Effect of Temperature on Conidial Germination and Systemic Infection of Maize by *Peronosclerospora* Species

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ABSTRACT

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Peronosclerospora maydis from Java, Indonesia, and the maize strain of *P. sorghi* from Thailand, both apparently infective only to maize, and *P. philippinensis* from the Philippines had very broad optimum temperature ranges for germination (at least 10–30 C) and germ tube growth (18–30 C); they produced large numbers of conidia from 18 to 23 C (the optimum temperature for sporulation) in presence of dew for 5–6 h. *P. maydis* usually, and the maize strain of *P. sorghi* always, caused high levels of systemic infection from 8 to 36 C. *P. philippinensis* consistently had less systemic infection with dew periods at the lower temperatures of 10–16 C. This lower systemic infection for *P. philippinensis* is similar to that previously reported for *P. sacchari,* an organism we believe to be conspecific with *P. philippinensis.* The sorghum strain of *P. sorghi* (true *P. sorghi*), common in many countries on sorghum and/or maize but not found in Thailand or Java, was characterized by a relatively narrow optimum temperature range for germination (about 12–20 C), relatively short germ tubes at the optimum temperature for germ tube growth, and low amounts of systemic infection at temperatures less than about 15 C and greater than 30 C.

Downy mildews of sorghum, maize, and sugarcane are among the world's most destructive diseases (11,12). *Peronosclerospora sorghi* (W. Weston & Uppal) C. G. Shaw, the causal agent of sorghum downy mildew of sorghum and maize found worldwide wherever sorghum is grown, is the only *Peronosclerospora*-downy mildew pathogen, aside from *P. globosa,* which is present in Texas on wild cupgrass (*Eriochloa contracta*) (14), known to be present on a graminaceous crop in the New World (1). Although the "sorghum strain" of *P. sorghi* can readily infect maize in the field, this fungus is primarily a pathogen on sorghum. In Texas, disease incidence has exceeded 30% on sorghum (10).

A so-called maize strain of *P. sorghi* rarely infects sorghum but has caused large losses to maize (6). The term "maize pathotype of *P. sorghi,*" first coined by Payak (17), referred to both the Thailand downy mildew of maize and that of Rajasthan, India. The latter subsequently was shown to attack the wild grass *Heteropogon contortus* (L.) P. Beauv. ex Roem. & Schult., producing oospores in that plant, and was named *P. heteropogoni* Siradhana, Dange, Rathore & Singh (22). The "maize strain" mentioned here is not related to the Rajasthan fungus.

P. philippinensis (W. Weston) C. G. Shaw, the causal agent of Philippine downy mildew of maize, has caused losses of 40–60% in susceptible maize varieties in the Philippines (9). Isozyme analysis, morphology, and host range studies indicated it is closely related to (or the same as) *P. sacchari* (T. Miyake) Shirai & Hara, the causal agent of sugarcane downy mildew of sugarcane and maize in Asia (2,4,15).

P. maydis (Racib.) C. G. Shaw, the causal agent of Java downy mildew, was the first *Peronosclerospora* downy mildew pathogen described on maize anywhere in the world and has been reported to cause nearly 100% loss to late-planted maize in Java, Indonesia (20).

Identification of *Peronosclerospora* species often is difficult. They may be easily divided into three categories according to shape of conidia: globose, ovoid to slightly elongate, and long or slipper-shaped, but within each group there are usually only minor morphological differences. Some of the described species have been reported to infect maize, of which five are considered economically important and belonging to the genus *Peronosclerospora* (1). The described species are differentiated by only small variations in the size and shape of their conidia and conidiophores, and sometimes by differences in host ranges, presence or lack of oospores, and differences in their morphology (13).

When our studies were initiated, we believed there was a possibility that *P. maydis* obtained from Java was the same (or nearly the same) as the maize strain of *P. sorghi* from Thailand because 1) both organisms have been reported to infect only maize and teosinte (6,18); 2) Indonesia and Thailand are geographically close;

3) downy mildews of maize from Java or Thailand have not been found to form oospores; and 4) some reports (e.g., 16) described conidia of *P. maydis* from Java that were similar in shape to those of the Thailand fungus. It became clear that true *P. maydis* from Java had globose conidia (13,18,19), whereas it was another species from Java, described as *P. javanica* Palm by Palm (16), which resembled both the true *P. sorghi* and the so-called maize strain of *P. sorghi* from Thailand in having more or less ovoid conidia. The Java isolates we tested had globose conidia, hence were of true *P. maydis*.

In an attempt to determine the threat of foreign maize downy mildew pathogens to U.S. agriculture, Foreign Disease-Weed Science Research has conducted several epidemiological studies on the sorghum and maize strains of *P. sorghi* and on *P. sacchari* present in much of southeast Asia, India, Papua New Guinea, and Australia (2,5,8). Specific information on temperature and moisture effects on disease has been used to determine whether these pathogens might be particularly damaging under environmental conditions common to the major maize-growing areas of the United States. To broaden the study, we present detailed information on the effects of temperature on germination, germ tube growth, and initiation of systemic infection in maize by *P. philippinensis* from the Philippines and *P. maydis* from Java, Indonesia. For the purpose of comparisons here, we include previously published data of two isolates of the sorghum strain and two of the maize strain of *P. sorghi,* respectively (5). In order to verify the identity of isolates used in this study, conidial morphology was examined for each isolate.

All research using the living organisms was conducted in the USDA plant disease containment facility at Foreign Disease-Weed Science Research, Frederick, MD, with approval of the appropriate state and federal agencies.

MATERIALS AND METHODS

Pathogen cultures. Isolates of the sorghum strain of *P. sorghi* were obtained from Texas, United States (pathotype 1) (R. A. Frederiksen), in 1972, and from Mysore, India (S. S. Bhat), in 1980. These were transferred to maize by inoculations of maize seedlings with oospores collected from leaves of systemically infected sorghum (*Sorghum bicolor* (L.) Moench). Isolates of the maize strain of *P. sorghi* were obtained from maize in Pak Chang, Thailand, in 1975 and 1985 (B. L. Renfro and C. De Leon, respectively). Isolates of *P. philippinensis* were obtained in 1975 and 1979 from maize in Los Banos, Philippines (O. Exconde), and isolates of *P. maydis* were obtained from maize in East and West Java, respectively, in 1988 (H. D. Vermeulen and Sumartini). The maize strain of *P. sorghi, P. philippinensis,* and *P. maydis* each were sent to Foreign Disease-Weed Science Research at various times in systemically infected maize seedlings. All isolates were maintained on maize (*Zea mays* L. 'Pioneer 3369A') in the disease containment greenhouses.

Preparation of inocula. Conidia were collected from infected donor plants of Pioneer 3369A previously inoculated and maintained in a greenhouse for 3–5 wk. Before spore collection, the donor plants were exposed to supplemental light from 1,000-W Metalarc high-intensity lamps (Sylvania Lighting Center, Danvers, MA) for approximately 16 h (from 1600 to 0800 hours) and then placed in a dark dew chamber at 21 C for 5–6 h to induce sporulation. Conidia were collected by washing the spores from the surface of maize leaves with cold (approximately 5 C) distilled water delivered by an atomizer at approximately 34.5 kPa (5 lb/in.^{2}) air-line pressure. The spore suspension was filtered immediately through a 150-μm (100 mesh) screen, quantified by counts with a hemacytometer, and adjusted to 1.0×10^4 spores per milliliter by dilution with cold distilled water.

Systemic infection studies. A series of experiments was conducted to determine the relationship of air temperature during inoculation dew periods and the incidence of systemic infection subsequently developing in inoculated plants. Each isolate was used in at least two experiments and the entire temperature range was tested in each experiment.

Pioneer 3369A maize seedlings in the two-leaf stage (two per 10-cm-diameter clay pot) were placed in dew chambers at selected constant (±1 C) air temperatures usually ranging from 9 to 38 C. After seedlings equilibrated to the temperature in each chamber (1 h), 1.0 ml of a spore suspension (1.0×10^4 conidia per milliliter) was sprayed onto the plants in each pot. Inoculated plants were incubated in the dew chambers for 18 h. Sixteen to 20 plants were used for each temperature-dew period treatment in each experiment. Generally, only one pathogen isolate was tested in a chamber. When two or more isolates were compared in the same dew chamber, plants were removed from the chamber, sprayed with the inoculum, and immediately replaced into the chamber. Each isolate was tested for the entire temperature range at least twice. Plants sprayed with distilled water and incubated in a dew chamber at 20 C, which is favorable for infection, served as controls.

During the dew period, air temperatures in each chamber were monitored continuously with a thermocouple and recorder. After the dew period, inoculated and control seedlings were placed in the greenhouse. All plants were examined for symptoms of systemic infection for 4 wk after inoculation. Normally the air temperature in the greenhouse fluctuated from 21 to 28 C; however, occasionally during summer months it approached 34 C shortly after noon and returned to the normal temperature range within 3 h.

Conidial germination and germ tube growth. To compare conidial germination and germ tube growth at specific temperatures, conidia of each isolate of each *Peronosclerospora* spp. were sprayed onto 1.5% water agar in plastic petri plates (35 × 10 mm). In at least two experiments for each isolate, three to five replicate plates per experiment were incubated at each temperature for each incubation period; the spore density on the agar surface was from 1.6 to 12 spores per square millimeter. Agar-plate temperatures were equilibrated with the chamber air temperatures before seeding plates with spores as described above, and air temperatures in chambers were monitored throughout incubation with thermocouples and a recorder. Prior tests with calibrated mercury-bulb thermometers showed that the mean temperature of the agar surface was always within ±1.2 C of the stated mean temperature, even when the chamber door was open during seeding of plates.

After 2 or 5 h of incubation, the plates were opened and placed over 38% formaldehyde in a desiccator jar to kill the spores quickly. Germination percentages were determined by microscopic observation of 100 spores per each of at least three plates for each incubation period at each temperature. A spore was considered germinated if the length of the longest germ tube exceeded the width of the spore. The germ tube lengths of 20 or 50 (number depending on the particular experiment) randomly selected germinated spores per petri plate were measured at 100× magnification after 2-h incubation. If a spore had more than one germ tube, only the longest was measured.

Sporulation. Three to five weeks after inoculation, Pioneer 3369A plants infected with the *P. maydis* strain from West Java, the 1985 *P. sorghi* maize strain, or the 1979 isolate of *P. philippinensis* were incubated in the dark in dew chambers at constant air temperatures of 8, 12, 15, 18, 21, 23, 26, and 32 C (±1 C) for up to 10 h. At 1-h intervals between 4 and 10 h of initiation of incubation, leaf pieces were excised from areas of leaves displaying systemic symptoms, stained in 0.1% aniline blue in lactophenol, and observed microscopically for the presence of conidiophores and conidia.

RESULTS

Conidial germination and germ tube growth. The effects of temperature on germination and germ tube growth are usually indistinguishable for *P. maydis,* the maize strain of *P. sorghi,* and *P. philippinensis* (Figs. 1A, B, and D, 2A, B, and D). Each organism usually had high germination from at least 10 to 35 C; however, in one experiment (Fig. 1A), germination was less for *P. maydis* at the extreme temperatures.

The typical sorghum-infecting isolates of *P. sorghi* were characterized by always having both a narrower optimum temperature range for germination (about 12–20 C) than the other pathogens and relatively short germ tubes (Figs. 1C and 2C).

Systemic infection of maize. *P. maydis* and the maize strain of *P. sorghi* both had very broad optimum temperature ranges for germination and development of systemic infection with generally little or no difference in percent systemic infection from 8 to 36 C, the entire range tested (Fig. 3A and B). In some experiments, however, systemic infection was reduced at the extreme temperatures for *P. maydis*. This reduction was not observed with the maize strain of *P. sorghi*. Infection was lower at the lowest temperature tested for *P. philippinensis* (Fig. 3D) and at both the lowest and highest temperatures with the sorghum strain of *P. sorghi* (Fig. 3C).

Sporulation. The optimum temperature range for sporulation of *P. maydis*, the maize strain of *P. sorghi*, and *P. philippinensis* was 18–23 C. At these temperatures mature conidia were abundant in 5–6 h in dew. At 6 h some conidia had dropped from the conidiophores onto the leaf surface and germinated with *P. maydis* and the maize strain of *P. sorghi*. Each organism produced fewer conidia at 26 C than at 18–23 C, and only abnormal, rarely branched conidiophores and only rare conidia at 32 C. Fewer mature conidia were produced by all three organisms at 12–15 C than at more optimum temperatures, and none at 10 C by 10 h.

DISCUSSION

Raciborski (18) in 1897, in Java, was the first to describe a downy mildew disease of maize. He named the causal agent *Peronospora maydis* Racib. Butler (7) in 1913, while observing a downy mildew fungus in India and erroneously believing he was looking at Raciborski's species, changed the genus name to *Sclerospora*, hence the species *S. maydis* (Racib.) Butler. This name persisted until 1978 when C. G. Shaw (21) changed the genus name to *Peronosclerospora*. Today, the accepted name of the causal agent of the typical Java downy mildew is *P. maydis* (Racib.) C. G. Shaw.

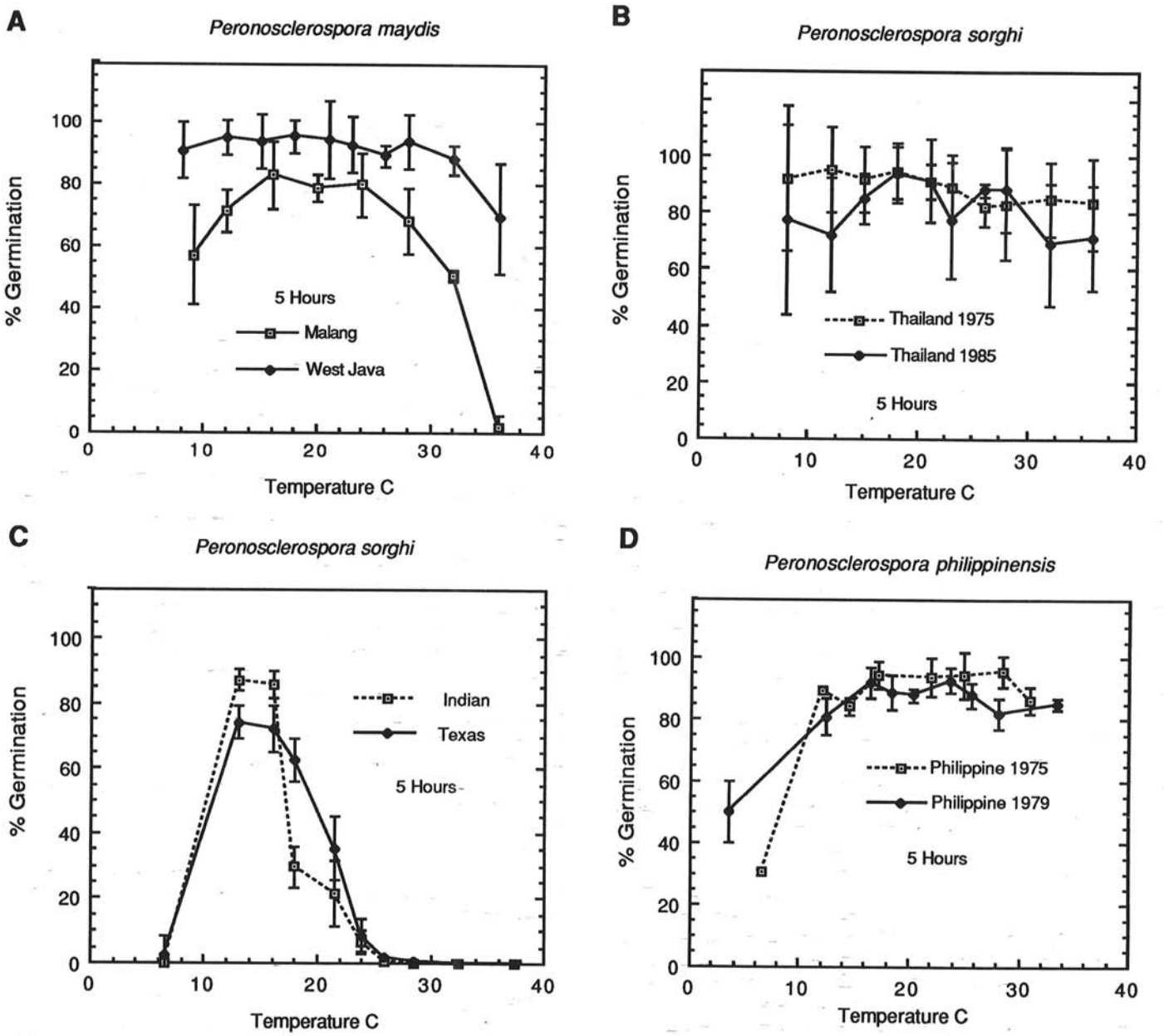

Fig. 1. Percent germination of conidia of *Peronosclerospora* spp. after 5-h incubation on 1.5% water agar at specific temperatures. **A,** *P. maydis* from West Java and Malang, East Java, Indonesia, respectively; **B,** two isolates collected in 1975 and 1985, respectively, of the maize strain of *P. sorghi* from Pak Chang, Thailand; **C,** the sorghum strain of *P. sorghi* from Mysore, South India, and Texas, U.S.; and **D,** two isolates of *P. philippinensis* from Los Banos, the Philippines. Confidence limits (95%) indicated.

Examination of the literature suggests that there are two maize downy mildew pathogens in Java going under the same name. Each apparently lacks oospores and has no other known natural hosts other than maize and teosinte (6,20). One of the organisms produces conidia that are globose when mature as described by Raciborski (18) in 1897, Rutgers (19) in 1916, and Kimigafukuro (13) in 1979. The second organism produces ovoid to only slightly elongate conidia when mature, as described by Palm (16) in 1918 and named *Sclerospora javanica* Palm. Palm erroneously considered it synonymous with *Peronospora maydis* Racib. The organism used in our study apparently is the same as that described by Raciborski; that is, having globose conidia (Fig. 4A). Of many dozen experiments in which our two isolates have been used, the conidia always have been round. This is in striking contrast to the ovoid to somewhat elongated conidia (when mature) of the maize strain of *P. sorghi* from Thailand (Fig. 4B).

Both *P. maydis* and the maize strain of *P. sorghi* have been shown to infect only maize in nature (6,20). It is possible that the maize strain of *P. sorghi* from Thailand is the same as the organism observed by Palm in Java. The Thailand strain of *P. sorghi* has conidia averaging 20.1 × 16.0 μm (length/width ratio = 1.25) as compared with 19–26 × 15–20 μm as described by Palm for *P. maydis*. Our isolates of *P. maydis* average 20.0 × 18.5 μm (length/width ratio = 1.08). It is important for us to establish at this time the identity of the isolates used in our study so as to allow a means of reference for other workers in the future.

When we began this study, we believed it was possible that the maize strains of *P. sorghi* (from Thailand) and *P. maydis* (from Java) might be a single organism, or at least very similar. Besides the morphological differences we observed, a concurrent study comparing isozymes of 34 isolates of *Peronosclerospora* (*P. sorghi* from Asia, Africa, India, South and North America, *P. sacchari* from Taiwan, *P. philippinensis* from the Philippines, and *P. maydis* from Java) downy mildew pathogens strongly indicated *P. maydis* is a separate species (15). Whereas the intraspecific simple matching coefficients (SSM) were 0.77–0.95 for the sorghum strain of *P. sorghi, P. sacchari,* and *P. philippinensis,* the highest SSM comparing *P. maydis* with any of the others was very low (only 0.14), suggesting a separate species for *P. maydis.*

In this study the two isolates of the maize strain of *P. sorghi* from Thailand behaved similarly (Figs. 1B, 2B, and 3B), but are distinctly different from all isolates of the sorghum strain of *P. sorghi* (Figs. 1C, 2C, and 3C) (5). Conidia of the maize strain of *P. sorghi* could germinate (Fig. 1B) and establish systemic

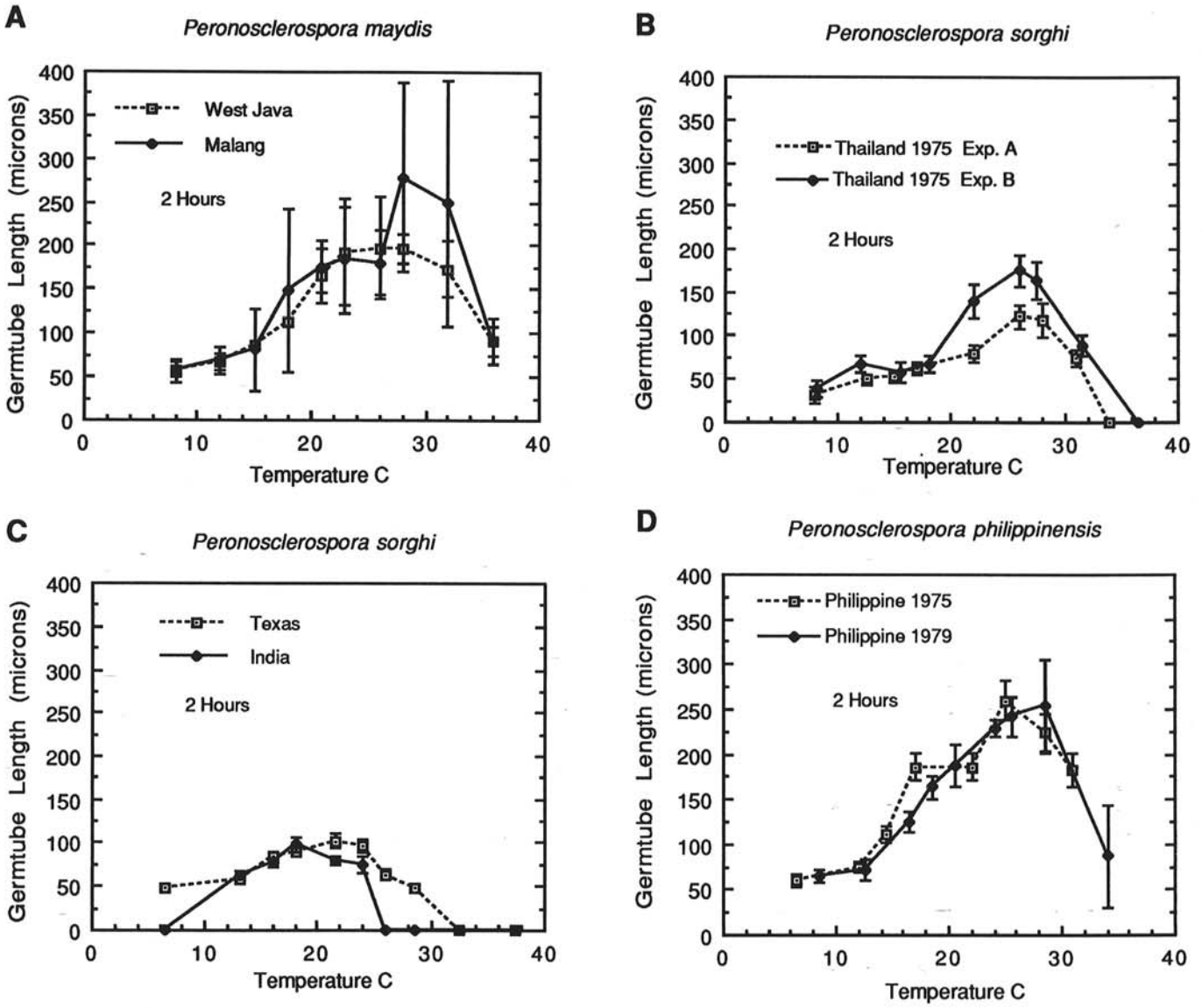

Fig. 2. Germ tube lengths (μm) of conidia of *Peronosclerospora* spp. after 2-h incubation on 1.5% water agar at specific temperatures. **A,** *P. maydis* from West Java and Malang, East Java, Indonesia, respectively; **B,** the 1975 isolate of *P. sorghi* from Pak Chang, Thailand, in two experiments; **C,** the sorghum strain of *P. sorghi* from Mysore, South India, and Texas, U.S.; and **D,** two isolates of *P. philippinensis* from Los Banos, the Philippines. Confidence limits (95%) indicated.

infection (Fig. 3B) at both higher and lower temperatures than isolates of the sorghum strain of *P. sorghi* from Texas, India (Figs. 1C and 3C) (5), or Brazil (5) when tested on maize. Furthermore, conidial germ tubes of the maize strain tended to grow faster than those of the sorghum strain over much of the temperature range tested (Fig. 2B and C), and the pathogen produced five times as many conidia on systemically infected maize as the sorghum strain on maize (8). Although we do not have precise data, the maize strain of *P. sorghi* always has caused higher percentages of systemic infection on maize than the sorghum strain at the same conidial inoculum concentrations (Fig. 3B and C). We believe the maize strain of *P. sorghi* (from Thailand) is much more aggressive than the sorghum strain of *P. sorghi* in causing infection of maize.

P. maydis and *P. philippinensis* also have broad temperature ranges for germination (Fig. 1A and D) and initiation of systemic infection (Fig. 3A and D). However, the latter consistently appears to cause infection in somewhat lower percentages at the lower temperatures (10–15 C). The germination vs. temperature and systemic infection vs. temperature response curves for *P. philippinensis* are essentially identical with those for *P. sacchari* (3), which is what we might expect since we believe the organisms to be very similar, if not the same, based on isozyme analysis, morphology, and host range (15). *P. maydis* in three of four experiments germinated at very high levels from 8 to 36 C (Fig. 1A), and in three of four experiments caused nearly the maximum amount of infection over the entire temperature range (Fig. 3A).

Considering sporulation potential, *P. maydis* and the maize strain of *P. sorghi* from Thailand are the most threatening in an agronomic system where maize is constantly present in the field. Besides the capability of conidia to germinate over a very broad temperature range, these pathogens have the highest sporulation potentials. Duck et al (8) found the maize strain of *P. sorghi* to produce five times as many conidia as the sorghum strain on maize and considerably more than *P. sacchari* or *P. philippinensis*. We believe *P. maydis* from Java produces nearly as many conidia as the maize strain of *P. sorghi*. However, because these organisms have narrow host ranges (perhaps infecting only

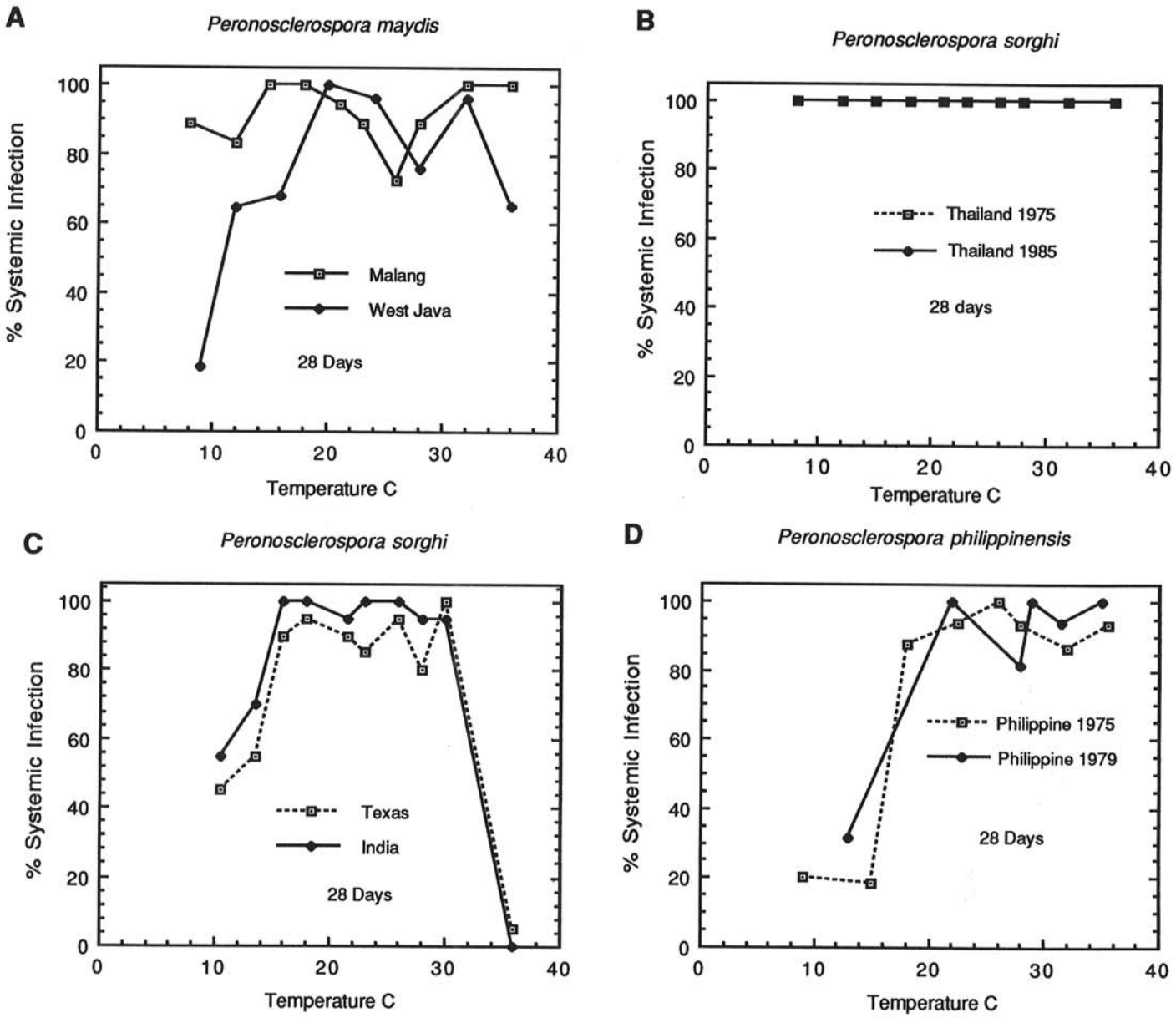

Fig. 3. Percent systemic infection of maize plants inoculated with conidia of *Peronosclerospora* spp. at the two-leaf stage and incubated 18 h in dew chambers at constant specific air temperatures. **A,** Isolates of *P. maydis* from Malang, East Java, and West Java, Indonesia, respectively; **B,** two isolates of the maize strain of *P. sorghi* acquired in 1975 and 1985, respectively, from Pak Chang, Thailand; **C,** *P. sorghi* sorghum strain from Texas, U.S., and Mysore, South India; and **D,** two isolates of *P. philippinensis* from Los Banos, the Philippines. Each isolate was tested at least twice (e.g., four tests per organism) for the whole range of temperatures without replication within experiments.

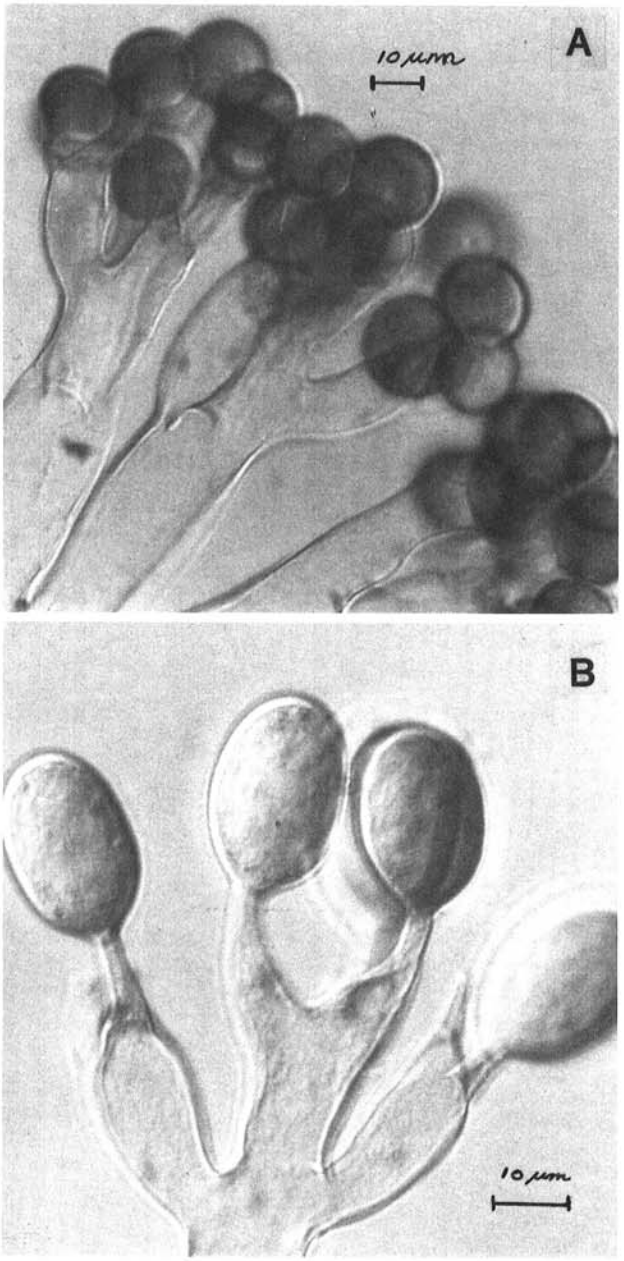

Fig. 4. Conidiospores of *Peronosclerospora* species infecting maize. **A,** Conidia of *P. maydis* originally collected from maize in Java, Indonesia. (Conidia are always globose in shape when mature.) **B,** Typical mature conidia of the maize strain of *P. sorghi* from Thailand. Notice the oval shape of the spores.

maize in the field) (1), and because they apparently do not produce oospores (1), they probably are of little threat to maize in the United States in areas with seasonal cropping to break the disease cycle.

Whether or not *P. maydis* and the maize strain of *P. sorghi* from Thailand are actually closely related is still unknown. Their behavior, as shown above, points toward taxonomic closeness, but conidial shape differences militate against that hypothesis.

P. philippinensis and *P. sacchari* have very broad host ranges and in the greenhouse can infect grasses common in the United States (3). Although the importance of oospores is uncertain, there is little doubt that at least *P. sacchari* has been widely disseminated by means of mycelium in infected sugarcane cuttings (1). Although initiation of infection is restricted by temperatures during the dew period of less than 18 C, these downy mildew pathogens pose some threat to maize in the United States and countries of a similar climate.

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