristics of the pathogen. There are two main races, one that infects cucumbers and melons, and one that infects pumpkins and squash. This disease can spread via air, water, and on agricultural equipment and human hands. In this review, special emphasis is given on host-pathogen interactions between P. cubensis and its economically important cucurbit hosts (Cucumis sativus, Cucumis melo, Cucurbita momordica, Cucurbita maxima, and Citrullus lanatus); pathogenic variability in P. cubensis at the species, genus, population levels and differentiation of races. This review serves to summarize the current status of this major pathogen and most important topics for future research and international collaboration.

Keywords: *Downy mildew, Biology, Cucurbits, Pseudoperonospora cubensis, Host-pathogen interactions, Classification, geographical distribution, Life cycle, Epidemiology*

Introduction

The most species used as human food of the plant groups is the family Cucurbitaceae. Downy mildew is a major disease of cucurbits with a global distribution (Palti and Cohen 1980). The causal agent, *Pseudoperonospora cubensis* (Berk. & Curt.) Rost. (Oomycota, Peronosporaceae), is an obligate biotrophic pathogen that infects over 40 host plant species belonging to 20 different genera of the family Cucurbitaceae. ucurbit plants are found in both tropical and temperate regions, and the ones that produce edible fruits were among the earliest to be grown by people. Cucurbit downy mildew is one of the most important foliar diseases of family Cucurbitaceae. It is caused by the fungus-like water mould *Pseudoperonospora cubensis*. The pathogen has a wide geographical distribution and has been reported in over 70 countries. (Lebeda and Urban, 2007). This disease spreads from the south to the north through tiny spores called sporangia, which form on sick plants. It cannot live in places where the winter gets very cold and freezing. Once it appears, the disease spreads fast and reduces both fruit quality and yield. It attacks cucumbers, melons, watermelons, squash, pumpkins, and gourds. Cucumbers are the most affected. There are different types of this disease, but each type only infects plants from the Cucurbit family. For example, the one that infects cucurbits does not attack legumes or spinach. The disease mainly damages leaves, which reduces photosynthesis. In suitable weather, it can destroy whole fields in a week. Fruits from infected plants are usually small.

Taxonomy And Morphology

According to recent taxonomic classification (Göker et al. 2007; Voglmayr 2008), *Pseudo Peronospora cubensis* belongs to

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Kingdom	Chromista
Subdivision	Peronosporomycotina
Class	Peronosporomycetes
Order	Peronosporales
Family	Peronosporaceae
Genus	*Pseudoperonospora*
Species	*cubensis*

Peronosporomycetes is comprised of 900 species, 75 genera and 19 families (Dick 2001a, c), and new genera were recently discovered (Göker et al. 2007; Voglmayr 2008). Among the five recognized species of the genus *Pseudoperonospora*, the type species is *Pseudoperonospora cubensis*. The genus includes *Ps. cubensis*, *Ps. humuli*, *Ps. cannabina*, *Ps. celtidis*, and *Ps. urticae*. *(Choi et al., 2005). Peronospora cubensis is the original name when discovered in Cuba by Berkeley and Curtis in 1868, Ps. cubensis was reclassified in 1903 after further observations of sporangia germination (Rostovzev, 1903). Pseudoperonospora species have true sporangia that germinate via cytoplasmic cleavage to produce zoospores (Fig. 1c), whereas species of Peronospora have sporangia that germinate directly via a germ tube (Palti and Cohen, 1980; Rostovzev, 1903).*

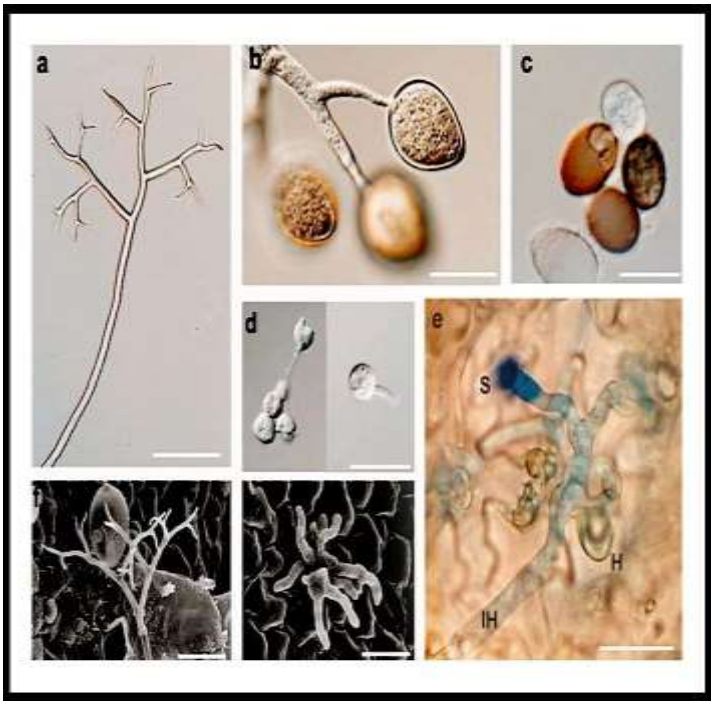

Fig.1 Morphology of *Pseudoperonospora cubensis*

(a) Sporangiophore (scale bar = 50 μm).
(b) Sporangia at the tip of the sporangiophore.
(c) Sporangia germinating through cytoplasmic cleavage.
(d) Zoospores and encysted zoospore with a germ tube.
(e) Intercellular growth showing haustorium [H], intercellular hyphae [IH], and stomata [S].
(f) Scanning electron image of a sporangiophore (scale bar = 20 μm).
(g) Sporangiophores emerging through stomata (scale bar = 20 μm).

Morphological characters may not provide sufficient information for the characterization of *Ps. cubensis* isolates, or even for differentiation between species of *Pseudoperonospora* (Runge and Thines, 2010). *Pseudoperonospora cubensis* sporangiophore morphology can vary in different environmental conditions like air temperature, soil temperature, humidity and sporangia dimensions are influenced by the cucurbit host (Iwata, 1942; Waterhouse and Brothers, 1981). Recent studies using a single isolate of *Ps. cubensis* on six different cucurbit species showed that the host plant influences five features of the pathogen's structure: sporangial length and width, sporangiophore length, length of the final branchlets, and the ratio of sporangial length to width. (Runge and Thines, 2010). The differences in these morphological features were clearer in hosts that are not closely related. These findings suggest

that using genetic markers is important when studying the evolutionary relationships of *Pseudoperonospora* species.

Signs And Symptoms

Downy mildew can attack plants of any age. It mainly affects leaves, but early infection can reduce photosynthesis, causing slow growth and lower yields, especially in cucumbers. Losing leaves early can also make fruits get sunburned. Symptoms look different on different cucurbit crops. The disease usually starts as small yellow or water-soaked spots on older leaves. The center of the spots turns brown and dies. The yellow spots often look greasy and have no clear edges. In wet weather, the infection can spread to upper leaves. In cucumbers, spots are usually angular, in melons they are irregular, and in watermelons they are smaller and round. As the disease spreads, spots increase in number and size, turning the field brown. In humid conditions, a fuzzy growth appears on the underside of the yellow spots. This is most visible in the morning after wet weather or dew. The underside may have dark purple or black sporangia that can be seen with a hand lens. This fuzzy growth is a key sign of the disease. Sometimes other bacteria or fungi infect the spots too. Because the disease spreads fast and symptoms show up 3–10 days after infection, control measures must start before symptoms appear.

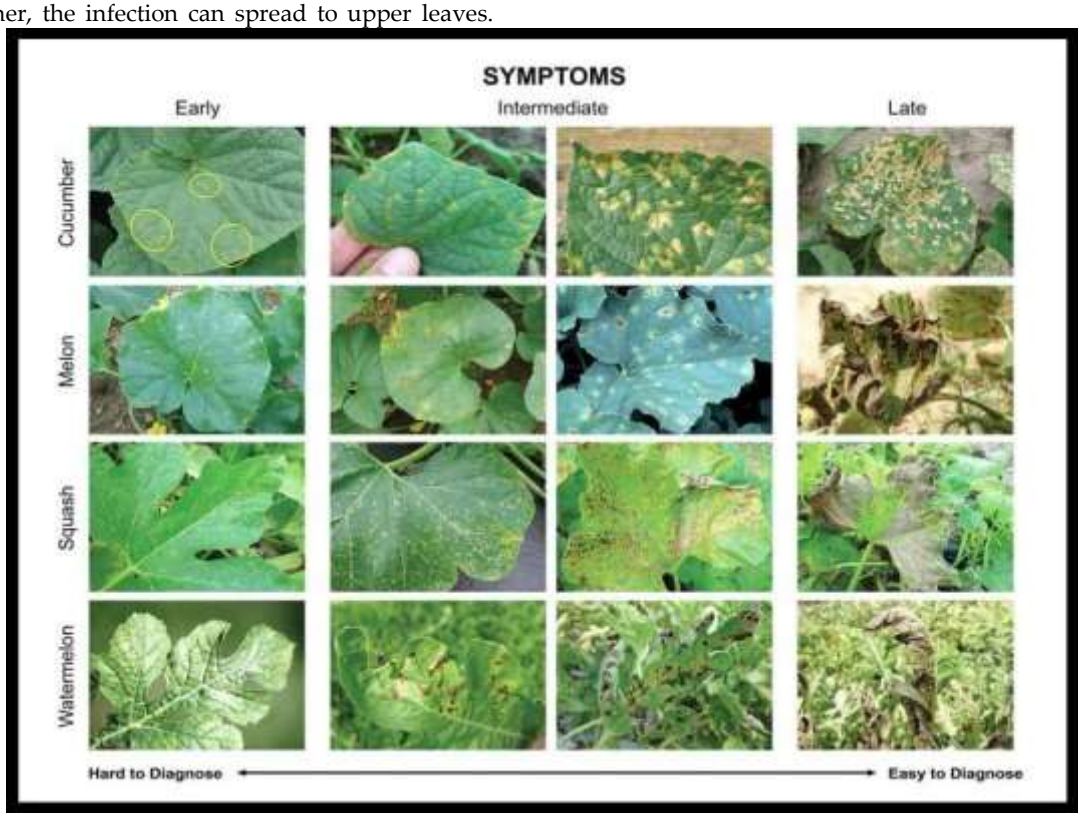

Fig.2 Downy mildew symptoms on four major cucurbit hosts (Cucumber, Melon, Squash, Watermelon) at early, intermediate and late stages of disease development. (*Photos Courtesy of G. J. Holmes*)

Life Cycle and Epidemiology

Reproduction of downy mildew pathogen is by sexual as well as asexual means. During the sexual phase, oospores are formed. Oospores are thick-walled and long lived therefore enable the pathogen to survive without host (Payak, 1975b; Ramalingam and Rajasab, 1981; Singh, 1995). Oospores are the main source of infection. The asexual phase happens when weather conditions are favorable. In asexual reproduction, the main infective units are spores, such as conidiospores and zoospores (Fig. 3). This happens through the production of conidia or sporangia. Sporangia release zoospores that infect new plants, while conidia can germinate directly to cause infection. Pathogens produced by conidia are evolutionary more advanced than those produced through sporangia (William, 1984a). Sporangia are generally elliptic in shape and measure is 15 to 25×20 to 35 µm (Skalicky, 1961). Sporangia are commonly light-grey to purple in colour at the time of maturity (Thomas 1996). The spores are easily released from the sporangiophores and spread by wind or splashing water. After landing on a leaf, they need wet conditions to germinate and infect the plant. High humidity is also required for spore production. Asexual spores of downy mildew do not last long, so quick dispersal and infection are

important. Factors like wind speed, temperature, leaf wetness, humidity, and sunlight affect how far the spores travel and how long they stay viable.

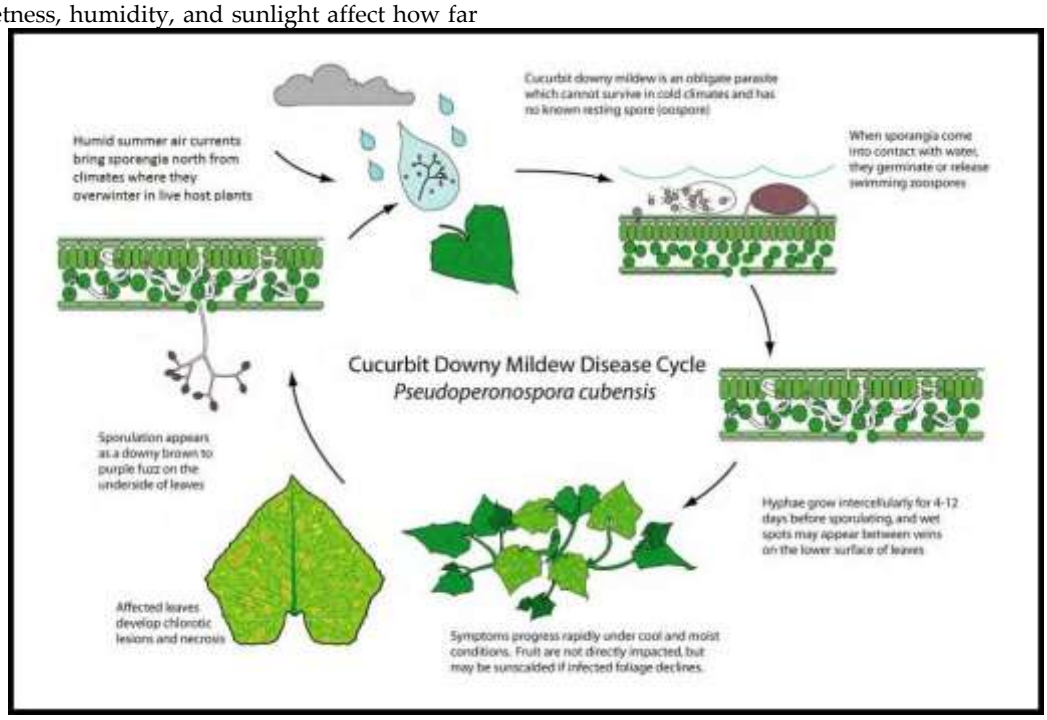

Fig. 3 Life cycle of *Pseudoperonospora cubensis (Graphic: R.A. Clark & A.J. Gevens)*

The type of germination is indirect, the multinucleate protoplast is differentiates into 5 to 15 biflagellate zoospores that emerge through a papilum (Palti and Cohen 1980). The zoospores swim in the direction of stomatal apertures where they settle and lose their flagella and encyst (Cohen 1981). A germ tube grows from the cyst and forms an appressorium. From this, a penetration hypha develops and enters the leaf through the stomata into the inner leaf tissue (Fig. 3). The penetration through stomata is the most frequent mechanism of penetration of *Pseudoperonospora cubensis* (Cohen 1981). A direct penetration occurs rarely (Lebeda 1990). Under suitable environmental conditions and in a susceptible host, the colonization of the parasite in tissue proceeds quickly and sporangiophores emerge from stomata between 5 to 8 days, predominantly on the lower side of the leaves where stomata are more frequent (Cohen 1981). On susceptible plants, a new infection can occur every 7 to 14 days, depending on the weather. *Pseudoperonospora cubensis* goes through multiple infection cycles in one season (Kranz 2003).

Result

The use of resistant cultivars, early disease detection, and timely use of fungicides are some combinations use for management of cucurbit downy mildew disease. Resistant cultivars are developed for cucumber and muskmelon, and to a lesser extent for squash and pumpkin. Higher air and soil temperatures increase downy mildew, while higher humidity reduces it. Resistant cucurbit plants used to control the disease well, but now they only slow it down. Resistant varieties cannot manage the disease alone.

Conclusion

Identifying the disease correctly is very important. In cucumber germplasm, genes for resistance to downy mildew caused by *Pseudoperonospora cubensis* should be introduced into high-yielding varieties, while improving the resistance traits in cucumber cultivars. Because of unpredictable climate changes, it is essential to continuously monitor soil and environmental conditions for disease assessment. Local soil and environmental data can help evaluate risk and predict disease outbreaks. Agronomic practices such as crop rotation, deep ploughing, proper watering, and fertilization, along with the use of herbicides, pesticides, and fungicides, help manage downy mildew. Due to the fast and aggressive nature of the disease, early detection and preventive fungicide use are crucial for control.

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Conflicts of interest
The authors declare that there are no conflicts of interest regarding the publication of this paper

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