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Abdelhak Rhouma
Higher Agronomic Institute of
Chott Meriem Sousse,
University of Sousse, Tunisia

Kabita Kumari Shah
Institute of Agriculture and
Animal Science, Gokuleshwor
College, Tribhuvan University,
Gokuleshwor, Baitadi, Nepal

Divya Pant
Department of Plant Science,
Pennsylvania State
University, University Park,
State College, United States of
America

Mohammad Imad Khriebe
National Center for
Biotechnology (NCBT),
Researcher Doctor at NCBT,
Damascus, Syria

Downy mildew of cucurbits caused by *Pseudoperonospora cubensis*: Disease profile and management

Abdelhak Rhouma, Kabita Kumari Shah, Divya Pant and Mohammad Imad Khriebe

Abstract

In recent years, the emergence of downy mildew had a significant impact on the production of cucurbits and disease control systems at multiple scales. Downy mildews wreak havoc on vital crops around the world, causing massive production losses. In order to achieve successful disease control, accurate identification and monitoring of these plant pathogens, as well as working on management strategies, is critical. Plant pathogens that cause epidemics are mostly responsible for successful disease management, thus it's critical to grasp their taxonomy, symptoms and indicators, and infection process before implementing any control strategies. Knowing the presence or absence of the pathogen, the volume of inoculum and their infection process, crop loss, the appropriate time to start chemical applications, and how to apply efficient remedies would all help to reduce cucurbit downy mildew losses. This review summarizes the current knowledge of taxonomy and morphology, disease development, signs and symptoms, infection process, pathogenicity, and control of *Ps. cubensis* with integrated disease management. In addition, the aim of this review paper is to develop both short- and long-term control measures of cucurbit downy mildew following chemical, cultural and biological control and host plant resistance are discussed.

Keywords: Host plant response, *Pseudoperonospora cubensis*, Downey mildew, Management practice, Cucurbits

1. Introduction

Cucurbit downy mildew is one of the most important foliar diseases of cucurbits caused by the fungus *Pseudoperonospora cubensis*. It is an important disease of cucurbits worldwide and has caused considerable yield losses in the Tunisia, United States, Europe, China in recent years. Downy mildew is caused by a water mold that infects cucurbits (Lebeda and Cohen, 2011) [18].

The obligate oomycete pathogen *Pseudoperonospora cubensis* infects *Cucurbitaceae* crops. Berkeley and Curtis (1868) [4] initially documented the disease in Cuba in 1868, hence the species name "*cubensis*". The pathogen was originally classified as *Peronospora*, but Rostovtsev proposed changing the name to *Pseudoperonospora* in 1903 (Palti and Cohen, 1980) [22]. It's an obligatory parasite, meaning it can only survive and reproduce if it has access to live host tissue. On the abaxial side of the leaf, the disease is marked by angular chlorotic lesions and a downy or felt like appearance. Small, water-soaked lesions form on the underside of cucurbit leaves as disease symptoms. Downey mildew is the most serious disease in cucurbits globally, causing up to 100% production loss, and *Ps. cubensis* strains have developed resistance to fungicides as well as overcoming resistance in cucumber germplasm (Savory *et al.*, 2011) [31]. As a result, established management measures are required to control downy mildew in cucurbits. Although resistant cultivars and chemical control-fungicides are the mainstays of *Ps. cubensis* management, there are other types of management strategies, such as cultural activities, that can help to reduce the disease severity. A thorough understanding of *Ps. cubensis* epidemiology, infection processes, and effective management methods is now lacking, but it will be required to guide future efforts in the development of innovative integrated management practices, host resistance management, and biological and chemical control (Porchas and Matheron, 2010; Simko *et al.*, 2014; Patel *et al.*, 2021; Salcedo *et al.*, 2021) [23, 24, 30, 31].

The aim of this paper is to briefly outline what is now known about *Ps. cubensis*, the pathogen that causes cucurbit downy mildew, including taxonomy, disease progression,

Correspondence
Abdelhak Rhouma
Higher Agronomic Institute of
Chott Meriem Sousse,
University of Sousse, Tunisia

signs and symptoms, control strategies, and management.

2. Taxonomy and Morphology

The family *Peronosporaceae* is the largest oomycete family and contains about 800 species of obligate biotrophic downy mildews. This pathogen belongs to the kingdom *Straminipila*, the phylum *Oomycota*, the subphylum *Peronosporomycotina*, the class *Peronosporomycetes* (Oomycetes), the order *Peronosporales* (downy mildews), and the family *Peronosporaceae* (Göker *et al.*, 2007; Savory *et al.*, 2011) [12,31]. The economically most important species on *Cucurbitaceae* crops are *Pseudoperonospora cubensis*. It is the type species of the genus *Pseudoperonospora*, which includes five recognized species: *Pseudoperonospora cubensis*, *Pseudoperonospora humuli*, *Pseudoperonospora cannabina*, *Pseudoperonospora celtidis*, and *Pseudoperonospora urticae* (Choi *et al.*, 2005) [8]. Downy mildew of cucurbits caused by this airborne pathogen occurs in almost of all cucurbit-growing countries (Runge and Thines, 2012) [28]. In 1868, originally named '*Peronospora cubensis*' when discovered in Cuba by Berkeley and Curtis (1868) [4]. In 1903, *Ps. cubensis* was reclassified after further observations of sporangia germination. *Pseudoperonospora* species have true sporangia which germinate via cytoplasmic cleavage to produce zoospores, whereas *Peronospora* species have sporangia that germinate directly via a germ tube (Savory *et al.*, 2011) [31]. Iwata (1942) [15], and Voglmayr *et al.* (2004) [33] noted that the morphology of sporangiophore can vary with temperature, and sporangia dimensions are influenced by the cucurbits host. *Ps. cubensis*, as a result, has a high level of pathogenic and genetic plasticity. Runge and Thines (2009) [27] showed that the cell matrix of the cucurbits host plays an important role in influencing five morphological criteria (sporangiophore length, length of ultimate branchlets, sporangial length, and width, and the ratio between sporangial length and width). Sporangiophores emerging through the stomata were tree-like, slightly curved, straight or hyaline, and monopodially branched in 3-4 orders (Dong *et al.*, 2021) [10]. Runge *et al.* (2012) [29] pointed out that the lengths of *Ps. cubensis* sporangiophores varied according to cucurbit species; *Bryonia dioica* (530 µm), *Citrullus lanatus* (397 µm), *Cucumis anguria* (498 µm), *Cucumis melo* (642 µm), *Cucumis sativus* (606 µm), *Cucurbita maxima* (425 µm), *Cucurbita moschata* (422 µm), *Lagenaria siceraria* (498 µm), *Luffa cylindrical* (500 µm), *Cyclanthera pedata* (497 µm), *Sicyos angulatus* (584 µm) and *Thladiantha dubia* (649 µm). Ultimate branchlets were in pairs, straight to slightly curved 9.0 µm long, 1.69 µm wide at the base, with a truncate or rarely swollen tip (Dong *et al.*, 2021) [10]. Runge *et al.* (2012) [29] revealed that the overall length of ultimate branchlets varied from 2.1 to 21.4 µm according to species of cucurbits. Sporangia were brownish, ovoidal, or lemon-shaped, measuring 24.8-16.7 µm, with a length/width ratio of 1.49 (Dong *et al.*, 2021) [10]. The differences among these morphological characteristics were more obvious in phylogenetically unrelated hosts. Many researches indicate that it is desirable to include information from genetic markers when resolving phylogenetic relationships in species of *Pseudoperonospora*. Choi *et al.* (2005) [8] revealed that the internal transcribed spacer region sequences of *Ps. cubensis* and *Ps. humuli* are highly similar, which suggests that *Ps. humuli* could be a taxonomic synonym of *Ps. cubensis*.

However, Mitchell *et al.* (2009) [20] using single nucleotide polymorphisms indicates that two nuclear and one mitochondrial gene support the separation of *Ps. cubensis* from *Ps. humuli*. In the same way, host range studies have demonstrated pathogenic differences between *Ps. cubensis* and *Ps. humuli* that further support the separation of these species (Gent *et al.*, 2009) [11].

Runge *et al.* (2012) [29] demonstrated that the sporangiophores length and the branching order correlated positively indicating a genetic pattern and it seems likely that proper nourishment, caused by adaptation to the host plant, results in longer and more frequently branched sporangiophores carrying more sporangia. Consequently, branching order is also correlated to the number of possible infections for the next generation.

3. Taxonomic Tree

Domain: *Eukaryota*

Kingdom: *Straminipila*

Phylum: *Oomycota*

Class: *Oomycetes*

Order: *Peronosporales*

Family: *Peronosporaceae*

Genus: *Pseudoperonospora*

Species: *Pseudoperonospora cubensis*

4. Symptoms and Signs

Pseudoperonospora cubensis the causal agent of cucurbit downy mildew is one of the most important foliar pathogens infecting cucurbits (Lebeda and Widrlechner, 2003) [19]. *Ps. cubensis* has several persistent identifying traits such as lesion development, form, color, and size, which vary according to on the host plant. Symptoms may differ in terms of cucurbit species and varieties, environmental factors, and parts infected. Infection of cucurbits by *Ps. cubensis* affects fruit quality and crop yield (Fig.1) (Savory *et al.*, 2011) [31].

Downy mildew of cucurbits is a foliar disease and is simply identifiable by the progress of chlorotic lesions on the adaxial surface of the leaf, sometimes with necrotic centers. Primary lesions range in size from 3 to 10 mm in diameter; as the disease progresses, the lesions merge to produce larger lesions that finally cover the entire leaf (Lebeda and Cohen, 2011) [18]. The intensity of the symptoms is determined by the pathogen's virulence and the host plant's susceptibility. The leaf vein might confine these diseases, giving them an angular look. As the infection progresses, the chlorotic lesions enlarge and may become necrotic. Within days after the initial infection, entire leaves may die as lesions expand and coalesce. Low canopy leads to fruit development cessation and exposure to sunlight (Keinath *et al.*, 2017) [17]. Despite the fact that the illness mainly affects the leaves, a loss in photosynthetic activity early in the plant's growth results in stunted plants and lower yields. Fruit sunscald can occur as a result of premature defoliation due to overexposure to direct sunshine. The symptoms of downy mildew infection vary depending on the type of cucurbit crop. Disease severity is also influenced by plant age, health, and vigor (Fig.1) (Patel *et al.*, 2021) [23].

Producing a high-quality cucurbit crop necessitates effectively managing downy mildew. This foliar disease is common in the northeast because the pathogen produces a large number of asexual spores that are easily dispersed long distances by wind, which enables it to spread widely.

Downy mildew appears as little, water-soaked patches on the leaf. Lesions start off yellow-green and then turn bright yellow on the upper leaf surface. Lesions grow angular, brown (necrotic), and deformed as they advance, and plants may defoliate. The existence of a downy growth on the underside of the lesion is critical in determining the disease's diagnosis. The pathogen does not affect fruit directly; however, affected leaves die prematurely which

results in fewer fruit and/or fruit of low quality (misshapen cucurbits, poor flavor, sunscald, poor storability). Secondary infections, such as soft rot bacteria or other fungi, can sometimes invade lesions. Because these pathogens infect a wide range of hosts, symptoms differ greatly from one host to the next, even within cultivars, making generalizations regarding downy mildew symptoms problematic (Fig.1) (Boregowda *et al.*, 2017) [6].

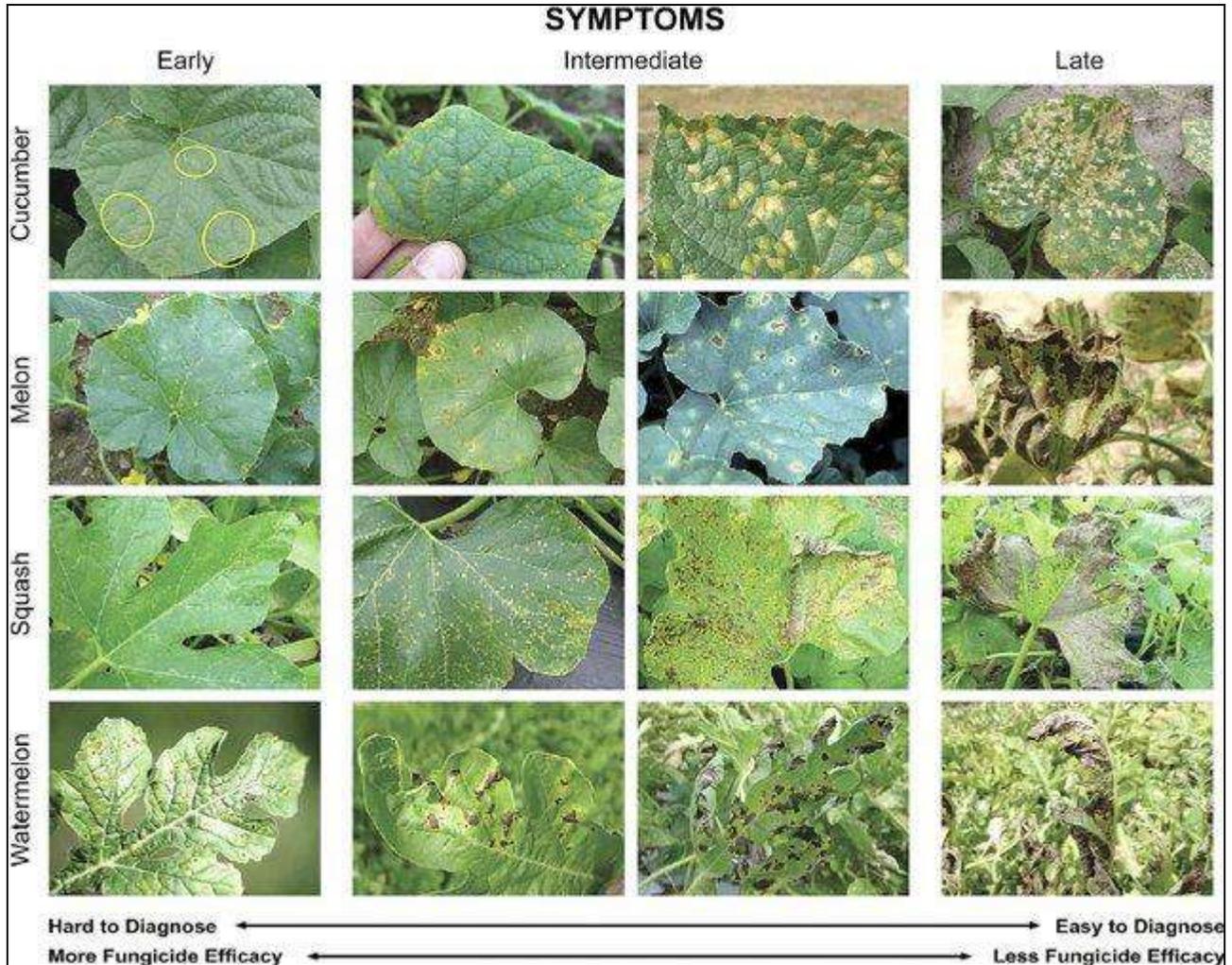


Fig 1: Early, intermediate, and late stages of downy mildew disease development with corresponding symptoms on four important cucurbit hosts (Photos Courtesy of G. Holmes) (Holmes *et al.*, 2015) [14].

5. Infection process

Pseudoperonospora cubensis causes a polycyclic disease in which the predominant inoculum comes from sporangia. Sporangia are carried by wind currents from sick plants to nearby or distant locations (Lebeda and Cohen, 2011) [18]. The fungus survives the winter as mycelium or oospores in or on plant components which is thick-walled, gumball-like structures that form the resting stage of the pathogen. The pathogen's development is influenced by temperature and humidity. Downy mildew outbreaks develop when germinating oospores form sporangiophores, which happen under cool and wet environment conditions. Although the liberation and dispersal of sporangia occur under conditions of low leaf wetness, cucurbit leaf moisture is essential for *Ps. cubensis* to successfully germinate and infect the host cucurbits. At the optimum temperature (15 °C) and at least two hours of moisture in cucurbit leaves, infection occurs with high levels of inoculums. Sporangia may also

germinate and cause infection at temperatures ranging from 5 to 28 °C, but longer periods of leaf wetness are required under these conditions or when less inoculum is present (Cohen, 1977; Patel *et al.*, 2021) [9, 23]. As a result, *Pseudoperonospora cubensis* dispersal potential appears to be restricted primarily by sporangia generation in source fields and the availability of susceptible hosts, rather than sporangia survival during transit. The incubation period depends on leaf wetness duration, temperature, inoculum concentration, and photoperiod, and can vary from 4 to 12 days (Cohen, 1977) [9]. The sporangia germinate by cleavage of the cytoplasmic, resulting in the release of 2 to 15 biflagellate motile zoospores (Palti and Cohen, 1980) [22]. And each sporangium contains dozens of zoospores that swim to vulnerable plants, preferring to open stomata, where they encyst and infect them even when just a thin film of free water is present (Fig.2) (Lebeda and Cohen, 2011) [18].

Germ tubes form from encysted zoospores and produce appressoria. A penetration hypha develops from the appressorium and penetrates through the stomatal opening into the leaf tissue. Hyaline coenocytic hyphae form and then grow intercellularly through the mesophyll and palisade tissues. Clavate-branched haustoria are established within mesophyll cells where they invaginate the cell membrane of cucurbit plants (Voglmayr *et al.*, 2004) [33]. These specialized structures are the site of pathogen uptake

of nutrients and delivery of effects or proteins that could potentially function to redirect host metabolism and suppress defense responses (Whisson *et al.*, 2007) [35]. The disease cycle takes seven to ten days from the first infection to the formation of more spores and secondary infection, although it can take as little as four days in humid conditions again, this varies depending on the downy mildew species and the host's susceptibility to infection (Fig.2) (Lebeda and Cohen, 2011) [18].

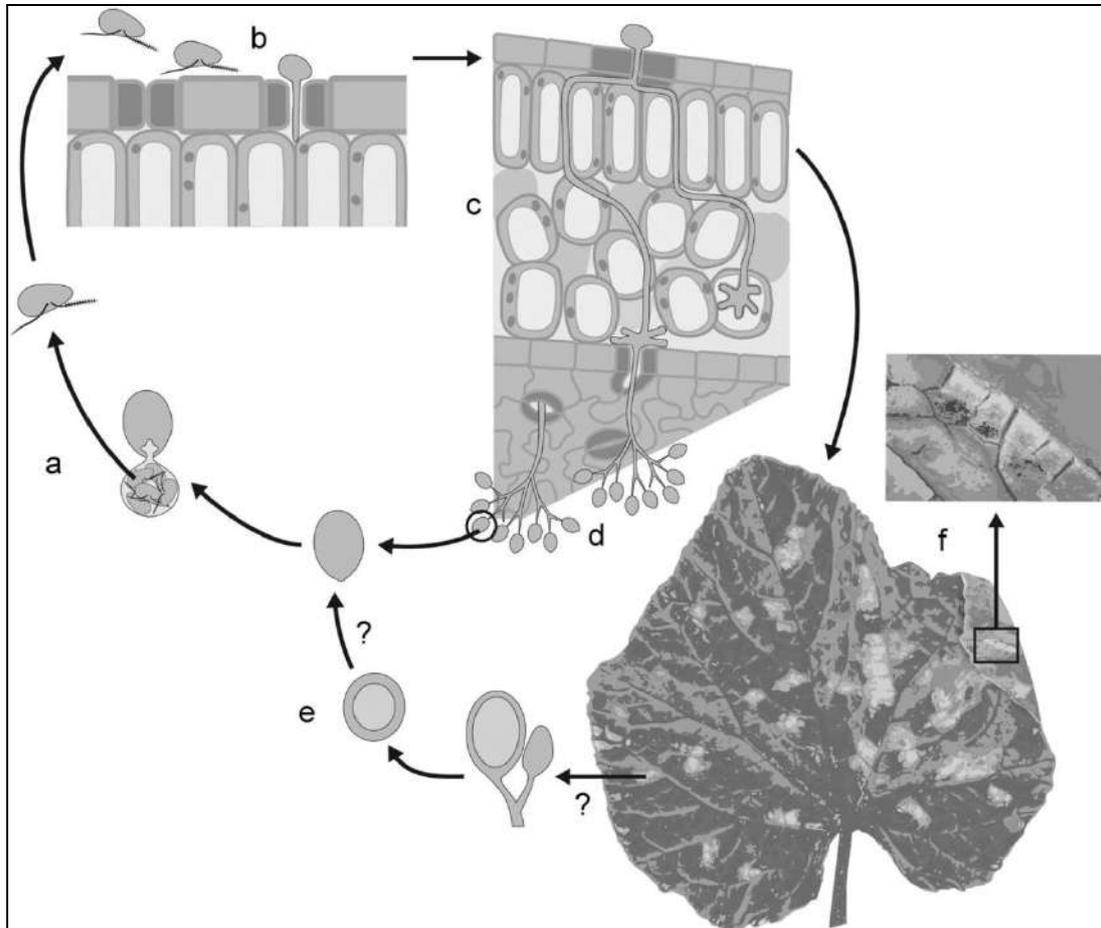


Fig 2: Life cycle of *Pseudoperonospora cubensis*: (a) Grey-purple lemon-shaped, aerially dispersed sporangia land on the leaf surface and germinate in free moisture to form biflagellate zoospores. (b) Zoospores swim to and encyst in the stomata, then penetrate the leaf surface via a germ tube. (c) Hyphae colonize the mesophyll layer, establishing clavate-branched haustoria within plant cells. (d) The diurnal cycle triggers sporulation and up to 6 sporangiophores emerge through each stomate, bearing sporangia at their tips. Sporangia are dislodged from sporangiophores by changes in hydrostatic pressure and are picked up by wind currents that carry them to their next host. (e) Chlorotic, angular lesions bound by leaf veins are a symptom of *Ps. cubensis* infection visible on the adaxial leaf surface. On the lower leaf surface, sporulation is visible (inset). (f) The role of the sexual stage of *Ps. cubensis* is unknown.

6. Integrated disease management

Effective downy mildew management necessitates an integrated pest management approach that considers all elements influencing disease development (pathogen, host, and environment), which is critical for controlling and predicting future cucurbit downy mildew epidemics (Lebeda and Cohen, 2011; Holmes *et al.*, 2015) [14, 18]. Management with a multi-faceted approach including cultural practices to decrease moisture in the plant canopy, avoidance by changing the planting date, using disease resistant or tolerant varieties, and applying effective fungicides can greatly control downy mildew infestation. Both the plant and the fungus are affected by the environment, with cool, damp weather providing ideal circumstances for downy mildews to invade. Further, the condition is typically difficult to identify due to the variety of lesion color and

size, as well as the severity of infection. To manage downy mildew and reduce reliance on pesticides, it's crucial to understand the disease cycle. This helps with early diagnosis, which is crucial for cucurbit downy mildew management (Patel *et al.*, 2021; Salcedo *et al.*, 2021) [23, 30]. Downy mildew is difficult to control if chemical sprays are not used promptly. As a result, an effective, appropriately scheduled fungicide treatment is the most crucial component of a successful downy mildew control strategy. And the key to doing so is using pathogen-specific mobile fungicides as soon as there is a danger of the pathogen being present. Broadly an integrated approach includes biological, chemical, cultural, and genetical control practices (Lebeda and Cohen, 2011; Holmes *et al.*, 2015; Patel *et al.*, 2021; Salcedo *et al.*, 2021) [14, 18, 23, 30].

Table 1. List of integrated management strategies that can prevent or reduce downy mildew infestation.

S.N.	Management strategies to control downy mildew
1.	Scout fields for symptoms of the disease every week - more often if possible. In shady sections of the canopy, scout the undersides of leaves, petioles, and stems.
2.	Use resistant (tolerant) varieties.
3.	Increase airflow by reducing plant density.
4.	Adjust planting dates to avoid favorable conditions for disease infestation.
5.	Early sowing to avoid moist conditions, destruction of weed hosts, proper nutrition and reducing the amount of moisture among the cucurbits.
6.	Follow the disease's progress on the cucurbit downy mildew forecast website throughout the growing season to apply timely fungicide treatments.
7.	Pruning and thinning plants to prevent overcrowding in the landscape and open up a thick canopy encourages quick leaf drying by increasing air circulation and light penetration.
8.	Wider space between plants reduces relative humidity in the plant canopy, therefore practice spacing that reduces relative humidity surrounding plants.
9.	Make sure your cucurbit transplants are disease-free before planting them.
10.	Keep weeds under control in the field. In surrounding fence rows and field margins, control alternative weed hosts (wild cucumber, golden creeper, and volunteer cucumbers).
11.	Reduce the quantity of leaf wetness early in the day (by watering in the late afternoon or switching from overhead irrigation to drip irrigation) and the disease will spread less.
12.	Excessive overhead watering should be avoided. Consider irrigating in the late morning to help the leaves dry quickly.
13.	Prior to an overhead watering event, apply a preventive fungicide. Use trickle irrigation if at all feasible.
14.	Consider washing equipment and tools before moving from one field to another.
15.	Ensure field workers wash their hands before moving from one field to another and, if possible, wear freshly laundered clothing each day.
16.	Apply fungicides immediately if symptoms are present, reapplying on a 7-day interval.

6.1 Cultural control

Cultural practices for prevention focus on reducing the period of leaf wetness including early planting, selecting sites with good air circulation, increasing planting space, avoiding overhead irrigation, and increasing air circulation within the canopy by trellising. Cultural practices aimed at alleviating high humidity can help prevent the disease or decrease its severity (Holmes *et al.*, 2015; Patel *et al.*, 2021) ^[14, 23]. The use of resistant varieties can delay disease onset by suppressing sporangia production by the pathogen and reducing disease inoculum (Mohamed *et al.*, 2016) ^[21]. Downy mildew severity can be decreased by taking actions that encourage airflow and reduce leaf wetness. Because early-morning leaf dampness is crucial for downy mildew growth. High relative humidity and free water encourage pathogen growth and dissemination, and extended leaf wetness encourages spore germination, keeping plants dry reduces disease transmission. However, such actions are often insufficient during prolonged, favorable environmental conditions and in the presence of high inoculum levels. Growing cucurbits in environments where humidity levels can be manipulated can help to manage downy mildew. For example, trellising cucurbits, increasing plant or row spacing, or growing in passive or traditional greenhouses can help reduce relative humidity and leaf wetness (Patel *et al.*, 2021) ^[23].

In the eastern United States the presence of downy mildew is an annual event in fall cucurbit production. Depending on the latitude of the production area, if a grower has the option to plant earlier in the spring, the disease may be largely avoided. For example, in North Carolina pickling cucumbers can often be planted in late-April and harvested before downy mildew has arrived. Conversely, in some mid-Atlantic states, pickling cucumbers are not planted after July because disease pressure is high and the cost of controlling the disease makes profitability much less likely (Mohamed *et al.*, 2016) ^[21].

Because this disease is carried to most fields on light winds,

cultural practices like crop rotation and sanitation have a limited effect on the incidence of downy mildew. Still, there are several things that growers can do to suppress the disease (Agrios, 2005) ^[1]. Growing vigorous plants, capable of withstanding or repelling disease onslaughts, is the first step. Further cultural considerations include selecting growing sites with good air drainage, full sunlight, and low humidity. Using drip irrigation, or scheduling overhead irrigation to avoid excessive leaf wetness, will also reduce disease incidence. When detected early, disease spread might be slowed somewhat by removing and destroying infected plants, and by taking care not to transport the disease by hand or on infected tools and equipment (Goldenhar and Hausbeck, 2019) ^[13]. It's critical to remove infected plants as soon as they're discovered to decrease the quantity of inoculum accessible to spread illness. Sanitation reduces the quantity of inoculum that overwinters in or on plant components such as mycelium or oospores, lowering the risk of infection to surrounding plants.

6.2 Host plant resistance

Host plant resistance is a practical and economic method of control for downy mildew. The adoption of resistant cultivars is one of the most significant parts of controlling *Ps. cubensis*. This is a unique technology embedded in seed, without direct cost to farmers, and does not require extra effort and understanding for its use. The use of host plant resistance requires: an effective screening technique; good sources of genetic resistance; a proper breeding method to efficiently incorporate the resistance; a sound strategy for cultivar deployment; and an effective monitoring system for pathogen virulence and resistance durability (Akem and Jovicich, 2013) ^[2].

An increasing number of cucurbit varieties are available that have some resistance to downy mildew. The use of these varieties does not necessarily assure that downy mildew will not become a problem, but rather, it can delay the onset of the disease or slow its development. Varieties that get their

resistance from both parent lines (homozygous) are more effective than those that get resistance from just one parent (heterozygous). In catalogs, these two types of varieties may be described as resistant and tolerant, respectively. The best way to manage downy mildew on organic farms is to use varieties with resistance to downy mildew in combination with timely applications of an effective, organically approved fungicide (Rajni *et al.*, 2018) ^[26].

Over the years, plant breeders have incorporated genetic resistance to downy mildew in some cucurbit varieties to combat this disease. The pathogen is known to overcome host plant resistance and develop resistance to fungicides. Genetic resistance to downy mildew can be a highly effective disease management tool, as it is active for the life of the plant. However, the use of genetic resistance against downy mildew does have limitations. Firstly, cucurbit cultivars and varieties resistant to all known races of the pathogen and suitable for all planting windows may not be available (Porchas and Matheron, 2010) ^[24]. Also, *Ps. cubensis* is a very adaptable pathogen, having the ability to develop new races which in time can overcome the genetic resistance within cucurbit cultivars and varieties. Finally, the races of the pathogen present in fields may differ from year to year, making decisions on cucurbit variety and cultivar selection difficult (Porchas and Matheron, 2010) ^[24].

Most popularly used cultivars of cucumber and cantaloupe, and to a lesser extent squash and pumpkin, have some level of downy mildew resistance bred into them. Even though cultivars with downy mildew resistance may become diseased, disease onset may be delayed, the disease may be less severe or the pathogen may produce fewer sporangia than on cultivars without resistance. However, since a new, more virulent strain of *Ps. cubensis* arrived in the eastern United States in 2004, cucumber production cannot rely solely on downy mildew resistant cultivars for control (Rajni *et al.*, 2018) ^[26].

6.3 Chemical control

Due to a lack of significant resistance in cultivars and efficient fungicides, fungicides are often used to treat downy mildew in cucurbits. When climatic circumstances encourage disease growth, an active fungicide program is typically required for crop prevention and protection to minimize output losses (Savory *et al.*, 2011) ^[31]. An effective, correctly scheduled fungicide application is the most crucial component of a successful downy mildew control program. As a result, when environmental circumstances promote disease growth, early and frequent fungicide treatments are essential to preserving the crop (Savory *et al.*, 2011) ^[31]. And the key to that is applying mobile fungicides targeted to the pathogen starting when there is a risk of the pathogen being present. Mobile (or translaminar) fungicides are needed for control on the underside of leaves. Each year there can be changes to the fungicides recommended as the pathogen develops resistance or new products are registered. Because these fungicides have targeted activity, additional fungicides must be added to the program when there is a need to manage other diseases such as downy mildew. Most targeted fungicides effective for downy mildew are also effective for Phytophthora blight (Keinath *et al.*, 2017) ^[17].

Prior to the reappearance of cucurbits downy mildew in the United States, resistance to phenylamide and strobilurin

fungicides had been seen in other countries. In the United States, the disease was shown to be resistant to mefenoxam in 1987, and strobilurin and carboxylic acid amide fungicides are no longer advised for cucurbits downy mildew. Fluopicolide, a pyridinylmethyl-benzamide fungicide, was recently shown to have decreased field effectiveness (Brzozowski *et al.*, 2016; Keinath, 2016; Rahman *et al.*, 2017; Goldenhar and Hausbeck, 2019) ^[7, 13, 16, 25].

There are quite a few materials that are labeled for control of downy mildew that can be used by organic farmers. Many of these materials, including several bio-fungicides, can provide some suppression of the disease if applied in a timely fashion. However, only a few materials provide consistent levels of control, according to ongoing research by Dr. Meg McGrath at Cornell's Long Island Horticultural Research and Extension Center. Her studies show that sulfur and 'stylet' oil are the most effective materials for managing downy mildew. Fixed copper fungicides have overall been less effective, but can be highly (in the case of preventive control) (Babadoost *et al.*, 2004) ^[3].

Organically-approved fungicides (as well as conventional materials) work by preventing infection of healthy tissue, so starting treatment early is key to their effectiveness. uncontrollable, established downy mildew colonies [spots] not only do not disappear when treated, but they also continue producing 100s of spores. These give the spots their downy appearance. The more spores, the more opportunity that some will land by chance on leaf tissue lacking spray deposit (Wehner *et al.*, 1997; Agrios, 2005; Mohamed *et al.*, 2016) ^[1, 21, 34]. Therefore, the most important component of an effective management program for downy mildew is an effective, properly-timed fungicide program (Keinath *et al.*, 2017) ^[17].

When planting cucurbit transplants, ensure that the transplants are free from disease. Apply a fungicide on field-planted transplants before installing a row cover or tunnel and immediately after the row cover or tunnel is removed (Wehner *et al.*, 1997; Akem and Jovicich, 2013) ^[2, 34]. Select fields and manage the crop to promote air movement and reduce humidity levels inside the crop canopy. Avoid excess overhead irrigation. Consider irrigating during the late morning to facilitate rapid leaf drying. Apply a preventative fungicide prior to an overhead irrigation event. If possible, use trickle irrigation (Babadoost *et al.*, 2004) ^[3].

Follow a preventative spray program. Vegetable Production Recommendations, for registered fungicides that can be applied to control downy mildew. Under wet and humid conditions, apply a fungicide every 5-7 days. When dryer weather occurs, the interval between applications can be relaxed to 7-10-day intervals. Always apply fungicides with at least 250-300 L of water per hectare (25-30 gal/acre). Ensure adequate coverage and spray penetration into the canopy. Rotate between fungicides from different chemical families (Babadoost *et al.*, 2004) ^[3].

Downy mildew spreads via airborne conidia and half spore, will travel. It's also possible to have local sources of initial infection, from greenhouse-grown cucurbits and verbena planted prior to field production. In addition, successive cucurbit plantings can lead to the spread of infection from field to field on a farm so new plantings should be physically separated from older plantings to limit the movement of conidia (Agrios, 2005; Akem and Jovicich,

2013) ^[1, 2]. Downy mildew can spread quickly because it only takes 3 to 7 days from initial infection to the appearance of symptoms, and a large number of conidia can be produced in a short time. Favorable conditions for the disease include dense plant growth, low light intensity, and high relative humidity. Infection can occur at 50 to 90 degrees F but 68 to 80 degrees F is ideal. If it gets very hot, over 100 degrees F, the disease does not spread.

Since there are growing concerns regarding pollinator health, chemical treatment should be used when other control techniques seem to be unsuccessful under integrated management. Where chemical management is required, it should be applied in a way that minimizes pollinator exposure to fungicides like chlorothalonil, and when practical, the fungicide should be applied when fewer pollinators are foraging and visiting flowers. In trials conducted to identify alternatives to tank mixing with chlorothalonil, both Tritex (mineral oil) and Microthiol Dispers (sulfur) were determined to be equally effective tank-mix partners and pose less of a risk to bee health (Akem and Jovicich, 2013) ^[2]. Chemical control, on the other hand, is not always viable due to the high price of fungicides and their application.

6.4 Biological control

Although downy mildew is an important pathogen on a number of high-value crops, there has not been the volume of research on biocontrol measures as has been conducted for chemical control measures. Results from studies conducted to date reveal the most promising products are formulations of different bacterial strains including those of *Bacillus* and *Streptomyces*. However, levels of control are not as high as those achieved with conventional chemistries. As such, much research is needed in this area (Keinath *et al.*, 2017) ^[17].

Fortunately, cucurbit downy mildew is one of the easier diseases to manage organically and there are a number of options including oil-based products like Eco E-rase (jojoba oil), JMS Stylet oil (paraffinic oil), Trilogy (neem oil), and Organocide (sesame oil), as well as potassium bicarbonate-based products such as Kaligreen and MilStop to name a few. With these products, spray coverage is essential since they are only effective at the site of application. So apply them in a large enough volume of water at a higher pressure to move the spray and penetrate the plant canopy. Genetic resistance can often both delay the onset of downy mildew and reduce overall disease severity (Wehner *et al.*, 1997) ^[34].

7. Conclusion

Over the last decade, significant progress has been made in understanding the biology, epidemiology, and treatment of *Ps. cubensis* caused downy mildew of cucurbits, but there is still more to learn. To enable proper management and increased resistance in the future, we must advance our understanding of pathogen taxonomy and morphology, signs and symptoms, pathogenicity and infection process, and integrated disease management—chemical, cultural, and biological control, host plant resistance. Although various integrated disease management techniques are used to control downy mildew in cucurbits, disease management will most likely be achieved in the long run through a combination of host resistance and well-timed fungicide applications driven by real-time pathogen detection to

ensure fungicide activity and genetic resistance. To avoid cucurbit downy mildew outbreaks and losses, an integrated strategy that encompasses all elements impacting disease development and control strategies is required.

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9. Declaration of Conflict

The authors declare that they have no conflict of interest. Informed consent was obtained from all individual participants included in the study. This article does not contain any studies with human participants or animals performed by any of the authors.

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