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DOWNY MILDEW OF CUCURBITS *(PSEUDOPERONOSPORA CUBENSIS)*: THE FUNGUS AND ITS HOSTS, DISTRIBUTION, EPIDEMIOLOGY AND CONTROL

By

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Taxonomy of the genus *Pseudoperonospora*, morphology of *Pseudoperonospora cubensis* (Berk. et Curt.) Rostow. and occurrence of its oospores, are described briefly. A list is presented of over 40 cucurbitaceous host species, representing about 20 genera, on which *P. cubensis* has been recorded. Two or more races exist in Japan and the United States, but not in Europe or the Middle East. The distribution of *P. cubensis* is widest on all continents on cucumbers (70 countries) and muskmelon (50 countries); on *Cucurbita* and watermelons it extends to about 40 and 25 countries, respectively.

P. cubensis may overwinter as oospores, though this seems rare, and on wild hosts or crops grown in the open or under cover. Airborne sporangia may also reach cooler countries from regions with mild winters.

Apart from the leaf wetness essential for infection, the factors determining disease progress are: rate of foliage growth and physiological age of the host; amount of primary inoculum available, light, and the rate at which lesions necrotize. The interaction of these factors is described for early, mid-season, and late crops. Losses caused by *P. cubensis* depend on the growth stage at which the crop is attacked, and on the rate of foliage and pathogen development. Breeding has produced downy mildew resistant lines of cucumbers, used chiefly in the United States, and some resistant lines of melons and watermelons. The most important agricultural practices used to restrict downy mildew development are proper irrigation management and avoidance of sowing in proximity to infected crops.

Success of control by protectant chemicals depends largely on proper timing of applications. Proximity of inoculum sources, hours of leaf wetness, age of crop, and irrigation practices are the principal factors that determine when to begin treatments. These factors and rate of leaf formation determine the frequency of applications. Application of systemic fungicides is much easier to time correctly.

KEY WORDS: Downy mildew; *Pseudoperonospora cubensis;* cucurbits; cucumber; melon; watermelon; epidemiology; resistance breeding.

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INTRODUCTION

Downy mildew of cucurbits, caused by *Pseudoperonospora cubensis* (Berk. et Curt.) Rostow., was first recorded from Cuba in 1868 (15). About 20 years later it was reported from Japan (80). It has since spread to almost all countries in which cucurbits are grown commercially. The disease is destructive in many parts of the world, and especially in countries with warmer climates. With the advance of agriculture in these countries, cucurbits and their diseases are of increasing economic importance.

Research on this downy mildew has been carried out over many years. In the 1930s and 1940s in the U.S.A., most of these studies centered on chemical control and breeding for resistance, while host range studies proceeded in Japan. More comprehensive work on the biological and epidemiological aspects of this downy mildew has been in progress over the past 10-15 years, chiefly in Japan and Israel, and lately also in India and the U.S.A.

This review describes the taxonomy, morphology, symptoms, host range, specialization, distribution and epidemiology of this downy mildew, the economic losses that it causes, as well as its control by breeding for resistance, cultural practices, and fungicides. It is intended to publish in the future a more extensive review on the symptoms, which will include a detailed discussion of factors affecting each stage of disease development: sporulation, dispersal, viability and germination of spores, infection, colonization, and lesion development. The interplay of these factors is also described by Cohen (32).

TAXONOMY, MORPHOLOGY AND SYMPTOMS

TAXONOMY OF THE GENUS *PSEUDOPERONOSPORA*

The basis for generic delimitation in the Peronosporaceae is the sporophore and its sporangia. This fact has been the cause of much controversy, especially in the differentiation between the genus *Pseudoperonospora* and the two genera closest to it, *Peronospora* and *Plasmopara.*

The principal feature dividing *Pseudoperonospora* from *Peronospora* is that the spore wall in the latter is non-poroid, uniformly thick, and germination can only be by germ tube, whereas the spores of *Pseudoperonospora* are true sporangia with a poroid apex (141) and germinate by zoospores. What distinguishes *Pseudoperonospora* from *Plasmopara*, which also has a poroid spore wall and germinates by zoospores, is the way the sporophores branch and terminate. These branches in *Plasmopara* are at right angles, or nearly so, to the axis and their tips are blunt; in *Pseudoperonospora* branches arise at acute angles to the axis and their tips are acute.

The genus *Pseudoperonospora* is at present held to comprise five species: *P. cubensis* attacking Cucurbitaceae and four morphologically similar species – *P. humuli* (Mig. & Tak.) G.W. Wils., *R. urticae* (Lib.) Salm. & Ware, *P. cannabina* (Otth.) Curzi and *P. celtidis* (Waite) G.W. Wils. – which attack the closely related host families Urticaceae, Cannabinaceae and Ulmaceae and might prove to be forms of one species (141).

PSEUDOPERONOSPORA CUBENSIS AND ITS MORPHOLOGY

Mycelium, sporangiophores and sporangia

Mycelium hyaline, coenocytic and intercellular, develops abundantly in the mesophyll, but also penetrates palisade tissues. Hyphae diameter 5.4-7.2 μ. Small, ovate, intercellular haustoria, sometimes with branches.

Sporangiophores, 180-400 μ in length, 5-7 μ in width, basally inflated, dichotomously branched in their upper third, emerging in groups of 1-5 from stomata. The sporangia are borne singly on the sporiferous tips (Fig. 1).

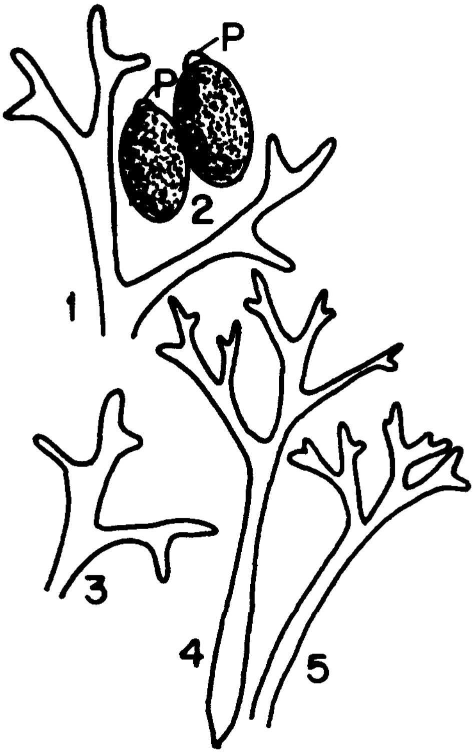

Fig. 1.

Pseudoperonospora cubensis (from Rostowzew, ref. 110).
1 and 3: upper parts of sporangiophores (x 900);
2: two sporangia, with papilla (p) (x 900);
4 and 5: two sporangiophores (x 450).

Sporangia grayish to olivaceous-purple, ovoid to ellipsoid, with a papilla at the distal end, measuring 20-40 x 14-25 μ. Sporangia germinate by production of 2-15 zoospores with two lateral flagellae; they measure 10-13 μ in diameter. Zoospore germ tubes attain lengths of 50-95 μ (80).

Oospores and their distribution

Oospores have been observed on cucumber leaves in open fields in the U.S.S.R. (110), Japan (60) and North China (27), and recently in protected culture sites in Italy (45). According to Hiura and Kawada (60), oogonia are obovoid to ellipsoid or irregular pyriform, and measure 28-56 x 24-44 μ, the antheridia are clavate to globose and measure 14-22 x 10-16 μ; oospores are spherical, rarely obovoid to ellipsoid, with hyaline to pale yellowish, smooth walls 1.5-3.5 μ thick, with a diameter of 22-42 μ. Chen *et al.* (27) and Rostowzew (110) mention the presence of oil globules in the oospores. Hiura and Kawada (60) found oospores even in young lesions showing little discoloration and observed mature oospores commonly present in the lesions of apparently vigorous leaves attached to the plant. However, D'Ercole (45) found the oospores on senescent leaves on the soil as the season advanced toward its end.

Bains and Jhooty (6), in India's Punjab, searched for, but failed to detect, oospores on diseased leaves of *Cucumis melo, C. callosus, Luffa aegyptiaca, L. acutangula,* and *Lagenaria siceraria.* However, oospores were found to have formed on *Melothria maderaspatana* when infected leaves were incubated at 20°C in a moisture-saturated atmosphere. These oospores were light yellow in color and 13.5-19.8 μ in size (10). In addition, Khosla *et al.* (79) reported smooth globose oospores, averaging 22 μ in diameter, on *Trichosanthes dioica,* which is cultivated as a cucurbit crop in some parts of India.

HOST PARTS AFFECTED AND SYMPTOMS

By far the most frequent part to be attacked by *P. cubensis* is the leaf blade, and in many hosts this is the only part affected. The downy mildew may appear on the cotyledons, but is rare or absent on very young true leaves when they are in the process of unfurling or immediately thereafter.

On cantaloups, Van Haltern (136) has found sporangiophores of the mildew on stems, leaf petioles, tendrils, and the peduncles of blossoms of heavily infected vines, but not on small cantaloup fruits. When the main stems of runners were sectioned, mycelium and haustoria of the fungus were found in the cortex.

To the best of our knowledge, only D'Ercole (45) in Italy has recorded the mildew on cucumber fruits. The symptoms that he observed quite frequently on cucumbers grown under cover were watery spots, and subsequently fungal fructifications on the fruit; growth of infected fruits was retarded, and their taste was insipid.

Symptoms on the leaf blades of different species of cucurbits vary somewhat, and may even vary on varieties within the same species. On most hosts, the very first symptom is the appearance of a small water-soaked lesion on the underside of the leaf. This lesion, when viewed from the upper side of the leaf, rapidly assumes various shades of yellow and is covered on its underside by a violet-gray to blackish down. The lesion subsequently becomes necrotic, beginning at the center, while its periphery is still yellowish-green. The down is absent from the necrotic tissue on the underside of the leaf except on veins running through the lesion. The discrete lesions measure

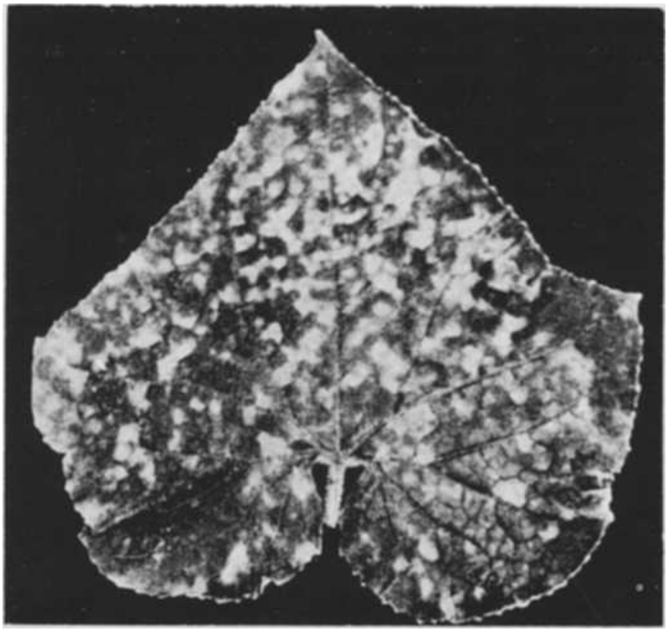

Plate 1. Symptoms of downy mildew on the upper side of a cucumber leaf.

3-15 mm in diameter. At a later stage the lesions may coalesce, giving the leaf a checkered appearance, with at first yellow, then brown spots predominating. Eventually the leaf blades become dry and curl upward while the petioles remain green, but ultimately the petioles also become dry, although the leaf is not shed.

On cucumbers, the downy mildew produces a very bright yellow lesion on the upper leaf surface in many varieties. This lesion is often sharply delineated by leaf veins, and thus assumes a distinctly angular shape. Plate 1 shows the symptoms of downy mildew on a cucumber leaf.

On melons and watermelons, the downy mildew in most varieties develops lesions which are neither as bright nor as angular as those commonly observed on cucumbers. On these hosts the lesions appear more roundish or indefinite and often blend gradually into the surrounding green leaf tissue.

On squash, symptoms have been described as round to angular brown leaf spots, sharply defined by veins, surrounded by a halo, with the underside biscuit-brown or covered with gray mould (18).

Bains and Jhooty (7), comparing downy mildew symptoms on various cucurbits, found symptoms on *Luffa acutangula* and *Lagenaria siceraria* to resemble those on melon, while on *Luffa aegyptiaca* and *Benincasa hispida* lesions coalesced more slowly and were invariably purplish in color.

HOSTS AND PHYSIOLOGICAL SPECIALIZATION

HOST RANGE

P. cubensis occurs in nature only on plants of the Cucurbitaceae, and is found on species belonging to four out of the five subfamilies (100). The hosts on which it has been recorded in the literature are listed below. Countries in which these records have been made are indicated for the rarer hosts only, since distribution of the disease on its common crop hosts is outlined in the section on its geographical distribution. Hosts recorded as infected only by artificial inoculation are marked with one asterisk. The hosts belong to more than 40 species in about 20 genera of the Cucurbitaceae.

HOSTS OF PSEUDOPERONOSPORA CUBENSIS

Host	**Country of record and reference source**
**Actinostemma lobatum* Maxim.	Japan (65)
Adenopus rufus	Sierra Leone (CMI)** (44)
Benincasa hispida Cogn.	U.S.A. (3, 48), Japan (68), India (7), Hong Kong (83)
Bryonopsis laciniosa Naud.	U.S.A. (3, 48)
Citrullus colocynthus Schrad.	Israel (30), India (7)
C. lanatus (Thunb.) Mansf.	New Zealand (47), Barbados (95)
C. vulgaris Schrad.	see section on distribution
Coccinia indica W. et K	U.S.A. (29), Japan (65)
Cucumis angulatus Forsk.	U.S.A. (145)
C. anguria L.	U.S.A. (3, 29)
C. callosus (Rotl.) Cogn.	India (7)
C. dipsaceus Ehrb.	U.S.A. (117)
C. erinaceus Hort.	U.S.A. (117)
C. melo L.	see section on distribution
C. odoratissimus Moench.	U.S.A. (117)
C. prophetarum L.	Israel (30)
C. sativus L.	see section on distribution
C. trigonus Roxb.	W. Pakistan (CMI)
Cucumis spp.	Indonesia, Rhodesia (CMI)
**Cucurbita foetidissima* H.B.K.	U.S.A. (136)
C. maxima Duch.	see section on distribution
C. moschata Duch.	see section on distribution
C. pepo L.	see section on distribution
****C. verrucosa* L.	U.S.A. (117)
Cucurbita spp.	Hong Kong, Tonga, Sudan, Mozambique (CMI), U.S.A. (29)
Echinocystis lobata (Michx.) Torr. and Gray	U.S.A. (3, 29)

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*Infected by artificial inoculation only.

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****C. verrucosa* is mentioned by Selby (117) as a doubtful host.

Host	Country of record and reference source
Gynostemma pentaphyllum Makino	Japan (67)
Lagenaria siceraria (Mol.) Standl.	U.S.A. (3, 48), New South Wales (CMI)
L. leucantha Rusby	India (7)
L. sphaerica	Tanzania (CMI), India (24)
L. vulgaris Ser.	Sarawak (134), Israel (30), India (138), U.S.A. (29)
Luffa acutangula Roxb.	U.S.A. (3), Hong Kong (73), Indonesia (CMI), India (7), Sri Lanka (102)
L. aegyptiaca Mill. – (*L. cylindrica* Roem.)	U.S.A. (48), Puerto Rico (3), India (7), Jamaica (89), Malaya (72), Philippines (142), Pakistan, Indonesia, Nepal (CMI)
Melothria maderaspatana Cogn.	U.S.A. (28), India (10)
M. pendula L.	U.S.A. (136)
M. scabra Naud.	U.S.A. (3, 29), Kenya (CMI)
Melothria sp.	U.S.A. (3)
Micrambeles lobata Mich. – (*Echinocystis lobata* (Michx.) Torr. and Gray)	U.S.A. (117)
Momordica balsamina L.	U.S.A. (3, 29), Israel (30)
M. charantia L.	U.S.A. (3), India (7), Indonesia, Malaya (CMI), New Guinea (119), Philippines (142), Thailand (25)
Momordica sp.	India (7)
Mukia scabrella Arn.	U.S.A. (117)
Sechium edule (Jacq.) Sw.	U.S.A. (118)
Sicyos angulatus L.	U.S.A. (48)
Trichosanthes anguina L.	U.S.A. (29), Sri Lanka (CMI), Japan (65), India (7)
T. cucumerina L.	India (24)
T. dioica Roxb.	India (7)
T. japonica Regel	Japan (65)
Zehneria scabra (L.f.) Sond.	Kenya (90)

It is interesting that, in addition to *P. cubensis*, a species of *Plasmopara*, *P. australis* Speg., has been recorded on *Sicyos angulata*, and an unidentified species of *Plasmopara* has been recorded on *Cyclanthera* sp., a host on which *P. cubensis* has not been found (100).

PHYSIOLOGICAL SPECIALIZATION

In discussing host specificity and physiological specialization of *P. cubensis*, one must take into account: (i) the experimental evidence supplied by cross-inoculation tests and field inoculations; (ii) the morphological studies of the fungus derived from various hosts; (iii) field observations relating to transmission of the disease from infected crop species to other species growing in the immediate vicinity under comparable conditions; and (iv) records of pronounced changes in the susceptibility of the same host in the same locality.

By far the most comprehensive cross-inoculation studies with *P. cubensis* have been carried out in Japan, by Iwata (64, 67, 68, 69). The results he obtained by inoculating 17 wild and cultivated species of cucurbits with inoculum from five cucurbit crops, have been compiled in Table 1. They show that in Japan sources of *P. cubensis* can be divided into two groups: Group 1 comprises the fungus derived from *Cucumis sativus, C. melo* var. Conomon, and *Lagenaria vulgaris* var. *clavata.* Inoculations with members of this group were generally negative (or very slightly positive) on cucurbits of the genus *Cucurbita* and on *Luffa cylindrica.* Group 2 comprises the isolates derived from *Cucurbita moschata* var. *melonaeformis* and from *Benincasa hispida* and is capable of infecting, in addition to all the hosts of Group 1, also hosts of *Cucurbita* and *Luffa*

TABLE 1

RESULTS OF IWATA'S CROSS-INOCULATIONS WITH *PSEUDOPERONOSPORA CUBENSIS* FROM FIVE HOSTS TO 17 CULTIVATED AND WILD CUCURBITS (refs. 64, 67, 69)

Plants inoculated	**Sources of inoculum**				
	Cucumis sativus	*Cucumis melo* var. Conomon	*Cucurbita moschata* var. *melonaeformis*	*Lagenaria vulgaris* var. *clavata*	*Benincasa hispida*
Cucumis sativus	+	+	+	+	+
C. melo var. Makuwa	+	+	+	+	+
C. melo var. Conomon	+	+	+	+	+
Cucurbita moschata var. *melonaeformis*	±	–	+	–	+
C. maxima	–	*	+	±	+
Lagenaria vulgaris var. Gourda	+	+	+	+	+
L. vulgaris var. *microcarpa*	+	*	+	+	+
L. vulgaris var. *clavata*	+	+	+	+	+
Benincasa hispida	+	+	+	+	+
Citrullus vulgaris	±	–	±	–	–
Luffa cylindrica	–	–	±	–	+
Melothria japonica	±	–	±	–	+
Momordica charantia	±	+	±	–	–
Trichosanthes cucumenoides	–	–	–	–	–
T. anguina	+	+	+	+	+
T. japonica	+	+	+	+	+
Actinostemma lobatum var. *racemosum*	±	+	±	*	*
Gynostemma pentaphyllum	±	*	±	*	*

±Positive results from some sources, and negative results from other sources of inoculum.
*Cross-inoculation not performed.

cylindrica. These Japanese sources of *P. cubensis* infected watermelons only very slightly.

Doran (48), in Massachusetts (U.S.A.), grew 19 species of cucurbits side by side, alternating with rows of cucumbers, and inoculated all by three applications of a water suspension of spores from leaves of cucumber. The resulting infection levels were very severe on cucumber, moderate on melon and *Bryonopsis laciniosa*, and did not exceed trace amounts on watermelon, *Sicyos angulatus, Luffa cylindrica, Benincasa hispida, Lagenaria leucantha* and *Trichosanthes anguina*. Plants not infected at all were *Cucurbita pepo* (squash), *C. maxima* and *C. moschata, Echinocystis lobata, Melothria scabra* and *Momordica balsamina*, all of which have been recorded as hosts of the fungus elsewhere in the United States (3, 29).

Bains and Jhooty (7, and personal communication) have reported the following results of inoculation tests: Inoculum from *Benincasa hispida, Momordica charantia, Lagenaria siceraria, Luffa aegyptiaca, Cucumis melo* var. *otilissimus* L., *Cucurbita moschata* and *C. pepo* proved pathogenic to muskmelon; however, inoculum from muskmelon was not pathogenic to *B. hispida.*

In Israel, Cohen (30) has carried out cross-inoculation experiments on a much smaller scale using *P. cubensis* from *C. sativus* as inoculum, and concurrent field observations on the extent to which various cucurbits were infected by the fungus when placed near a heavily diseased cucumber plot. The results obtained in this study are summarized in Table 2.

These results show that in Israel, as in Japan, *P. cubensis* from *C. sativus* failed to

TABLE 2

SUSCEPTIBILITY OF VARIOUS CUCURBITS TO *PSEUDOPERONOSPORA CUBENSIS* FROM *CUCUMIS SATIVUS* IN ISRAEL (ref. 30)

Species	**Results of inoculation in the greenhouse***		**Field observations on plants placed next to severely infected cucumbers**
	Infection rating	Degree of sporulation	
Cucumis sativus cv. Bet Alpha	4	free	Rapidly and severely infected
C. prophetarum	5	free	
Citrullus colocynthus	5	free	
Luffa cylindrica	5	free	Not infected
Momordica balsamina	5	free	Slightly infected
Lagenaria vulgaris	3.5	slight	Infected later; disease progressed slowly
Cucurbita maxima	0.1	none	
C. moschata cv. Sichi Lavan	0.1	none	
Bryonia multiflora	0		
Ecballium elaterium	0		

*Estimated on a scale of infection ratings from 0 (no infection) to 5 (very severe infection).

infect species of *Cucurbita* but did infect *Lagenaria.* However, in Israel, the fungus from this source also infected *Luffa cylindrica* in artificial inoculations, but not in the field. A species of *Citrullus* was infected both in artificial inoculations and in the field.

In the southern United States, Hughes and Van Haltern (62) carried out tests with isolates from cucumber and watermelon inoculated on cucumber, cantaloup and watermelon. The isolate from cucumber caused severe and rapid damage to cucumber and cantaloup, but only mild symptoms on watermelon. The watermelon isolate infected cucumber and cantaloup less severely than did the cucumber isolate, but caused much damage to watermelon. The conclusion that the two isolates represented distinct biological forms is further supported by the fact that the symptoms they caused differed considerably. On all three hosts, the watermelon isolate caused yellowish blotches that spread widely over the leaf with several days elapsing before the leaf tissue was killed; the cucumber isolate caused tiny spots, surrounded by narrow yellowish bands, and the center of these spots rapidly turned necrotic.

Field inoculations: Doran (48) has reported the following experiment carried out in eastern U.S.A. Sixteen species of cucurbits, including vegetable, ornamental and wild species, were grown in a field plot with alternate rows of cucumbers. All plants were inoculated three times by application of water suspensions of sporangia of *P. cubensis* obtained from cucumber leaves. The cucumbers were very severely infected; of the others, *Cucumis melo* and *Bryonopsis* sp. were infected with moderate severity, while only trace infection occurred on *Citrullus vulgaris, Benincasa hispida, Lagenaria leucantha, Luffa cylindrica, Sicyos angulatus* and *Trichosanthes anguina. Cucumis anguria, Cucurbita pepo, C. moschata, C. maxima, Melothria scabra* and *Momordica balsamina* were not infected.

Morphological and physiological characteristics: Iwata (66, 67, 68, 69) has paid special attention to the characteristics of *P. cubensis* derived from various hosts in Japan. He found that the size of sporangia and sporangiophores was markedly influenced by the temperature at which they were formed. Moreover, even at the same temperatures, their size was not constant even when derived from the same host, if isolates had been collected from different regions. With these reservations in mind, Iwata arrived at the conclusion that there were no constant differences in the size of sporangia derived from *Cucumis sativus, C. melo* var. Conomon, *Lagenaria vulgaris* var. *clavata*, and *Benincasa hispida*, but those from *Cucurbita moschata* were slightly larger at all temperatures tested. As regards sporangiophores, there were no differences in the length and number of branchings of fungi derived from the first four of the above hosts. However, when compared with sporangiophores from *C. moschata*, those from *Benincasa hispida* were longer, and those from some collections of *C. sativus* differed in their temperature relations: those from *C. sativus* attained their maximum length at 22-26°C, those from *C. moschata* at 14-18°C, and there was little difference between the two at 11° and 30°C.

Field transmission to neighboring cucurbits: In evaluating transmission from one species of cucurbit to another in neighboring fields, interpreted as evidence of physiological specialization, it must be remembered that lack of such transmission may be due to varietal resistance. Alternatively, differences in host reaction under various environmental conditions may account for lack of transmission, even though there is no physiological differentiation between the fungi. Nevertheless, the information available on such field transmission observations is relevant here.

One of the earliest contributions to the subject comes from Rostowzew (110), who observed that in the gardens of the Botanical Institute at Moscow, *P. cubensis* from severely infected cucumbers failed to infect nearby plots of *Bryonia, Luffa* and *Ecballium elaterium.*

In Japan, Iwata (64) reported that *Cucurbita moschata* growing next to severely infected fields of *Cucumis sativus*, remained entirely free of downy mildew.

In Israel, of the four principal cucurbit crops, cucumber and squash are grown under regimes of frequent irrigation (about once a week), while large areas of melon and watermelon are grown either without irrigation or with auxiliary irrigation only (two or three irrigations at 3-4-week intervals). These crops are most commonly grown in neighboring plots. Cucumber and melon are severely infected by downy mildew, especially in summer and autumn, but infection in adjoining plots of squash or watermelon has never been found.

In Mysore (India), the disease was observed to spread in the field from severely infected cucumbers to watermelon (*Citrullus vulgaris*), sweet melon (*Cucumis melo*), and bottle gourd (*Lagenaria vulgaris*); this was the first record on watermelon and bottle gourd in India (138).

Changes in the susceptibility of certain crops or varieties: Epps and Barnes (53) have reported that in South Carolina (U.S.A.) the cucumber variety Palmetto, which had previously been highly resistant to downy mildew, suddenly, in 1950, became susceptible. They attributed this phenomenon to the appearance of a new race of the pathogen.

Conclusions: The evidence presented above undoubtedly supports the conclusion that races with various physiological specializations, and perhaps even slight morphological differences, do exist in various countries. Thus, it has been established that in Japan there are at least two races, one which attacks chiefly crops of *Cucumis* and *Lagenaria*, and another which attacks these hosts as well as *Cucurbita* and *Benincasa*. Neither of these races attacks *Citrullus vulgaris*. In the southern United States there are also at least two races, one which is destructive on species of *Cucumis*, but much less so on *Citrullus vulgaris*, and a second which is more destructive on the latter than the former. In the absence of cross-inoculations performed with races from one country to hosts in another, the question as to the similarities of races from various countries remains open.

As is evident from the geographical distribution of the fungus on its major crop hosts (see below), a race (or races) which affects watermelon is considerably more common on the American continent than elsewhere. In the U.S.A. watermelons are attacked under conditions closely resembling those which prevail in countries of other continents where the crop is not affected. Thus the disease attacks watermelon in California and states along the eastern seaboard in the U.S.A. (3), and in Central America under conditions corresponding, respectively, to those of Israel, southern Europe, and equatorial Africa, where it is absent from this crop.

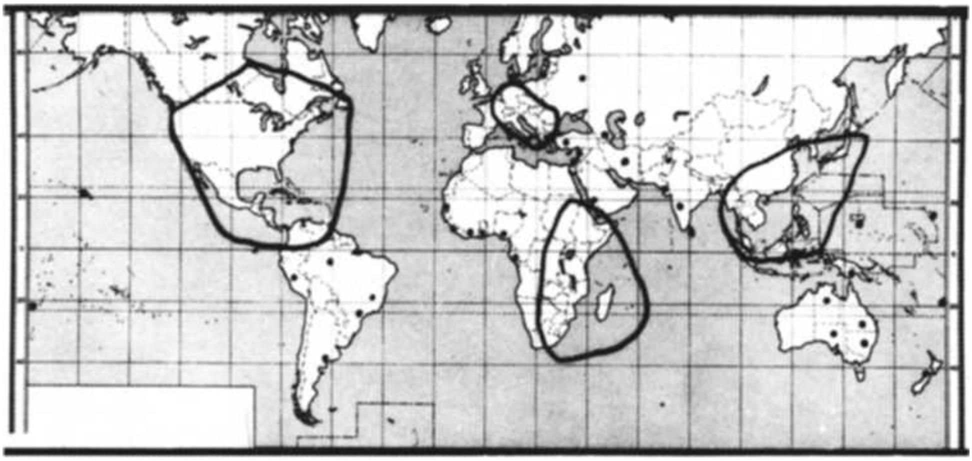
The races which attack species of *Cucurbita* appear to be of wide distribution in most countries in which the disease affects *Cucumis* spp., with the exception of Europe and the Mediterranean region. In many countries two or more races of the fungus seem to exist side by side, a fact that should not be overlooked in breeding cucurbits for resistance to downy mildew.

However, no final conclusions regarding the characteristics and distribution of races of *P. cubensis* should be drawn from the data published thus far. Such conclusions should be based on the effects of isolates of the fungus on differential hosts of well-established genetic make-up in various countries – a comprehensive task not yet undertaken.

GEOGRAPHICAL DISTRIBUTION

P. cubensis is widely distributed geographically but differs, due to physiological specialization, in its geographical host-range (see Maps 1-3, Table 3, and host list presented above). No unirrigated crops are infected in very dry areas. Boughey (22), in his survey of plant diseases in the Sudan, with areas ranging from practically rainless to humid tropical, found that the disease occurs only in regions with an annual rainfall exceeding 375 mm.

Distribution of the fungus is widest on crops of the genus *Cucumis* (*viz.*, on cucumbers and melons) (Map 1), with records for cucumbers in close to 70 countries, and for melons in about 50. On the American continents this includes Canada, the whole of the United States, the entire region of Central America and the Caribbean, the northern states of South America, as well as Brazil and Argentina. In Europe the disease has been reported from field-grown crops in western and central Europe, Italy and the Balkan countries, and in the U.S.S.R. as far north as the Moscow region. In Africa the mildew has not, to our knowledge, been recorded on *Cucumis* crops in



Map 1. Distribution of *Pseudoperonospora cubensis* on *Cucumis* crops.

Map 2. Distribution of *Pseudoperonospora cubensis* on *Cucurbita* crops.

Map 3. Distribution of *Pseudoperonospora cubensis* on *Citrullus* crops.

countries north of the Sahara, although it would be expected to occur there. However, the disease does occur in all East African states, in the equatorial West African states, and in South Africa. In Asia the disease occurs in the Middle East, Israel, Lebanon, and even Saudi Arabia, the Indian sub-continent, China, Japan, Indonesia, and the Philippines. It is also found in Australia in all but the western part, in New Zealand, and on islands in the Pacific Ocean. The disease thus occurs in tropical regions all over the world, in some semi-arid regions (U.S.A., Middle East), and in temperate regions of America, Europe, Japan, Australia, and South Africa.

TABLE 3

DISTRIBUTION OF *PSEUDOPERONOSPORA CUBENSIS* ON THE GENERA *CUCUMIS, CUCURBITA, CITRULLUS* AND *LUFFA*

Country or	*Cucumis*		*Cucurbita*	*Citrullus*	*Luffa*	Reference
area	*C. sativus*	*C. melo*	spp.	spp.	spp.	no.
Asia						
Armenia	+	+				(98)
Cambodia	+	+		+		(85)
China	+		+		+	(27)
Hong Kong	+	+	+		+	(83)
India	+	+		+	+	(7, 138)
Indonesia	+	+	+		+	(85)
Iran	+	+	+	+		(114)
Israel	+	+				(106)
Japan	+	+	+			(64, 65)
Jordan	+	+				(139)
Korea	+		+			(4)
Laos				+		(74)
Lebanon	+					(112)
Malaya	+	+	+		+	(72)
Nepal					+	CMI*
Pakistan	+	+			+	CMI
Philippines	+		+		+	(143)
Sarawak	+				+	(134)
Saudi Arabia	+	+	+			(88, 92)
Sri Lanka (Ceylon)	+				+	(102)
Thailand	+	+		+		(25)
Turkey	+					(78)
Africa						
Egypt			+	+		(52)
Ethiopia	+	+		+		(128)
Gabon		+				(11)
Ghana	+	+				(81)
Ivory Coast	+					(20)
Kenya	+	+				(2, 93)
Madagascar	+	+	+			(41)
Malawi	+	+	+			(126)
Mauritius	+	+	+			(61)
Mozambique	+		+			(43)
Nigeria		+				(5)
Rhodesia	+	+	+			(144)
Senegal	+	+	+			(23)
Sierra Leone	+					(44)
South Africa	+	+	+	+		(18)
Sudan	+		+		+	(21)
Tanzania	+		+		+	(140)
Togo		+				(94)
Zambia			+			CMI

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*Commonwealth Mycological Institute, Kew, Surrey, U.K.

Country or area	*Cucumis*		*Cucurbita* spp.	*Citrullus* spp.	*Luffa* spp.	Reference no.
	C. sativus	*C. melo*				
Europe						
Austria	+					(59)
Bulgaria	+					(51)
Czechoslovakia	+					(124)
France	+					(111)
Germany	+					(39)
Greece	+	+				(101)
Hungary	+	+				(84)
Italy	+	+				(42, 147)
Netherlands	+					(137)
Romania	+	+				(56)
U.S.S.R.	+		+			(96, 110)
Yugoslavia	+	+	+			(40)
Australia and the Pacific Ocean						
Australia	+	+	+	+		(91, 122)
Fiji Islands	+	+	+	+		(55)
Guam	+	+	+			(1)
Hawaii	+	+	+			(103)
New Guinea	+	+	+			(119)
New Zealand	+	+	+	+		(47)
Samoa	+					CMI
Tonga Islands		+				CMI
America						
Argentina	+		+	+		(113)
Barbados	+	+	+	+		(95)
Bermuda		+	+			(142)
Brazil	+		+	+		(57)
Canada	+	+				(36)
Colombia			+			(26)
Cuba	+	+				(15, 121)
Dominican Republic			+			(28)
El Salvador	+	+		+		(38)
Guiana				+		(16)
Jamaica	+	+	+	+	+	(82)
Mexico	+	+	+	+		(108)
Nicaragua	+	+	+	+		(86)
Panama		+		+		(133)
Peru		+		+		(46)
Puerto Rico	+	+			+	(37)
U.S.A.	+	+	+	+	+	(3, 116)
Venezuela	+	+	+	+		(105, 127)

On crops of the genus *Cucurbita* (*viz.*, on squash, pumpkins and marrows), distribution of *P. cubensis* is somewhat more limited (Map 2), but still covers almost 40 countries. In America (3) it is less widely distributed in the U.S.A., frequent in Central America and the Caribbean, but has been recorded in only three of the South American countries. The disease has not been found on these crops in Europe or the Middle East (except in Iran and Saudi Arabia). In Africa, infected *Cucurbita* crops have been found in Senegal and the Sudan, and countries of East and South Africa, but not in the numerous West African countries in which it occurs on *Cucumis* crops. In Asia, records of downy mildew on *Cucurbita* crops are limited to China, Japan, Hong Kong, and Malaya. The disease has been found in Australia, New Zealand, and islands in the Indian and Pacific Oceans. In sum, the distribution of the disease on *Cucurbita* crops is more restricted than it is on *Cucumis* crops in the more northerly states of the Northern Hemisphere, and in other parts of the world it occurs mainly in limited geographic foci, *e.g.* Central America, southeast Asia, and southeast Africa.

On crops of the genus *Citrullus* the distribution of *P. cubensis* is even more restricted (Map 3) and has been recorded in about 25 countries. These include a large group of countries in Central America and in adjacent regions to both the north and south. On other continents records of the disease on these crops are dispersed and limited to three or four countries each in Africa, Asia, and Australia – New Zealand. In the Northern Hemisphere downy mildew has not been found to infect *Citrullus* crops above 30° latitude N.

The distribution of *P. cubensis* on hosts belonging to other genera of Cucurbitaceae is evident from the host list presented above. Many of these hosts are wild cucurbits that grow chiefly in hot and humid climates, and distribution of downy mildew on such hosts is accordingly limited.

EPIDEMIOLOGY

OVERWINTERING AND SPRING INFECTIONS

Possible modes of local overwintering of an obligate parasite such as *P. cubensis* are persistence by oospores, and perpetuation of inoculum on overwintering wild, feral or cultivated hosts. An additional important source of spring infection may be sporangia blown in from regions with mild winters, although such infection is in general held to be more efficient in diseases dispersed by more resistant spores (*e.g.* rusts) than by the short-lived sporangia of *P. cubensis*. It has been established that in a temperate climate with cold winters, inoculum cannot survive on leaves killed by the disease (87).

Oospores: Oospores have occasionally been reported from Japan, China, India, Italy, and the Moscow region of the U.S.S.R. They have been sought but not found in many other countries. Although it must be considered a possibility that oospores may serve to carry the disease over winter, this has not been proved.

Overwintering hosts: The large increase in area of cucurbits grown under glass or plastic cover in temperate and semi-arid regions makes these protected winter crops highly suspect as sources of downy mildew inoculum for field-grown crops grown in spring and early summer. In Israel, *P. cubensis* on cucumber and melon used to be limited to the months May to November. With the introduction of cucumber crops sown under plastic in autumn and ripening in March-April, downy mildew is now in evidence in every month of the year, and attacks crops in the open from April onward. However, in Massachusetts (U.S.A.), Doran (48) considered that only in exceptional cases would the mildew emanate from glasshouse crops to attack cucumber fields in spring. Referring to spring infection of watermelons in Florida, Schenck (115) has concluded from a review of downy mildew incidence from 1931-1959 that failure of the disease to develop in years following severe winters should be attributed to the winter kill of wild and cultivated hosts of *P. cubensis*. In India's Punjab, Bains and Jhooty (6) observed that *P. cubensis* survived as active mycelium on plants of *Luffa aegyptiaca* that were either self-sown or cultivated and grew in somewhat sheltered sites. Since inoculum from *L. aegyptiaca* has proved pathogenic to muskmelon, the authors consider this a possible mode of overwintering of the pathogen.

Spore influx from warmer regions: Much has been written in the United States about the likelihood of inoculum of *P. cubensis* from the south serving as the source of epiphytotics in more northerly states. Jenkins (70) has stated that "available evidence indicates that the fungus overwinters on live host plants along the Gulf Coast and in Florida and moves progressively northwards in the spring." Conditions governing such movement are discussed in the section on prediction of the occurrence of downy mildew on cucurbits.

PROGRESS OF DISEASE TO EPIDEMIC PROPORTIONS

Once inoculum reaches a field, onset of an epiphytotic of the disease depends on two principal factors: (i) the effects of environmental and host-pathogen factors on each successive stage of the disease, which is discussed in detail in a coming publication, and (ii) the overall effects of weather and cultural factors on the seasonal development of the pathogen.

Sources of wetness

The limiting point in every epidemiological consideration of *P. cubensis*, as with other downy mildews, is leaf wetness. Unless free moisture is available on the leaf surface for germination of sporangia and for penetration of germ tubes into the host, all other factors become irrelevant.

Rain has variously been correlated with development of this mildew. Thus Schenck (115) has reported that in Florida (U.S.A.), where the 57-year mean for May-June rainfall is 23.4 mm, the following rain-mildew relations were found: in five years with abundant mildew on watermelon, the rainfall was 54.6, 52.0, 42.2, 26.7 and 26.9 mm, respectively; in four years with moderate mildew incidence, 36.6, 22.1, 23.9 and 23.1 mm; and out of 17 years with slight mildew or only traces of disease, six had rainfall considerably below normal and six had normal rainfall preceded by unusually severe winters.

Rain may, of course, play an important role in mildew development, for a variety of reasons. Rainfall during the daytime will extend wetness periods beyond those provided by dew at night, and will often provide wetness at higher temperatures. Rain penetrates to most of the lower leaves and may also splash inoculum about just when conditions for infection are favorable.

Under conditions in which rain periods in the daytime are infrequent, dew may be regarded as the most important source of wetness for development of this mildew. Duvdevani *et al.* (49) have clearly shown that, in the absence of rain, prevention of dew largely precludes development of the disease on cucumbers in Israel under conditions in which exposure of the leaves to dew leads to severe incidence of the disease. Thomas (131) has likewise found dew periods to be the determining factors for the onset of downy mildew on cantaloups in southern Texas (U.S.A.): epiphytotics did not occur until dew periods were of at least 5-6 hours' duration, although inoculum was present and temperatures were favorable. The specific advantages of dew for mildew development are that it forms a steady water film that persists continuously for several hours, with none of the washing-off of sporangia that is caused by rain or sprinkling. Dew formation occurs largely during the cooler hours of the day, which may limit its usefulness to the mildew in cooler seasons, but provides wetness under temperature conditions optimal for infection in warmer seasons. In crops with mostly horizontal leaves, such as melon, cucumber and watermelon, the upper leaves may partially shield the lower ones from dewfall, and this would reduce the amount of foliage likely to be infected.

Duvdevani *et al.* (49) expressed the opinion that the small amount of downy mildew that developed in their studies, even on plants protected from dewfall, may have been due to the presence of guttation moisture.

The effect of irrigation on downy mildew development is twofold. Every type of irrigation, whether applied by furrows, flooding, sprinkling, or trickling, promotes the general growth of cucurbits, causes foliage to be denser, and rows to close at an earlier stage, thus altering the microclimate. Overhead sprinkling alone has additional effects, the most obvious of which are wetting of the foliage and splashing about of inoculum. The effects of sprinkling differ greatly from those of rain. When plants are sprinkled in clear weather, the relatively dry air surrounding the field will stream into the strip just sprinkled immediately after application of water has come to an end. This contrasts with the effect of rain, which often falls on cloudy days with high relative humidity, which persists after the rain stops.

In the view of Duvdevani *et al.* (49), the above direct effects of sprinkling on the downy mildew disease are less important than the indirect ones. Since sprinkling wets the entire surface of the soil as well as the foliage, atmospheric humidity in the plot is increased much more than in furrow-irrigated plots, where only up to about 30% of the soil surface and little of the foliage is wetted. The amount of dew forming on sprinkled plots is therefore likely to be greater. These authors, moreover, cited evidence that sprinkling increases the rate of guttation under conditions of little or no dew, and this further changes conditions in favor of the disease.

The effect of sprinkling on downy mildew depends greatly on the frequency of application. In crops on heavy soils, with applications made once in 2-3 weeks or at even longer intervals, the effect will be limited. However, where cucurbits on light soil have to be sprinkled as often as twice a week, mildew development may be greatly enhanced. This was found to be the case when cucumbers were grown on sandy soil in Israel's southern coastal belt; here, the substitution of trickling (drip irrigation) for sprinkling has made cucumber cultivation economically feasible.

Effects of leaf wetness and high relative humidity on overall mildew development

Periods of wetness are essential for liberation of zoospores and penetration of germ tubes into the host. High relative humidity is also required for sporulation, but limits the period over which sporangia retain their viability. Except for extreme temperatures of 5° and 30°C, sporulation requires 6-12 hours of saturated atmosphere, with a clear optimum at 15°C. Of far greater importance is the interaction effect with regard to infection: at the lowest spore loads there is no infection with less than 6 hours' wetness, at intermediate loads the minimum period of wetness is reduced to 2 hours at 20-25°C, and the highest spore load will ensure infection at these temperatures as well as at 15°C (32, 35). Temperatures of 15-20°C are common (but not predominant) during dew periods in regions and seasons suitable for growing cucurbit crops. The significance of this interaction between spore load and wetness period is thus obvious, and will be discussed below as one of the central factors in the onset and progress of mildew development.

All the above refers to continuous wet periods. However, wet periods due to rain or sprinkling are often discontinuous, and it must be remembered that intermittent wetting and drying has been shown to reduce the viability of sporangia, especially if the wet period lasts for less than two hours (34).

High temperature limitations and the effect of light

The maximum temperatures for the various stages of downy mildew development on cucurbits lie at or below 30°C, even when wet periods are long and inoculum is plentiful. Since many cucurbit crops are capable of growing at higher temperatures, the question arises whether high temperatures may limit disease development.

Bains and Jhooty (8) reported the development of *P. cubensis* on muskmelon in India's Punjab in months with mean temperatures of 29-30°C, 30-32°C, and 28-30°C, with maxima reaching 44° and even 48°C. The disease in the field continued to develop in these months, although established infections in laboratory studies were eliminated in plants exposed for six hours to 40-45°C. The temporary reductions in temperature effected by occasional rainfall, and the attendant long wet periods, were considered to maintain the disease even under these extreme conditions.

In Israel's Jordan Valley, downy mildew does not appear on cucumber in the rainless mid-summer months (with 28-30°C mean temperatures), unless the crop is sprinkled frequently.

The effects of light that are of epidemiological significance are as follows: (i) Extension of light periods that precede wet periods promotes sporulation (34). (ii) Dark periods in which leaves are dry, shorten the period of subsequent wetness (in the dark) required for sporulation; dark wet periods of as little as six hours then suffice for maximum sporulation on true leaves (33). (iii) Exposure of sporulating leaves to dry, hot sunlight reduces viability of sporangia (136). (iv) Weak light hastens necrotization of lesions and reduces the sporulation potential at 20-30°, but not at 15°C (30). (v) In all but its initial stage, lesion development is stronger at short (4-10 hours) than at longer photoperiods, but the sporulation potential of a lesion under 16-20-hour photoperiods greatly exceeds that at 8-hour photoperiods (30).

The above indicates that the effect of light on development of *P. cubensis* is highly complex, and that various stages of disease development are affected in different ways. This is bound to find expression in the overall development of downy mildew under the two sets of climatic conditions in which cucurbits are most commonly grown and attacked by the disease: temperate regions at higher latitudes, with long summer and autumn days and moderate levels of radiation and temperature (hereafter called LD regions); and regions at lower latitudes, with shorter summer and autumn days and higher radiation and temperature (SD regions).

In the LD regions, spore production in nights following long days may be stronger, although nightly dew periods may be shorter and their effect on sporulation will be supplemented by preceding dark dry periods. Lesion development in the long photoperiods will be slower, will take longer to reach the necrotization stage, and thus extend the period over which sporulation takes place. Moderate levels of radiation will tend to extend the period of spore viability. In sum, it is primarily the effect of light on the strength and duration of sporulation which, under suitable conditions of wetness and temperature, makes the mildew so dangerous in the LD regions.

In the SD regions, mildew development will be more rapid. The limiting effect on sporulation of the shorter day is partly compensated for by the dark, dry period preceding dewfall. Lesions reach the necrotic stage more rapidly, so that the sporulation period is shorter. However, the strong light increases the sporulation potential of the lesion before it turns necrotic. If sunlight is strong enough to affect seriously the viability of sporangia, this may be important, as it would prevent one morning's crop of sporangia from surviving long enough to take advantage of subsequent dew periods. It would appear that in the SD regions light can markedly affect downy mildew development on cucurbits only when wetness is not a limiting factor.

SEASONAL ADVANCE OF MILDEW DEVELOPMENT ON CUCURBITS

Three biological factors interact with meteorological parameters in determining both the onset and the curve of disease development: the rate of foliage growth and aging; the amount of spores initially available for infection and the subsequent rate and amount of sporulation; and the rate of necrotization of lesions, until they reach the stage at which sporulation ceases.

In the following we have devised three scenarios for downy mildew development in early, main, and late seasons. The assumption is that: early season crops follow a period in which there has been no mildew, the crops are grown in the open, and either rain or dew provides at least minimum periods of wetness, *i.e.*, conditions resembling those of Israel. These scenarios have been devised to exemplify the interplay of all the environmental and biological factors that have been mentioned above as influencing the course of epidemics. Different courses could evidently be charted for such epidemics where environmental factors differ, *e.g.* where summer rains prevail, as is the case in the southern United States.

Early season (spring and early summer): Temperatures and light intensity in this season can be expected to be moderate so that leaf and lesion development will be relatively slow. Thus, foliage will take a comparatively long time to close up the rows, aeration will be good, and dew will dry promptly in the morning. Inoculum, still at a low level, requires long wetness periods for infection, and cotyledons are unlikely to be infected. As the season advances, four things happen: temperatures rise, days lengthen, the foliar canopy closes, and the level of inoculum rises. This brings about a snowball effect: sporulation increases, the greater amount of inoculum at higher temperatures facilitates infection at shorter wetness periods, and this in turn multiplies lesions which duly sporulate. Since temperature and light intensity levels are still below those of mid-summer, necrotization is relatively slow and both the viability of spores and sporulation are prolonged. Thus, the sporulation period is extended and fairly large numbers of spores may survive until the next night's dewfall enables them to germinate. However, development of the mildew in early season crops is usually too slow and comes too late to assume epidemic proportions before much of the yield has been harvested.

Main season (mid-summer): Temperatures and radiation in this season reach their highest values, and light periods their greatest length; foliage develops rapidly and soon closes the rows, impeding aeration and raising the humidity. Inoculum in this season may be ample, so that infection will be effected even when wetness periods are relatively short. If these periods are long enough, cotyledons may be infected, and early infections enhance the above mentioned snowball effect. However, necrotization of lesions will be rapid and reduce the amount of sporulation on much of the infected foliage. Strong radiation and heat will reduce the viability of sporangia, and if daytime humidity is low, few or none of the sporangia may survive the day. However, this loss of daytime infection potential is compensated for by massive spore production at night, the amount of such production depending, evidently, on the frequency and length of wetness periods. As a result, development of the disease in this season may be so rapid that the yield is almost completely or totally destroyed.

Late season (autumn): Temperatures decrease as the days become shorter and light becomes less intense. Foliage development may initially still be rapid, but eventually slows down. The decisive factor in disease development is the level of inoculum. If the main season's crop has been heavily infected, inoculum may be so abundant that infection takes place even at low temperatures and/or in short wetness periods, and the snowball becomes an avalanche. In that case the crop may be totally destroyed at a fairly early stage of growth, but if it can hold out over its early growing period, the danger lessens progressively. Owing to the abundance of inoculum, late season crops may develop an epiphytotic of downy mildew under weather conditions which could never induce such development in the early season, and may extend the period of disease development into early winter months which in themselves are not favorable to the disease.

LOSSES CAUSED

Downy mildew is capable of completely destroying crops of its cucurbit hosts. However, as with many other diseases, the extent of the losses caused depends on the stage of growth at which the crop is attacked, the rate of disease increase, and the rate of foliage growth.

Stage of crop growth

As mentioned earlier, downy mildew may appear on cotyledons, but it does not do so in all countries, and has never been detected on cotyledons in the field in the southern United States. At any rate, it is not clear how much direct damage such an attack can cause to the plant. However, when the first true leaves are attacked, there may be total loss of the crop, but attacks at so early a stage are also infrequent in some parts of the world. Attacks at the fruiting stage are destructive everywhere, but attacks beginning later cause only limited damage. Van Haltern (136), noting that inoculum for mildew infection in the Atlantic states of the U.S.A. originated in Florida, reported that losses in these states depended on the rate at which such inoculum traveled north. If the inoculum arrived early, when crops were still young, the losses were very high, but in years in which it arrived late, the losses were limited.

Rate of disease increase

The rate of disease increase depends primarily on the frequency and length of wetness periods and the amount of inoculum available, with temperature and light playing secondary roles. The comparatively light losses caused by downy mildew to spring crops in Israel are undoubtedly due to the slow advance of the disease in this season, as contrasted with the rapid advance leading to heavy losses in summer and in many autumn crops. This has been demonstrated in a field trial, in which rate of disease increase on cucumbers sown in late summer was related to yield (50). In this trial, massive development of the downy mildew began only in early September, just before the first fruit was picked from the field sown in July, but even an epiphytotic spreading so late in the crop's growth period reduced the yield greatly. Plots effectively protected against the mildew yielded almost four times as much as the plots not protected against the disease. In effect, the latter plots ceased to yield about the middle of September, when the disease had infected more than two-thirds of the leaves, whereas the plot which was only slightly infected continued to yield for two more weeks.

Rate of foliage development

The relationship between rate of foliage and disease development in cucumbers was investigated by Cohen and Rotem (35) in growth chamber experiments. The plants were kept in moist chambers under minimum/maximum temperature regimes of 10/20°C, 15/25°C, and 20/30°C, and exposed to inoculum from a single diseased plant placed in each chamber. As seen from Fig. 2, total areas of foliage and lesions increased most under the 20/30°C regime, but the ratio of infected to healthy leaf area was highest under the 10/20°C regime, where leaf development was much less but lesion development was only slightly less than at 20/30°C. These results confirmed previous field observations that plants with less well developed foliage suffered comparatively greater damage.

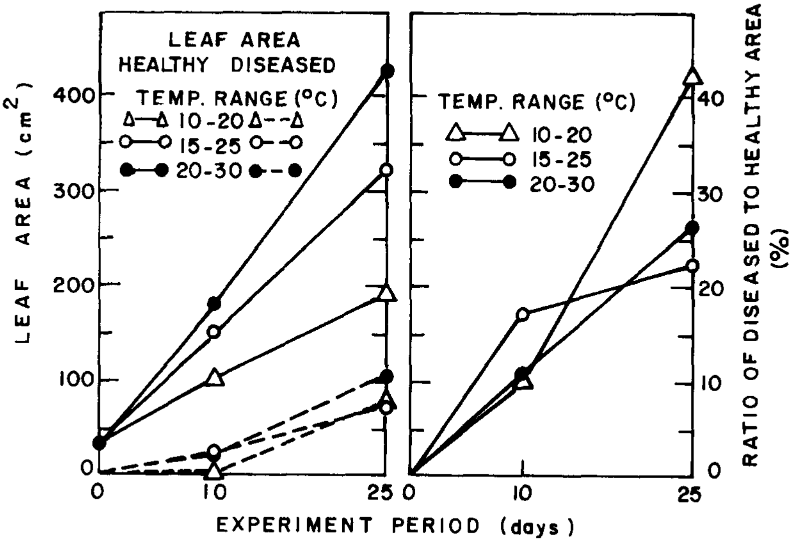

Fig. 2. The effects of temperature and time on epiphytotics of *Pseudoperonospora cubensis* on cucumbers in growth chambers (from ref. 35).

RESISTANCE OF CUCURBITS TO DOWNY MILDEW

The ecological amplitude of *P. cubensis* in infecting its principal hosts, and the comparatively marked ability of its spores to survive somewhat uncongenial conditions (at least compared with species of *Phytophthora*), coupled with the fast growth of cucurbits under good conditions along with the difficulty of covering the underside of foliage close to the ground with fungicides – all these factors restrict the efficacy of fungicidal control of downy mildew and point to breeding for resistance as the most promising control measure. Such breeding programs have been carried out principally, but not exclusively, in the United States, on cucumber, melon, and watermelon. Much of the up-to-date information presented in the following sections has been supplied to us by Dr. C.E. Thomas of the U.S. Department of Agriculture, Weslaco, Texas.

Sources of resistance and varieties developed from them

At least five sources for breeding cucumbers resistant to *P. cubensis* have come to be known in the last 40 years.

In the Western Hemisphere a number of cucumbers growing in Puerto Rico, notably an introduction from China, have been found to be highly resistant. These have served for intensive breeding work, first in Puerto Rico (109) and subsequently in the U.S.A., in Florida and South Carolina (13, 58, 70). One of the outcomes of this work has been the production of the resistant Palmetto variety by crossing Puerto Rico 40 with the susceptible Cubit variety (12). However, after a number of years, this variety lost its resistance, at least in South Carolina, apparently as the result of the increase of a newly dominant strain of *P. cubensis* from among the mixed population of the fungus. Other varieties bred for resistance to downy mildew in the southeastern United States were derived from Puerto Rican sources and from resistant Chinese strains; they include Poinsett and Cherokee (17). Poinsett, in turn, has been used by Dutch breeders (137) and is still in use in the U.S.A.

Breeding for resistance has also proceeded in Japan, where Aojhai and other strains have been used as sources of resistance (54, 120). The Japanese material is being used for resistance breeding in the U.S.S.R. and one source (P.I. 212233) has been used in the U.S.A. Breeding in South Carolina has yielded the resistant Stono variety.

Most of the downy mildew resistance currently utilized in cucumbers in the U.S.A. stems from Barnes' work with Plant Introduction no. 197087 from India, especially the "Gy 1-A" developed by Barnes, as well as the varieties Calypso, Pixie, and Chipper.

Simanca *et al.* (121) published the results of field tests with 360 cultivars and lines of cucumbers, carried out in Cuba in 1974-1977 under conditions of fungicidal protection, natural infection, and artificial inoculation. Only five of these exhibited high resistance to *P. cubensis*, and three – Heiva 2841 and Mid 2861 from Japan and S2 Shimochirazu from the U.S.S.R. – also gave high yields. Thirteen other cultivars possessed moderate resistance.

Expression, mode of inheritance and quantification of resistance

Symptom expression on some of the source material used in breeding for resistance and on some of the varieties produced from such sources may deviate in important aspects from normal symptoms. On the resistant Plant Introduction no. 197087 from India, Barnes and Epps (14) found lesions formed after inoculation to be brown and irregular in shape, often with a water-soaked appearance; the spots readily changed to dark-brown, as tissues dried out. The tissues within the lesion, on inoculated as well as naturally infected leaves, never passed through the yellow phase, which may indicate a hypersensitive reaction (123).

Resistance may also be expressed as a low rate of sporulation. This has been indicated for the Palmetto variety by Barnes (12) and for P.I. 197087 by Barnes and Epps (14).

The nature of resistance and its mode of inheritance to *P. cubensis* in cucumbers have been studied in the U.S.A. and Japan. Jenkins (70, 71), in breeding with Puerto Rican sources, found resistance linked to indeterminate growth habit, but not significantly linked to color of spine or fruit, netting of mature fruit, spine texture, earliness, or fruit shape. On the other hand, Shimizu *et al.* (120), breeding with Aojhai as a source of resistance, concluded that resistance and green fruit color were linked.

In Japan, varieties more resistant to downy mildew seemed less resistant to *Fusarium oxysporum* var. *cucumerinum*, and *vice versa* (54). In Holland, Van Vliet and Meysing (137) considered one of the genes for resistance against powdery mildew to be linked with the recessive gene conditioning downy mildew resistance.

In the U.S.A., inheritance in crosses with P.I. 197087 as the source of resistance seemed controlled by one or two major genes and one or more minor genes (14). However, Van Vliet and Meysing (137), working in Holland with the U.S. variety Poinsett as a source of resistance, found resistance controlled by only one recessive gene. In Japan, Shimizu *et al.* (120) stated that the resistance of Aojhai was inherited as a triple recessive.

Cohen (31) attempted to quantify expression of resistance by visual distinction between greenish, yellow, and brown color of lesions; by determining the size of the infected area as a fraction of the area inoculated; by counting the number of lesions after inoculation; and by counting the sporangial yield of lesions. He showed that out of 14 varieties and lines of cucumbers tested, only Poinsett and Chipper were highly resistant. Resistance was expressed as: circular lesions instead of the angular ones in susceptible varieties, smaller lesion size (1-1.5 mm diameter *vs.* 2 x 2 - 2 x 3 mm area), smaller total infection area (64-77 *vs.* 540 mm^2), lower number of spores (6-100 *vs.* 80-500 per mm^2), and a considerable reduction in the number of lesions appearing at the target area on the lowest cucumber leaf, but not on leaves higher up on the stem.

MELONS

Studies of breeding cantaloup melons for resistance to downy mildew, as well as to *Aphis gossypii*, were carried out by Ivanoff (63) in Texas (U.S.A.). They included: *(a)* crossing of four resistant cantaloup varieties of West Indian origin (Cuban Castilian, Green Fleshed Rocky Dew, Orange Fleshed Rocky Dew, and Smith's Perfect) with susceptible commercial varieties, and *(b)* in-breeding and selection of Cuban Castilian and Green Fleshed Rocky Dew varieties. Resistance to downy mildew often seemed associated with resistance to the aphid, and resistance to both appeared in the F_1 generation as partly dominant. Highly resistant lines were isolated in later generations, and disease resistance was combined with shipping and other commercial qualities.

Smith's Perfect has also been mentioned as suitable for growing in Puerto Rico, both because of its downy mildew resistance and its keeping quality (107). Crossing of Smith's Perfect with a variety called Georgia 47 was carried out in Taiwan and yielded the strain P.I. 321005 (Tainan 2); this was shown to equal the highly resistant

Edisto and its parent varieties in its resistance to *P. cubensis*, and to be resistant also to the powdery mildew, *Sphaerotheca fuliginea* (125) races 1 and 2 but not race 3 (132).

The principal sources now used for breeding cantaloups resistant to downy mildew come from India. These include P.I. 124111 and especially P.I. 124112 from eastern India (Calcutta district), and P.I. 180280 from western India, originally chosen because of its resistance to the WMV 1 virus. All these sources have been found at 22° latitude N.

Thomas (130) has compared disease development and sporulation in susceptible and resistant cantaloups. In some varieties, such as Dulce, Edisto, and Edisto 47, delayed onset of infection was due simply to slower physiological development, since earlier maturing varieties and lines, *e.g.* Perlita, PMR 45, and 38-1, contracted the mildew at an earlier date. In other lines (83-1, 37-1), delay in infection seemed to indicate gene-conferred resistance: they ripened together with the early maturing group and yet showed a low rate of infection. The susceptible PMR 45 had an extremely high sporulation rate, the resistant 37-1 a very low one. However, the 83-1 line, although moderately resistant to infection, supported a high sporulation rate. One reason for the high sporulation rate of some commercial varieties, *e.g.* PMR 45 and Edisto 47, may lie in the abundance of their vegetation, since they produce more foliage tissue subject to infection than varieties such as Perlita, Dulce, and Edisto.

In studying the relation between lesion color and varietal resistance, Thomas (132) found in tests with seven breeding lines and five varieties of cantaloup that plants with brown lesions had the lowest percentage of necrotic leaves, plants with yellow lesions had the highest percentage, and plants with brown-centered lesions with yellow halos were intermediate.

For downy mildew resistance in honeydew melons, the variety Floridew was developed in Florida from an introduction from Iran (P.I. 223637).

In Israel, Karchi and Govers (77) crossed a selection from Spanish honeydew cultivars with a cultivar obtained from the late Dr. Glen Davis, of Davis, California. This resulted in production of a cultivar (Noy Zahov Amid) which is not only resistant to powdery mildew (*Sphaerotheca fuliginea*), but also rated "field resistant" to downy mildew. The nature of resistance of this cultivar is described as follows: the lesions are at first much smaller than in susceptible cultivars, and they do not appear at early growth stages; later, as the fruit approaches maturity, the number and size of lesions increase without, however, causing great losses.

WATERMELONS

Parris (104) reported that Dominican Republic strains of watermelon possess a useful degree of downy mildew resistance, although here, as in the above mentioned honeydew melons, the foliage also slowly succumbs to the disease as the fruits mature.

In testing some 300 watermelon introductions and breeding lines in North Carolina (U.S.A.), Winstead *et al.* (146) found two highly resistant lines (P.I. 179660 and P.I. 179875), and a number of moderately resistant lines.

Watermelon cultivars differing in their downy mildew susceptibility were shown by Thomas (129) to differ in the sporulation potential of the fungus on their leaves. Rapid necrosis of lesions and consequently limited sporulation were observed on Charleston Gray, while the susceptible Summerfield cultivar, on which lesions necrotized slowly, supported abundant sporulation. This characteristic is of primary importance in determining the field resistance of cultivars.

CONTROL BY CULTURAL PRACTICES

SOWING SEASON AND SITE

Season or date of sowing

In countries with well-defined warm and cool or wet and dry seasons, downy mildew will infect cucurbits in the open field as fairly wet conditions (dew or rain) coincide with rising temperatures. Since most cucurbit crops, especially those of the genus *Cucurbita*, will develop at temperatures below those favoring build-up of inoculum and infection by the downy mildew fungus, and under at least partly dry conditions (with or without irrigation), early sowing may be an important means of escaping the disease. In Israel's coastal plain, for example, cucumber and melon crops grown in the open are attacked before the second half of May only when in close proximity to winter-sown crops grown under cover. Crops sown in the open field in March or earlier thus escape downy mildew for the major part of their growth period (if not in close proximity to crops grown under cover).

Topography, shade, and dew

Under rainless conditions, dew, as mentioned above, is a major factor in downy mildew development on cucurbits (49). As soon as nights are warm enough for development of the disease, any factor extending the dew period in the morning therefore favors the disease. These factors are: crop density (see below); anything that provides shade; and sometimes nearby waterways, ponds, or other bodies of water. The effect of shade on persistence of dew and disease development can, of course, be observed near trees (windrows) and various structures in the field, but is particularly prominent on slopes which shield the crop from morning insolation for a period sometimes extending to 3-4 hours. Although this has been established experimentally only for *Phytophthora infestans* and *Peronospora tabacina*, it is reasonable to assume that shade would similarly favor development of *P. cubensis.*

CROP DENSITY AND AERATION

The density of the crop is the factor that most affects aeration, and therefore the humidity level in the crop, especially after dew-nights, rain, and irrigation. As a general rule, the denser the crop, the longer high humidity will persist in it and the greater the danger of downy mildew attack. This is particularly true where the length of the leaf wetness periods constitutes a limiting factor in disease development, *i.e.*, in open air crops growing in rainless seasons where relatively short dew periods provide the principal source of wetness. Crop density may be less important when the crop is grown in rainy seasons or under plastic cover, since in these cases periods of leaf wetness are otherwise prolonged.

Bohn *et al.* (19), in California, observed that cultural practices which promoted air circulation among the plants materially reduced the loss from downy mildew on muskmelons. In open fields aeration is also affected by the direction of the rows in relation to that of prevailing winds. In glasshouses, a proper aeration regime is probably the most basic measure for the control of downy mildew.

When downy mildew development depends on the presence of dew, the upper leaves that are most fully exposed to dew formation are those attacked most severely. In a dense crop, lower leaves may to some extent be sheltered from dew formation and are then less likely to be infected.

NEIGHBORING CROPS

Since a large amount of inoculum can to a large extent make up for environmental limitation to downy mildew development, the proximity of infected fields that may be the source of massive doses of inoculum is an important consideration. The practice of sowing cucurbits successively at short intervals in adjacent plots, convenient as it is for successive harvesting in large fields, is most undesirable in this respect, since it facilitates disease transmission from older to younger crops (35, 45, 99). If such adjacent sowings are unavoidable, care should be taken to sow the older crop downwind from the younger one, so as to prevent prevailing winds from blowing spores onto the younger crop.

IRRIGATION

The mode and frequency of irrigation greatly influence downy mildew development on cucurbits where humidity factors are prominent in limiting the disease. Under these conditions, irrigation by furrow, flooding, or trickling undoubtedly promotes the downy mildew much less than does overhead sprinkling. Although experimental data specifically concerning this disease are not available, it may be assumed that, under conditions similar to those of Israel, sprinkling in the morning, continuous with the dew period, favors infection more than sprinkling at mid-day or in the evening, because most of the sporangia are formed early in the morning and few, if any, survive dry days and are infective in the evening.

The frequency of overhead sprinkling has a definite effect on downy mildew attack. In seasons without rain, but rich in dew, the frequent sprinkling necessary on sandy soil may favor the disease to such an extent that it is practically uncontrollable with protectant fungicides. On all types of soil, intervals between sprinklings should be extended as much as soil and crop characteristics permit.

Cohen and Rotem (34) obtained evidence that one daily application of water to leaves in the field reduces infection of cucumber by downy mildew. This certainly deserves to be followed up as a possible means of control, especially where fixed sprinkler installations afford easy opportunities for such brief wetting of leaves.

MINERAL NUTRITION

The effect of nutrients on development of *P. cubensis* was studied by Doran (48) in the U.S.A. on cucumber, and by Bains and Jhooty (8) in India on muskmelon. Doran (48) came to the conclusion that potassic fertilizers have no effect on the disease. Bains and Jhooty (8) used sand culture techniques to determine the effects of different levels of nutrition on muskmelon kept under natural light conditions and temperatures of 20-28°C. They tested a balanced solution containing 5 ml each of $Ca(NO_3)_2$, $4H_2O$ and KNO_3, 1 ml of KH_2PO_4, 2 ml of $MgSO_4$, and 30 ml of NaCl stock solution per liter nutrient solution, in comparison with solutions in which one of the elements N, P and K was given in higher or lower concentrations, or in which a balanced solution was given at a reduced rate. Reduction of the general nutrient level increased susceptibility to infection, while some of the unbalanced treatments, especially high N or P, or low K, reduced it appreciably. Reduction of general nutrients failed to reduce sporulation, but all the unbalanced treatments, except high P, did so. None of the treatments affected size of sporangia. In sum, most of the unbalanced treatments reduced infection and sporulation, and balanced treatments – which were best for the muskmelon – were also best for the disease.

CHEMICAL CONTROL

TIMING OF THE START OF FUNGICIDAL TREATMENT

As mentioned in the section on overwintering, there may be three primary sources of spring infection of cucurbits by downy mildew in countries with cool winters: *(a)* oospores which have been found only in Russia, the Far East and Italy, and whose role in infection is not clear; *(b)* protected crops that carry inoculum throughout the cooler season; and *(c)* wind-borne inoculum blown in from warmer regions.

Since the ecological amplitude of *P. cubensis* is fairly wide, and the dispersing spores are rather more tolerant of dry conditions than those of some other downy mildews and *Phytophthora infestans* (34), it has not been possible to work out schemes of timing for the beginning of fungicide applications by meteorological indicators. Such timing should take into consideration: source, proximity and size of inoculum; source of leaf wetness and duration of wetness periods; age of plants; weather; irrigation regime; and type of fungicide (protectant or systemic).

Primary inoculum

Determination of the source of primary inoculum is probably the most important aspect of estimating the time of early outbreaks of downy mildew and of timing preventive control measures. When the source is local, and especially when it lies in protected crops, this presents no special difficulties, but when long-range transport of spores from warmer to cooler regions is involved, estimation of the availability of inoculum is much more complex.

A coordinated attempt was made to predict dates of spring outbreaks of downy mildew on cucumbers and melons in the Atlantic coast states of the U.S.A. according to the prevalence of the disease in winter crops in Florida and the Gulf states (89, 97). However, this attempt was abandoned as impractical, and no prediction schemes have been forthcoming elsewhere.

Level of inoculum

No reliable method for estimating levels of downy mildew inoculum as a guide to chemical control has been worked out. It can therefore only be stated in a general way that abundance of inoculum in neighboring fields necessitates early application of prophylactic sprays and sometimes shorter spray intervals. This is of particular importance for late-season sowings of cucurbits, where crops from early and main season sowings have already been infected and massive inoculum is available. As stated elsewhere, abundance of inoculum will maintain the momentum of infection even in seasons in which temperatures fall below optimal levels and wetness periods are relatively short.

Leaf wetness

The presence of free moisture on the leaf being a prerequisite for downy mildew infection, determination of wetness on the leaf and of length of wetness periods, assumes importance. This is true in particular when inoculum levels are still low, and only protracted wetness periods at fairly high temperatures will result in infection.

It may be stated with reasonable certainty that the disease will not assume epiphytotic proportions, and protective measures will seldom be required, where daily leaf wetness periods do not exceed 4-5 hours at temperatures not exceeding 12-15°C. In practice this means that in a rainless growing season, the length of the dew period is of primary importance in deciding when to start chemical control.

Thomas (131), in southern Texas, suggested that the monitoring of dew periods might maximize the efficiency of timely applications of preventive fungicides to cantaloups.

Age of plants, and irrigation regime

Where infection of cotyledons and young leaves occurs in open fields, it is common only where heavy inoculum pressure combines with highly favorable temperature and humidity conditions. Under most circumstances, the leaves of cucumbers show symptoms only after they are fully expanded. Where rains occur with any frequency during the growing season, no relationship can be established between host age and timing of the first fungicidal application. However, under rainless conditions, crops irrigated by means other than overhead sprinkling will require protection before expansion of the first true leaves only when growing in the proximity of older infected crops, and in nights with dew and temperature conditions highly favorable to the development of downy mildew.

Empirical establishment of treatment threshold

In field experiments on honeydew melons in Florida (U.S.A.), Jones (75) determined that spraying with chlorathonil did not give satisfactory results, if more than 3% of the leaves were infected when the first spray was applied.

TIMING OF PROTECTANT AND SYSTEMIC FUNGICIDE APPLICATIONS

Once the first symptoms of the disease have appeared in the field, timing of fungicide applications is subject to the following considerations: *(a)* expected rate of downy mildew development, especially as related to weather and proximity of sources of inoculum; *(b)* rate of foliage development; *(c)* irrigation intervals; and *(d)* type of fungicide chosen – protectant or systemic.

Protectant fungicides

Copper fungicides have long been used to protect cucurbits from downy mildew, but since copper has a phytocidal effect on leaves of many cucurbits, these fungicides have been replaced by others of the carbamate group as soon as they became available. However, in the control of downy mildew all protectant fungicides suffer from one important drawback: the disease attacks young tissues shortly after they have formed and, wherever vegetative growth is vigorous, protectants have to be applied at very short intervals.

When using any protectant fungicide maximum coverage of foliage is always important, but particularly so when inoculum and weather conditions favor rapid disease development. Cucurbit crops, which spread over the soil surface, are notoriously difficult to cover on the lower side of their foliage. Every single application will achieve only partial coverage, and the cumulative coverage provided by successive applications at the shortest intervals contributes markedly to the control effect.

The rate of foliage development differs greatly among cucurbits in different seasons. Under conditions extremely favorable to infection, true leaves should ideally not be left without protectant cover for more than 2-3 days after they have unfurled; this may mean twice-weekly applications of fungicides. Jones and Everett (76) stated that in Florida weekly spraying of cucumbers was inadequate and that twice-weekly spraying was required to protect the crop from downy mildew; this is in agreement with experience in Israel.

In irrigated crops, intervals between sprayings are of necessity related to irrigation intervals. Where irrigations are applied by any method other than overhead sprinkling, they affect spraying chiefly by their effect on soil conditions and the attendant technical difficulties of ground applications of fungicides. However, where overhead sprinkling is practiced, irrigation sometimes directly promotes disease development and each sprinkling also reduces the fungicide deposit on the foliage.

Experience in Israel has shown that the efficacy of protectant fungicides can be greatly improved if they are applied within 24 hours after sprinkling. On large areas this can be done by aerial application. On smaller areas, or where aircraft is not available, every effort must be made to spray as soon as possible after sprinkling, and this can be done by: *(a)* providing permanent pathways on which tractor-mounted sprayers can be driven even when the ground is wet; *(b)* application by knapsack sprayers; or *(c)* application of fungicides through overhead sprinkling systems.

Systemic fungicides

A turning point in the chemical control of downy mildews, including that of cucurbits, has been reached with the recent discovery of the systemic action of the acylalanine group on these diseases. Urech *et al.* (135) included the following data on control of *P. cubensis* on squash in the U.S.A.: Ridomil (DL-methyl N-(2,4-dimethylphenyl)-N-)2-methoxyacetyl) alaninate) was applied as a 50% wettable powder at the rate of 140 and 280 g a.i./ha at 14-day intervals. This resulted in a disease rating of 3.7 and 0.7 (on a scale of 0-10), respectively, as compared with 6.5 for the control and for mancozeb (1680 g a.i./ha), also applied once every 14 days.

The use of such systemic fungicides has made the timing of application against downy mildew much simpler. The intervals of application by spraying are much longer, usually 10-14 days, so that there is no difficulty in integrating the spraying with the irrigation schedules. Applications at shorter intervals are generally practiced only if leaf growth is very rapid, or if spraying has been delayed until infection has already reached a fairly high level.

OVERALL OUTLOOK FOR CONTROL

The data presented above on host range and geographical distribution of *P. cubensis* show that this pathogen is adapted to a fairly wide range of climatic conditions. The reasons underlying this adaptability will be examined in another publication, which will deal in considerable detail with the factors affecting each of the successive stages of disease development, the operative limiting factors at each stage, and also the success with which the pathogen can compensate for sub-optimal factors and produce epiphytotics under conditions in which the most crucial factor, moisture, is largely limiting.

The existence of genetic sources of resistance in the major crops, the development of systemic fungicides effective against this mildew, and our increasing understanding of the management of cultural practices for healthier cucurbit crops – all these combine to justify the statement that severe losses from this downy mildew can now be largely avoided.

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