

7. THE TAXONOMY OF GRAMINICOLOUS DOWNY MILDEWS, WITH EMPHASIS ON THOSE ATTACKING MAIZE**

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Nine species of *Sclerophthora* and *Sclerospora* have been reported to attack maize (*Zea mays* L.). A discussion in the chronological sequence in which they were described is most revealing regarding the development of taxonomic concepts of these species and and the changes in nomenclature necessitated thereby.

In 1876 P. A. Saccardo³⁾ described *Protomyces graminicola* from *Setaria verticillata* (L.) Beauv. collected at Selva (Treviso), Italy. Therewith started the taxonomy, and simultaneously the nomenclature, of the downy mildew fungi parasitic on Gramineae. Saccardo's initial description was based only on oospores; Saccardo described the imperfect state in 1882 on *S. viridis* (L.) Beauv. On the basis of the latter state he made the combination *Peronospora graminicola* (Sacc.) Sacc. Meanwhile P. Magnus in 1878 also described the oospores. Being uncertain of their mycological affinities, he assigned the obviously tentative name "*Ustilago* (?) *Urbani*". A year later (1879) Passerini described both the imperfect state ("Forma conidiophora") and the perfect state ("Forma oogoniophora") for the first time under the binomial *Peronospora Setariae*.

Saccardo's combination, *Peronospora graminicola* (Sacc.) Sacc., was actually a later homonym, since Schroeter in 1879 had already transferred the species to *Peronospora*. Thus in the genus *Peronospora* the correct author citation for the Graminicola downy mildew is *P. graminicola* (Sacc.) Schroet. dating from 1879. Simultaneously, Schroeter proposed *Sclerospora* as a subcategory ("Abtheilung" *sic*) within *Peronospora*, for *P. graminicola*, but did not treat it as a separate genus until 1886. Meanwhile, de Bary in 1881 (2) listed the valid genera of the *Peronosporaceae*, included *Sclerospora* in that list, and referred to Schroeter's (1879) use of the name as a subcategory in *Peronospora*. Even though de Bary did not publish the combination *Sclerospora graminicola*, by reference to Schroeter's publication he did typify the genus *Sclerospora*, and the genus should be cited *Sclerospora* (Schroet.) de Bary. Most authors, including Waterhouse (22), cite the genus as *Sclerospora* Schroet. or *Sclerospora* (Schroet. or *Sclerospora* (Schroet.) Schroet. (1886).

In ten years *Sclerospora graminicola* (Sacc.) Schroet (a) was described as new three times, (b) was the basis for a new genus, and (c) the specific epithet *graminicola* was transferred three times from *Protomyces* to other genera. A basis for extended nomenclatural confusion and disagreement existed, but little has resulted because taxonomists of the Phycomycetes and plant pathologists working with the graminicolous downy mildews concur in: (a) the necessity for the genus *Sclerospora* and (b) the validity of the type species of that genus (*S. graminicola*). Although varieties of *S. graminicola* have been proposed, none have stood the test of time and none are recognized today.

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Sclerospora graminicola, the Graminicola downy mildew, is world-wide in distribution and attacks a number of genera and species of grasses including maize, pearl millet (*Pennisetum typhoideum* (L. Rich.), and sorghum (*Sorghum vulgare* Pers.). In tropical areas it causes serious losses on pearl millet, on which the disease is known as Green ear disease. While it constitutes a potential threat to maize, it has so far proven to be little more than a mycological curiosity thereon.

S. graminicola was first reported on maize by Spegazzini from Argentina in 1909. Melhus and Van Haltern (6) successfully inoculated maize with oospores of *S. graminicola* in Iowa in 1925, but found the fungus on maize under natural conditions only twice during a three year period.

The next graminicolous downy mildew to be described that attacks maize was *Sclerospora macrospora* Sacc. in 1890. Saccardo's description was based solely on oospores found on *Alopecurus* sp. in Australia; these were sufficiently larger than those of *S. graminicola* that Saccardo considered it a distinct species. When the asexual stage was eventually found (by Tasugi in 1927 on rice, Peyronel in 1929 on wheat, and by Peglion in 1930 by germination of oospores from wheat, cf. 17), scientists were puzzled by the similarity of the sporangial stage of *Sclerospora macrospora* to that of *Phytophthora* spp. In 1940 Ito and Tanaka transferred the fungus to *Phytophthora* as *P. macrospora* (Sacc.) Ito and Tanaka. Hara is said to have placed the species in the genus *Kawakamia*, which Waterhouse (21, 22) rejected. Waterhouse maintains the species in *Phytophthora*, although most mycologists accept the genus *Sclerophthora*, erected with *S. macrospora* (Sacc.) Thirum. et al. as the type species after careful study of the development and structure of its sporangial stage, the oospores and oogonia (17). Payak, et al. (1970) have listed the characters differentiating *Sclerospora*, *Sclerophthora*, and *Phytophthora*. I agree with the generic characterizations therein, except that I (1970) consider the sporangiophores of *Sclerophthora* indeterminate in their development. In addition, the facultative saprophytism characteristically associated with species of *Phytophthora* and the Pythiaceae must be contrasted with the typically obligate parasitism of *Sclerophthora* and other genera of the Peronosporaceae. The limited success to date of growing *Sclerophthora* and *Sclerospora* spp. in axenic culture (1, 15, 18) in no way detracts from this basic physiologic difference.

Since *Sclerophthora* was erected, three new species (*S. cryophila* Jones, *S. lolii* Kenneth, and *S. rayssiae* Kenneth et al.; Shaw, 1970) and one variety (*S. rayssiae* var. *zeae* Payak and Renfro, 9) have been described. Of these, only *S. rayssiae* var. *zeae* attacks maize; it will be discussed later.

Sclerophthora macrospora is also of world-wide distribution in temperate or warm temperate climates; its reported host range is even greater than that of *Sclerospora graminicola*. There is great variation in size and sculpturing of oospores collected from different graminicolous hosts assigned to *Sclerophthora macrospora*; we are fortunate that a conservative species concept has prevailed to date. Careful study of oospores, oospore germination, and sporangiophore development on other hosts may justify description of additional species within *Sclerophthora*.

The first record of *Sclerophthora macrospora* on maize was from Italy in 1902 (Ullstrup, 1970). On maize, as a result of phyllody of the tassels and occasionally the ears, *S. macrospora* causes symptoms called Crazy top. In spite of its wide-spread occurrence and spectacular appearance, the pathogen is of minor importance on maize.

Brizi (22) described *Sclerospora oryzae* from rice in 1919; there is almost unanimous agreement that *S. oryzae* Brizi is a synonym of *Sclerophthora macrospora*. On rice the disease is known as Yellow wilt. *Sclerospora secalina* Naumov (22), of which only oospores are known, may also be a synonym, even though the oospores described by Naumov in 1949 are small for *Sclerophthora macrospora*. *Secale cereale* L. has been

reported a host for *S. macrospora*.

The third downy mildew attacking maize to be described was *Sclerospora maydis* (Racib.) Butl. Raciborski described it from Java in 1897 as *Peronospora maydis*, and Butler in 1913 inadvertently transferred it to *Sclerospora*. I say inadvertently because Butler was actually working in India with a different downy mildew on maize, but thought he had the same fungus as Raciborski had had. The International Code of Botanical Nomenclature (16) specifically states that the new combination applies to the original type, that is the material of the original author, not to the material of the second author. In such circumstances, if the material studied by the second worker is new, it remains unnamed. In 1916 Rutgers again described the downy mildew from Java; he called it *Peronospora maydis*, but apparently did not create a later homonym (22, pp. 8, 11). Palm, also working in Java, believing that *S. maydis* (Rac.) Butler was not available for the Javanese fungus, renamed it *Sclerospora javanica* Palm. The accepted common name for *Sclerospora maydis* is Java downy mildew of maize. It is of great importance in Indonesia.

Miyake described the next downy mildew attacking maize, *Sclerospora sacchari*, in 1911. As the name indicates, it was originally described from sugarcane, but Miyake himself demonstrated by inoculation tests that the downy mildew on sugarcane was also able to infect maize. Thus, he confirmed that a downy mildew he had found on maize in Taiwan in 1909 was the same as the one he shortly afterwards found on sugarcane. Sun (1970) has summarized our information on sugarcane downy mildew of maize, and has confirmed that in Taiwan Sugarcane downy mildew is far more serious on maize than on sugarcane and is actually the most destructive disease of maize. Sugarcane downy mildew has also been reported in other tropical areas, including Australia, Fiji, India, Guinea, the Philippines, and Thailand, on maize (7).

Sclerospora sacchari is of particular importance because of the observations and conclusions concerning this species published by S. Ito in 1913.

Ito recognized the significance of the fact that in *Sclerospora sacchari* the conidia germinate by germ tubes as in species of *Peronospora*, not by the production of zoospores which is typical of the type species, *Sclerospora graminicola*.

Ito established two subgenera within *Sclerospora*: *Eusclerospora* for species producing zoospores in the asexual phase and *Peronosclerospora* for those species, such as *S. sacchari* in which the asexual reproductive structure germinates by a germ tube. This significant difference, as Shaw (1970) has pointed out, is correlated with the basic distinction between sporangia and conidia; nevertheless, its significance, both taxonomically and phylogenetically, has been almost completely ignored by other workers on graminicolous downy mildews.

Since no mycologist has yet raised any objection to the basic importance of the morphologic and physiologic differences between sporangia and conidia, I have decided to raise Ito's subgenus to generic rank. This is being done in a separate paper.

In the same publication in which Miyake described *Sclerospora sacchari*, he described and named oospores found on *Miscanthis japonicus* Anderss. in Taiwan, *Sclerospora miscanthi* (as *S. mischanthi*). The binomial is usually cited as *S. miscanthi* T. Miyake apud Sacc. The conidia of this fungus were not described until 1953 by Chu (22), who reported germ tube germination for them. The pathogen has been given the common name Leaf-splitting downy mildew. It has been inoculated onto maize but has not been found occurring naturally thereon (3). Because of its natural nonoccurrence on maize over the past 60 years since its description, its potential threat to corn must be considered low.

Next, G. S. Kulkarni, without giving a formal diagnosis, described and illustrated *Sclerospora graminicola* var. *andropogonis-sorghii* in 1913. Interestingly enough, he illus-

trated and discussed germination of the conidia by germ tubes. In retrospect, it seems surprising he would consider the fungus merely a variety of a fungus with an entirely different method of germination of the asexual reproductive structures. Ito, in establishing the subgenus *Peronosclerospora*, commented that Kulkarni's variety was the second representative of the subgenus *Peronosclerospora*; apparently Ito was not aware of Raciborski's *Peronospora maydis* (= *Sclerospora maydis*).

Kulkarni found the fungus on *Andropogon sorghum* Brot., a synonym of *Sorghum vulgare* Pers. While discussed several times by other workers in the intervening years, it was not until 1932 that Weston and Uppal formalized their conviction that this fungus was a distinct species and named it *Sclerospora sorghi*. In describing it as a new species, they were free to utilize any available epithet; they were not committed to utilize the varietal epithet that Kulkarni had used (16). In that they chose not to use Kulkarni's epithet, Weston and Uppal were incorrect in citing the new species as *S. sorghi* (Kulk.) Weston and Uppal, but their doing so does not make the binomial incorrect. It should, however, be credited to Weston and Uppal alone.

The binomial published in 1951 by Mundkur, *Sclerospora sorghi-vulgaris* (Kulkarni) Mundkur, is considered by some (22) a *nomen nudum*; even if treated as a new name at the species level for *Sclerospora graminicola* var. *andropogonis-sorghi* Kulkarni, it is still a later synonym of *Sclerospora sorghi* Weston and Uppal.

Sclerospora sorghi, for which the common names Sorghum downy mildew and Sorghum downy mildew of maize have been approved, is undoubtedly the most destructive graminicolous downy mildew. Originally considered of primary importance on sorghum, it has become equally important on maize throughout the world. Its introduction and current importance in the United States resulted in a Workshop on the Downy Mildews of Sorghum and Corn (3) being held at Corpus Christi, Texas (U.S.A.) in June of 1973, and certainly is one of the species primarily responsible for this International Symposium. *Sclerospora sorghi* is found in Africa, India and Pakistan, Thailand, the U.S.A., and Mexico, where it was first found in 1961 (14). Frederiksen *et al.* (4) have recently published a comprehensive monograph on Sorghum downy mildew.

The next species to be discussed was studied extensively by H. H. Weston in the Philippines, and named by him *Sclerospora philippinensis* in 1920. Weston reported the extensive damage caused by this species on maize, its occurrence on sorghum and on teosinte (*Euchlaena mexicana* Schrad.). It has since been reported on other hosts, including sugarcane. Exconde (1970) has reported the oospores of this fungus. In spite of the logical common name for this downy mildew, Philippine downy mildew of maize and sugarcane, Weston's observations of it there were not the first. In the opinion of most taxonomists, the downy mildew that Butler called the Pusa downy mildew of maize in India in 1913 is actually *S. philippinensis*. As discussed earlier, Butler considered the downy mildew he was studying the same as Raciborski's *Peronospora maydis*. In 1931 Butler, realizing that the new combination he had made in 1913 could not be applied to the Pusa downy mildew of India, but still not realizing that the Pusa downy mildew was the same as *Sclerospora philippinensis*, proposed yet another new name, *Sclerospora indica* Butl. Reinking (10, 11, 12, 13) consistently referred the Philippine downy mildew material he studied to *Sclerospora maydis* (Rac.) Butl.; he did not publish a binomial, *Peronospora maydis* Reinking, as inferred by Waterhouse (22).

Philippine downy mildew is the most serious disease of maize in the Philippines. In addition to India, it also occurs in Indonesia and Nepal.

One year after describing *Sclerospora philippinensis*, Weston described another downy mildew on maize from the Philippines, *Sclerospora spontanea* Weston. This downy mildew, given the common name Spontaneum downy mildew by Ullstrup (4), was serious on maize in the Visayan Islands of the Philippines at the time of Weston's study; how-

ever, Exconde (1970) indicated that *S. spontanea* is rare on corn in the Philippines, and there is no positive report of it on this host from elsewhere.

From 1921 until 1967 no additional species of downy mildews were reported on maize. Additional species of *Sclerospora* and *Sclerophthora* were described on other graminicolous hosts, and two new downy mildews found on graminicolous hosts have been assigned to the genus *Plasmopara*—*P. oplismeni* Viennot-Bourgin (20) and *P. penniseti* Kenneth & Kranz (5). The latter species joined *Bremia graminicola* Naumoff (8) and *Basidiophora butleri* (Weston) Thirum. & Whitehead (22) as exceptions to the rule that all graminicolous downy mildews belong to either *Sclerospora* or *Sclerophthora*. The converse, that all species of *Sclerospora* and *Sclerophthora* occur on Gramineae, still holds.

In 1967 Payak and Renfro (9) described as new a downy mildew they had noted on maize since 1962 in India. The symptoms were distinct from those caused by all other species of *Sclerophthora* and *Sclerospora* that attack maize. Morphologically the fungus was similar to *Sclerophthora rayssiae* Kenneth, Koltin and Wahl, described on barley (*Hordeum vulgare* L.) from Israel (Kenneth, 1970). While differences were noted, these were not considered of sufficient magnitude to justify describing the fungus as a new species, so Payak & Renfro named it *Sclerophthora rayssiae* var. *zeae* (9).

These eight species, and a variety of a ninth, are the only species of downy mildew so far reported to attack maize. What of the future? We must not forget one very important fact regarding all the species of downy mildews on maize. Maize cannot be considered the original host for any of these species! No downy mildew was ever found on maize in Mexico prior to 1961 (14). Indeed, the first reported occurrence of a downy mildew on maize was Raciborski's description of *Peronospora maydis* thereon from Java in 1897! Thus, from the beginning of the 16th century when the Spaniards first began to take maize from Mexico and other locations in South and Central America to the rest of the world, almost four hundred years elapsed before a downy mildew was reported on this host. World-wide within the past seventy-five years, the downy mildews have become one of the most destructive group of diseases on maize.

The situation in regard to sorghum is markedly different. Futrell (3), applying Vavilov's (19) point of origin theory, hypothesizes that *Sclerospora sorghi* probably originated on *Sorghum* spp. in southern Africa, rather than in India where the early investigations of Sorghum downy mildew were conducted by Kulkarni, Butler and others.

Vavilov places the origin of cultivated sorghum in northeastern Sudan along the Red Sea. Futrell (3) states, "From testing we did in Nigeria and based on Vavilov's theory, it would appear that downy mildew became a major problem on sorghum grown near the equator and southward because sorghums endemic to southern Africa carry more resistance than did sorghums collected in northern Africa. This would indicate that sorghum downy mildew has been present in southern Africa for many years and many resistant lines have developed in nature and in primitively cultivated fields".

Can we by similar logic reach any conclusions regarding the possible origins of other downy mildews attacking maize? First, the production of zoospores by species of *Sclerophthora* and *Sclerospora graminicola* indicates these species are more primitive and of more temperate origin than the species of *Sclerospora* referable to *Peronosclerospora*. Original hosts for *Sclerospora graminicola* probably were species of *Setaria* and *Pennisetum* of the Tribe Paniceae; its possible place of origin could have been Eurasia.

I find it difficult to reach any conclusions regarding the origin of *Sclerophthora macrospora* because of its extensive host range. I would place its origin—together with that of other species of *Sclerophthora*—in the temperate region. The genus, with its obvious affinities to *Phytophthora*, is the most primitive in the Peronosporaceae.

The other species of *Sclerospora* (= *Peronosclerospora*) which produce conidia are

considered of tropical origin. *Sclerospora miscanthi* probably originated on *Miscanthus* spp., *S. sacchari*, *S. spontanea*, *S. philippinensis*, on *Saccharum* spp., all in the Southern Asia-Pacific area.

Little can be stated as to the origin of *Sclerospora maydis*, except that it is apparently native to Indonesia. Its original host is unknown. There are no confirmed reports of *S. maydis* occurring elsewhere, and Semangoen's (1970) attempt to inoculate other Gramineae were negative, except that *Euchlaena mexicana* (teosinte) became severely infected. Indeed, it is interesting to note that teosinte is also reported susceptible to *S. sorghi*, *S. sacchari*, *S. philippinensis*, *S. graminicola*, and *S. spontanea*.

The question has been asked how many species of downy mildew are there that attack maize? Are the nine species discussed here all worthy of recognition, or should the number be reduced to perhaps three—namely *Sclerophthora macrospora*, *Sclerospora graminicola*, and *Sclerospora* (*Peronosclerospora*) *maydis*? The epithet "*maydis*" would have priority if all the downy mildews which produce conidia reported on maize were considered synonymous.

The species now recognized have stood the test of extensive study and critical comparison by mycologists and the criteria of utility applied by plant pathologists. Certainly, we need to know more about all the species discussed here, and the other species attacking Gramineae, enumerated elsewhere (Shaw, 1970). Discovery of the imperfect states for those graminicolous downy mildews for which they are still not known and of the oospores for species and hosts from which they still remain undiscovered will amplify our knowledge and taxonomic concepts regarding all these species. Axenic culture (1, 15, 18) will assist not only the pathologist, but also the taxonomist by making possible the comparison of morphologic structures produced under identical environments. Axenic culture will speed inoculation studies and cytological investigations.

Certainly, the history of downy mildews on maize indicates there is tremendous genetic variability in these species. They have spread from their original hosts to maize, and probably some of them to sugarcane and other cultivated Gramineae. *Sclerophthora rayssiae* var. *zae* certainly did not originate on maize and, if native to India, probably was native to the northern foothills, not to the regions where it is now causing so much damage. *S. rayssiae* var. *rayssiae*, found on barey in Israel, is recognized by Kenneth (1970) as a cold-weather pathogen. *S. rayssiae* var. *zae*, if properly classified as a variety of *S. rayssiae*, has certainly become adapted to more tropical habitats.

Just as the cool-weather species producing zoospores (i.e. *Sclerophthora* spp. and *Sclerospora graminicola*) have adapted to hosts and habitats in the tropics, so have the tropical species of *Sclerospora* (= *Peronosclerospora*), especially *Sclerospora sorghi*, adapted to more temperate climates. The spread of *S. sorghi* in the United States as far north as Indiana indicates its plasticity to climate.

The extensive host range of every species with which inoculations have been attempted is also indicative of genetic plasticity and potential for change. Consequently, we should not be surprized if species now known to attack maize, but not now serious thereon, should in the future become serious. Nor should we be surprized if other species of *Sclerophthora* and *Sclerospora* which have not yet been reported on maize even as a result of inoculation, should be eventually found thereon.

Literature Cited

1. Arya, H. C., and M. M. Tiwari. 1969. Growth of *Sclerospora graminicola* on callus tissues of *Pennisetum typhoides* and in culture. *Indian Phytopathology* 22: 446-452.
2. Bary, A. de. 1881. Zur Kenntniss der Peronosporeen. (Schluss.). *Bot. Zeit.* 39: 517-625.
3. (Frederiksen, R. A.—Chm. & Ed.). 1973. A workshop on the downy mildews of

- sorghum and corn. Texas A. & M. University, Corpus Christi, June 6–8, 1973. 71 pp. (Mimeo.)
4. Frederiksen, R. A., *et al.* 1973. Sorghum downy mildew . . . A disease of maize and sorghum. Texas Agr. Expt. Sta. Res. Mono. 2. pp., illus.
 5. Kenneth, R., and J. Kranz. 1973. *Plasmopara penniseti* sp. nov., a downy mildew of pearl millet in Ethiopia. Trans. Brit. Mycol. Soc. 60: 590–593.
 6. Melhus, I. E., F. H. Van Haltern, and D. E. Bliss. 1928. A study of *Sclerospora Graminicola* (Sacc.) Schroet. on *Setaria Viridis* (L.) Beauv. and *Zea Mays* L. Iowa Agr. Expt. Sta. Res. Bull. 111: (293)–340.
 7. (Muller, G. J.). 1973. A compendium of corn diseases. Amer. Phytopath. Soc., Inc., St. Paul. 64 pp., illus.
 8. Naumoff, N. 1913. Materiaux pour la Flore mycologique de la Russie. Bull. Soc. Mycol. Fr. 29: 273–278.
 9. Payak, M. M., and B. L. Renfro. 1967. A new downy mildew disease of maize. Phytopathology 57: 394–397.
 10. Reinking, O. A. 1918. Philippine economic plant diseases. Philippine Jour. Sci., Sect. A, 13: 165–274.
 11. Reinking, O. A. 1919. Host index of diseases in the Philippines. Philippine Agriculturist 8: 38–54.
 12. Reinking, O. A. 1919. Diseases of economic plants in Southern China. Philippine Agriculturist 8: 109–134.
 13. Reinking, O. A. 1919. Philippine plant diseases. Phytopathology 9: 114–140.
 14. Reyes, L., D. T. Rosenow, R. W. Berry, and M. C. Futrell. 1964. Downy mildew and head smut diseases of sorghum in Texas. Pl. Dis. Repr. 48: 249–253.
 15. Shaw, C. G., and K. M. Safeeulla. 1969. Growth of two downy mildew fungi on semi-synthetic medium. XI Inter. Bot. Cong. Abstr.: 196. (Abstract).
 16. Stafleu, F. A. 1972. International Code of Botanical Nomenclature. Regnum Veg. 82. 426 pp. Internat. Assoc. Pl. Tax. Utrecht.
 17. Thirumalachar, M. J., C. G. Shaw, and M. J. Narasimhan. 1953. The sporangial phase of the downy mildew on *Eleusine coracana* with a discussion of the identity of *Sclerospora macrospora* Sacc. Bull. Torrey Bot. Club 80: 299–307.
 18. Tiwari, M. M., and H. C. Arya. 1969. *Sclerospora graminicola*—axenic culture. Science 163: 291–293.
 19. Vavilov, N. I. 1951. The origin, variation, immunity and breeding of cultivated plants. Ronald Press, New York. 364 pp., illus.
 20. Viennot-Bourgin, G. 1959. Champignons nouveaux de la Guinée. Bull. Soc. Mycol. Fr. 75: 33–37.
 21. Waterhouse, G. M. 1963. Key to the species of *Phytophthora* de Bary. Commonw. Mycol. Inst. Mycol. Pap. 92: 22 pp.
 22. Waterhouse, G. M. 1964. The genus *Sclerospora*. Diagnoses (or descriptions) from the original papers and a key. Commonw. Mycol. Inst. Misc. Publ. 17: 33 pp., illus.

Question and Answer

R. G. Kenneth, Israel: What is *Phytoph. omnivorum*? I think McMurphy mentioned it, ca. 1916, near San Francisco, on oats. It was mentioned on oats in Turkey. Could it be a *Sclerophthora*?

Answer: Without reference specimens, or good descriptions of the fungi upon which these reports are based, it is not possible to decide now whether one or both reports were actually *Phytophthora omnivorum*, *Sclerophthora macrospora* or some other pythiaceous fungus.

R. G. Kenneth, Israel: The taxonomic value of the formation of conidia vs. sporangia

would be strengthened if it could be shown that the oosporic stage also germinates in a like manner. Prof. Viennot-Bourgin informed me that *PLASMOPARA PYGMAEA* germinates by hyphal growth. Of course, many errors have been made in claiming germination of oospores. Comment?

Answer: To my knowledge, the oospores of all downy mildews which produce conidia, and of which the oospores have been germinated under carefully controlled conditions (surface sterilization, etc.) have produced germ tubes. Other types of germination have been reported but further study has disclosed that germ tube germination actually occurred. *Peronospora tabacina* was first reported to produce zoospores upon germination of the oospores, but additional careful work disclosed that the zoospores came from a parasitic chytrid attacking the oospores. After sterilization of the oospore, they produced germ tubes.

R. G. Kenneth, Israel: Is there any actual proof that *S. graminicola* attacks sorghum? Most, if not all, instances mentioned, were of *S. sorghi*, mostly before Weston & Uppals' work. Comment?

Answer: Again, in the absence of preserved specimens, or detailed descriptions, it is best to consider records of *Sclerospora graminicola* on sorghum as erroneous determinations. Also keep in mind that *Sclerospora sorghi* was first described under the trinomial *Sclerospora graminicola* vs. *andropogoniosorghi*. By omission of the varietal epithet, a record of *Sclerospora graminicola*, an entirely distinct species, on sorghum could result. The record of successful inoculation with *Sclerospora graminicola* on four varieties of *Sorghum vulgare* Pero by Melhus et al. (1928) seems authentic, but of course is not indicative of natural occurrence.

Nobuo Murata, Japan: Let me comment on your discussion on "genetic plasticity and potential for change" of downy mildew organisms. One time, there were arguments that phytopathogenic bacteria such as *Xanthomonas* species are convertible from one species to another, for these species are uniform in phenotypic characters but for pathogenic specificity. However, we have found that each of these species has segments of DNA specific to the species, which amount to more than 50% of the whole genome (Murata & Starr 1973, etc.). It is hardly possible they are mutually convertible. It will be interesting to see how closely *Sclerospora* and *Sclerophthora* species are genetically related by comparison of their DNA's or other means.

Answer: I know of no studies on DNA of downy mildews. Knowledge derived from such studies in the future will become part of the total pool of knowledge upon which taxonomic decisions should be based.

Joginder Singh, India: 1) Is it possible to relate the major taxonomic characters used in distinguishing the species or even genera to the disease symptoms produced on the plant?

2) Is it possible to distinguish various downy mildews of maize on the basis of symptom alone?

3) Could you kindly brief us the cytological information which has been used in the classification of downy mildew.

Answer: There is no constant correlation between the taxonomic characters useful in distinguishing species, genera or other taxa of parasitic fungi and the symptoms produced by them on their suscept.

2) The symptoms produced by some species on maize—e.g. *Sclerophthora macrospora* and *Sclerophthora rayssiae* var. *zeae* are in my opinion diagnostic. Those produced by other species are not diagnostic.

M. M. Payak, India: The main issue in the nomenclature of sorghum downy mildew is that Weston and Uppal did not describe *S. sorghi* as a new species without reference to Kulkarni's variety. In fact they established it as a new combination and not as a new

species. Hence a formal validation of *S. sorghi* Weston & Uppal is still necessary.

Answer: In the International Code of Botanical Nomenclature (Stafleu, 1972) *Rules* take precedence over *Recommendations* (See Preamble, page 15). The Rule applying to *Sclerospora sorghi* Weston and Uppal is Article 60: "When the rank of a genus or infrageneric taxon is changed, the correct name or epithet is the earliest legitimate one available in the new rank. In no case does a name or an epithet have priority outside its own rank". Weston and Uppal chose *not* to follow Recommendation 60 A (2): "When an infraspecific taxon is raised in rank to a species, . . . , the original epithet should be retained. . . .". Although Weston and Uppal confused the situation by citing "Kulk." in parenthesis, their doing so does not change the basic facts that (1) they did treat this fungus as a new species for the first time and (2) they did not use Kulkarni's epithet, but a new epithet. No validation is necessary, since the applicable conditions for valid publication (Arts 32-45) were complied with.

Sangam Lal, India: 1) I think that it would be the right time to solve and come out with distinguishing character(s) of various species or sub species, because the whole topic is so confusing that most of us, at least I would be in a difficult position for correct identification. On the basis of symptoms, I believe that you will agree, species of *Sclerospora* will not be identified.

2) On maize, on the basis of symptoms we can divide all the downy mildew diseases in two groups: (i) Those where we get systemic infection in the plants as in most of the *Sclerospora* sp. (ii) In *Sclerophthora rayssiae* var. *zeae*, we get non-systemic infection. The symptoms start from the lower leaves touching the ground, and spread upwards as in the case of other foliar diseases. Kindly comment.

3) Further, *Sclerophthora* can be cultured easily, whereas *Sclerospora* is difficult to culture.

Answer: (1) I agree that not all the species of graminicolous downy mildews currently accepted can be recognized on the basis of symptoms. However, suspect symptoms, at best, are only a helpful adjunct to the identification of parasitic fungi in general. (2) Not only downy mildews attacking grasses produce systemic symptoms; downy mildews on many other hosts—e.g. tobacco, hops, beets, peas, etc. can also produce systemic symptoms. These same downy mildews—and also most of the graminicolous downy mildews which produce systemic symptoms—can also produce local lesions—if older plants are inoculated. (3) The "ease" or difficulty of culturing either *Sclerospora* or *Sclerophthora* is relative. Only when reinoculation with axenic cultures has been accomplished, and the diagnostic morphologic structures have been again produced on the suspect, will we have conclusive proof of axenic culture.

O. R. Exconde, The Philippines: Can you offer some suggestions on how to resolve the taxonomic relationship of the nine species of downy mildew attacking corn?

Answer: The eight species and one variety currently recognized are generally accepted. This in itself is a strong basis for their continued acceptance. However, as we continue to study these taxa the number recognized may increase or decrease. Careful study of the *Sclerophthora macrospora* complex may result in dividing it into two, several or many species. Conversely, the conidia producing species of *Sclerospora* (= *Pero-nosclerospora*) may easily be grouped into two species—one with oval conidia and one with cylindrical conidia. Only after continued studies, are taxonomic decisions of such significance justified.